CUSHMAN FOUNDATION FOR FORAMINIFERAL RESEARCH

SPECIAL PUBLICATION NO. 19

STUDIES IN MARINE MICROPALEONTOLOGY AND PALEOECOLOGY
A MEMORIAL VOLUME TO ORVILLE L. BANDY

EDITOR

WILLIAM V. SLITER

August 1, 1980
Price $20.00 Individuals
$25.00 Libraries

Printed in the United States of America
by Allen Press, Inc., Lawrence, Kansas

PREFACE

The last two decades have seen major developments in marine geology including a revolution in an understanding of the development of the earth and its oceans. This success has resulted from interrelated advances in a number of areas of marine geophysics and geology, one of which is marine micropaleontology. Marine microfossils have provided critical information about the geological sequence, age and paleoenvironment of rocks. Hence they contribute greatly to both the understanding of the events of earth history especially biotic evolution, and dates for this flow of natural history. The progress in marine micropaleontology has advanced in parallel with an increase in focus on oceanographic problems during the last two decades. Programs such as the Deep Sea Drilling Project and other coring programs have provided critical material which has required the attention of large numbers of micropaleontologists. This trend has been further enhanced by the enlivened search for hydrocarbon resources in ever increasing water depths in the ocean and sharpened attention towards the global environment including its climatic conditions and paleoclimatic history.

This volume contains a group of papers that represent a wide spectrum of marine micropaleontological investigations. All the papers have in some way examined marine microfossils. Groups represented include forms such as the benthonic and planktonic foraminifera and the calcareous nannofossils, as well as the siliceous radiolaria. The majority of the papers deal with foraminifera. The range of geological problems is wide, encompassing marine sediments uplifted on land and sediments under the oceans from near-shore (estuarine) to abyssal depths. The late Orville Bandy's research touched on most of the avenues of investigation represented in this volume; some he pioneered. Thus the papers.presented here reflect something of the activity in micropaleontology during the last few years, but are by no means meant to be a comprehensive selection. Most of the papers are authored by past students and colleagues of Orville Bandy, and reflect in various degrees the influence that he exerted on their subsequent research activities.

The idea of a memorial volume of papers honoring Orville Bandy came naturally upon his passing and was acted on by Ronald Kolpack at the University of Southern California. A large number of Orville's colleagues and students were eager to organize and contribute to this undertaking and the length of the initial list of papers was in fact worrisome. In the end, delays due to publishing and manuscript problems reduced the number of contributions and William Sliter, Chief of the Branch of Paleontology, U.S. Geological Survey, agreed to edit the volume under the auspices of the Cushman Foundation for Foraminiferal Research. We regret the belated issuing of this testimony to Orville Bandy but are very pleased to be able to fulfill our wish for a lasting tribute to him. Many of Orville's concepts and his spirit are reflected in the papers presented herein. Those of us who were privileged to have worked closely with Orville are still much influenced by his multifaceted approach to micropaleontology and most especially by his unfailing enthusiasm for all aspects of earth history. Clearly, there were no limits to his thinking as demonstrated by the wide range of topics addressed in his published reports. In short, Orville Bandy was an inspirational scholar both in word and deed and a delightful human being, and we dedicate this volume to his memory.

CONTENTS

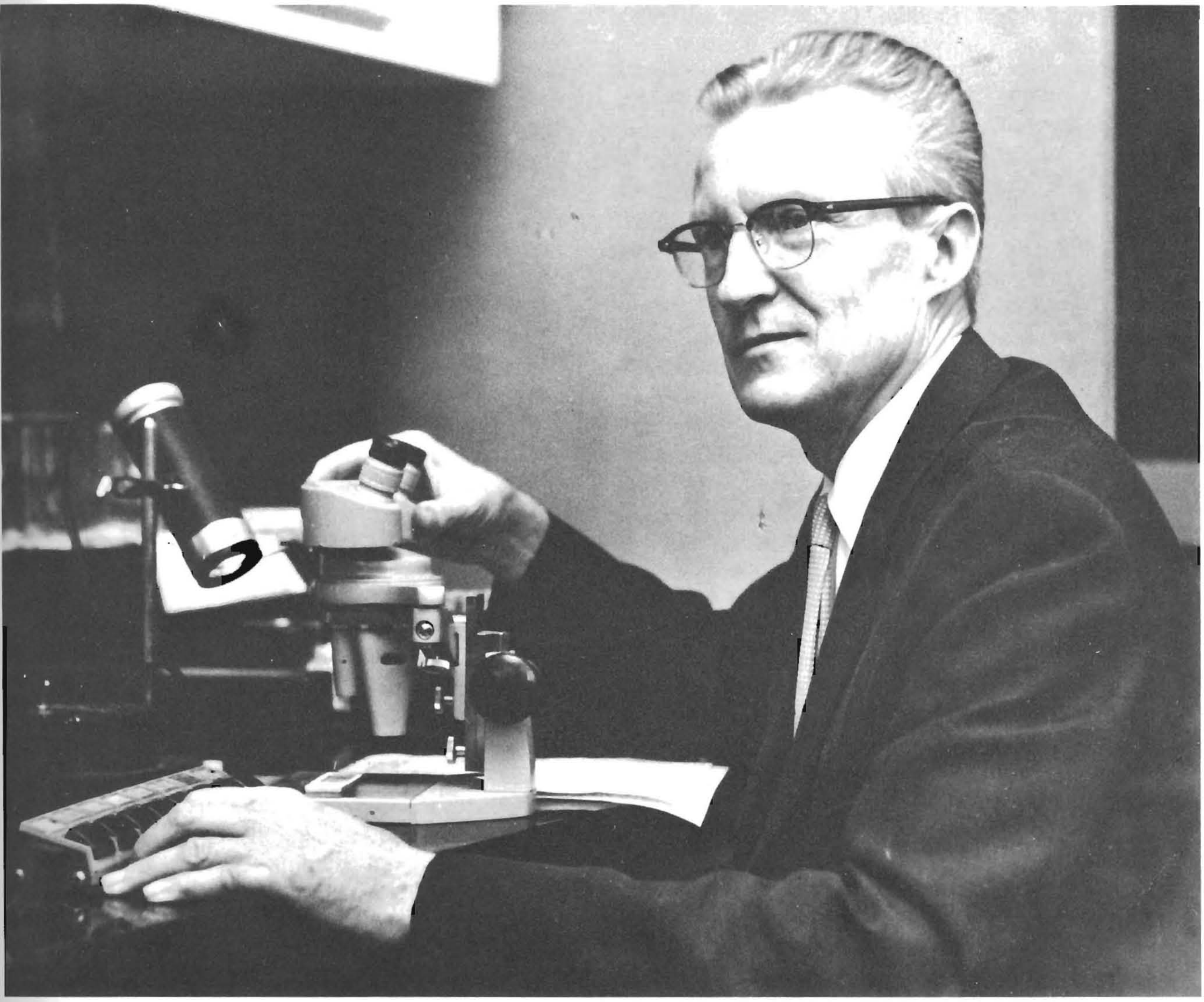
BENTHONIC FORAMINIFERAL ECOLOGY and PALEOECOLOGY

PLANKTONIC FORAMINIFERAL ECOLOGY and PALEOECOLOGY

TAXONOMIC STUDIES

STRATIGRAPHIC STUDIES

MEMORIAL



Orville Lee Bandy
(1917–1973)

The premature and tragic death of Orville Bandy (August 2, 1973) cut short, at its zenith, the dynamic career of this internationally recognized earth scientist. It is highly appropriate to comment on his life in this memorial volume, even though two lengthy memorials to Orville have already been published (Vincent, 1973; Easton, 1974) and two outstanding papers have been dedicated in his honor (Berggren and van Couvering, 1974; Stainforth, Lamb, Luterbacher, Beard and Jeffords, 1975).

Orville was born in Linden, Iowa on March 31, 1917, later moving to Corvallis, Oregon. He completed his B.S. and M.S. degrees in geology at Oregon State University in 1940 and 1941. Two of his earliest publications detail the results of his M.S. research on Cenozoic foraminifera from the Oregon coast. Interestingly, both of these publications were accompanied by Orville's excellent pencil drawings of species described; fine technical illustration was another of Orville's many talents. After completing military service in the U.S. Army Air Corps from 1942 to 1946, he worked as a micropaleontologist for Humble Oil and Refining Company in Houston, Texas. Although brief, this experience not only impressed Orville with the practical application of micropaleontology to oil exploration but also convinced him to seek further graduate education. In characteristic style, he promptly embarked on a doctoral program in 1946 under the renowned J. J. Galloway at Indiana University, aided by a Shell Oil Company Fellowship. There he completed his much referenced Ph.D. dissertation on "Eocene and Oligocene foraminifera from Little Stave Creek, Alabama" in 1948, once again fully documented with his excellent illustrations. The time constraints of finishing his dissertation demanded a non-stop bout of drawing species which apparently taxed even Orville's legendary capacity for intense concentration, and he was to produce his own illustrations for only a half dozen more of his 150 papers. Orville welcomed the arrival of the SEM-era of illustration with relish!

Orville joined the Geology faculty of the University of Southern California in 1948, a time when teaching loads were unusually heavy and space was at a premium. Bill Easton (1974) relates that Orville's first laboratory was a former chemistry stockroom known as "Bandy's broom closet." From this confined space, he produced a dozen papers in four years in addition to teaching a full load of courses. Eventually, Orville's laboratory was transferred to a cheery complex of rooms on the second floor of the Allan Hancock Foundation building. Fortuitously, these rooms were opposite those occupied by K. O. Emery's and later Donn Gorsline's marine geology laboratory. A mutually symbiotic relationship immediately ensued between these two groups periodically punctuated by friendly accusations regarding missing binocular microscopes and Tyler screens. In fact, K. O. insisted that all his marine geology students take Orville's course in introductory micropaleontology, much to the momentary chagrin and ultimate enlightenment of some of the more geophysically inclined types.

Shortly after his arrival at U.S.C., Orville began work on Recent benthic foraminiferal distributions off California, using older samples in the Hancock Foundation collections and samples collected by K. O. Emery and his students. This work resulted in a now classic set of papers with the general title, "Ecology and paleoecology of some California foraminifera." The second half of this contribution deals with the Cenozoic paleobathymetric histories of the Los Angeles and Ventura basins, clearly illustrating the use of biofacies analysis in estimating rates of subsidence and sediment accumulation. Orville first utilized a form of cumulative frequency diagrams in these papers which are still commonly referred to as "Bandy-grams" and which early demonstrated the usefulness of quantitative analysis of foraminiferal faunas.

Orville went on to study modern foraminiferal faunas from the Gulf of Mexico, Gulf of California, and elsewhere, generalizing his observations in an influential paper entitled, "General correlation of foraminiferal structure with environment." During this same period, with his first Ph.D. student, Robert Arnal, he completed work for Gulf Oil Company on the foraminifera from Oligocene and Miocene deposits in the San Joaquin Valley. This effort later yielded two important co-authored papers detailing both general concepts and excellent examples of paleoenvironmental analysis.

Orville hit his research stride during 1960 and 1961. In addition to papers dealing with the distribution and environmental significance of both modern and fossil benthonic foraminifera, he also published reports illustrating the use of planktonic foraminifera for paleoclimatic-paleoceanographic analysis, a subject of increasing importance in his later work. He early recognized the tie between surface water masses, surface temperatures and the distribution of planktonic foraminifera and initially noted, in 1959, the significance of coiling within *Neogloboquadrina pachyderma*.

By 1960, the increasing number, range, and importance of Orville's publications along with those of his growing group of students was reflected by the increasing number of graduate and post-graduate scholars populating his laboratory. All were inspired to unusual heights of activity by Orville's enthusiastic attitude about all things micropaleontologic. Discussions were non-ending and vigorous with some of the most stimulating sessions taking place during extended "coffee breaks" presided over by Orville in the U.S.C. cafeteria. Students began literally working around the clock in the micropaleontologic laboratory. Orville set the pace by working not only in the laboratory, but at home, on the road, in the air and in the field. Periodically Orville's family would attempt to get him to take a vacation, producing speculations by the students as to (a) whether he would leave at all and (b) for how long. In one instance, the entire family departed for a Hawaiian interlude with Orville sans microscope. The resulting "inactivity" was more than Orville could tolerate, and he was back in the laboratory days ahead of schedule. Another attempt saw Orville and family off to the mountains for a skiing holiday; in this case, Orville worked in the snow-covered cabin while the family enjoyed the snow. He simply could not be distracted from his passion for study.

One method by which Orville passes on his drive and knowledge was through an intensive one-to-one teaching style by which each student was required to make reasoned decisions regarding species' identification, ranges and paleoenvironmental decisions. His advanced micropaleontology course centered on a series of unknown samples of increasingly obscure origin, with each student responsible for identifying all species encountered and tabulating abundances, known ranges, etc., finally summarizing the origin, age and depositional environment of each sample. The moment of truth came when Orville sat down with each student and checked individually each species' identification. This activity went on long into the afternoon and evening, spiced with lengthy discussions until a sample's pedigree was established to everyone's satisfaction. Errors, oversights and sloppy thinking were soon exposed by this technique, and he would quickly provide an *F* or an *A* grade based on his intimate knowledge of a student's performance.

Although Orville was a hard task-master in the laboratory, he was a genial host in his truly beautiful home. Orville married his wife Alda in 1943, and they are survived by their son Donald and daughter Janet Lowinger. The Bandy family delighted in having groups of students, colleagues and friends over for an evening of gracious dining and relaxed conversation. One of Orville's specialties was "foraminiferal punch," which had the capacity to untie the tongue of even the most shy graduate student or scholarly adversary, thanks to the generous ratio between rum and other potables (not including the stray foraminifera).

It was obvious to all that Orville enjoyed his family as well as their many friends both within and outside of the micropaleontologic community. In fact, it was Orville's well known capacity to deal with people in a straight-forward yet genial and inspiring way which ultimately thrust him into a leadership role in 13 professional and honorary societies at the national and international level. He was a member of the board of directors of the Cushman Foundation for Foraminiferal Research and served as President of the Foundation in 1956–1967. Orville was also National President of the Society of Economic Paleontologists and Mineralogists in 1971–1972 and earlier served as President of the Pacific Branch of the Paleontological Society. He was a distinguished lecturer for the American Association of Petroleum Geologists in 1963 and 1964 and also served as a trustee of the Research Fund of this organization. His foreign professional associations included membership in the Asociación Mexicana de Geologos Petroleros, Société Géologique Suisse, and the International Subcommission on the Plio-Pleistocene Boundary of the International Geological Union.

Orville's leadership abilities were also fully utilized on his home campus, where he served on the U.S.C. Faculty Senate and became Chairman of the Department of Geological Sciences in 1967. He maintained this latter post through 1972—a period which saw the faculty increase by five members and programs added in geochemistry, geophysics and chemical oceanography. It was also a period which saw the departmental offices moved to expanded and newly renovated quarters. All in all, this was a remarkable set of administrative achievements carried out while Orville was simultaneously teaching courses, fulfilling the presidency of a national society, increasing his pace of publication, leading international oceanographic expeditions, and acting as consultant to the petroleum industry—and always with a smile and great courtesy to all.

Those of us privileged to have been students or close associates of Orville Bandy are still much infected by his ideas and attitudes toward the application of micropaleontology to fundamental questions regarding the later history of the earth. Using the fossil shells of long dead microscopic protozoans to unravel a planet's history may seem a bit much to the uninitiated. But, in fact, Orville played a special and pioneering role in demonstrating the power of micropaleontology to decipher the tectonic and depositional history of continental margins, major variations in the circulation of the oceans, and ultimately the climatic history of the earth—all topics which now occupy center stage in the earth sciences.

BIBLIOGRAPHY OF O. L. BANDY

1944 Eocene Foraminifera from Cape Blanco, Oregon: Jour. Paleontology, v. 18, p. 366–377.

1949 Eocene and Oligocene Foraminifera from Little Stave Creek, Clarke County, Alabama: Bulls. Am. Paleontology, v. 32, no. 32, p. 1–210.

—— Ontogenetic variation in *Eponides mexicanus* (Cushman) [abs.]: Geol. Soc. America Bull., v. 60, no. 12, p. 1949.

1950 Some later Cenozoic Foraminifera from Cape Blanco, Oregon: Jour. Paleontology, v. 24, p. 269–281.

1951 Bathymetric distribution of some shallow-water Foraminifera in the Gulf of Mexico [abs.]: Geol. Soc. America Bull., v. 62, pt. 2, p. 1521.

—— (and Merriam, R. H.) Test wall microstructures as a basis for separating *Nonion* and *Elphidium* [abs.]: Geol. Soc. America Bull., v. 62, pt. 2, p. 1521.

—— (and Burnside, R. J.) The genus *Siphogenerina* Schlumberger: Cushman Found. Foram. Research Contr., v. 2, no. 1, p. 13–15.

—— Upper Cretaceous Foraminifera from the Carlsbad area, San Diego County, California: Jour. Paleontology, v. 25, p. 488–513.

—— Miocene Foraminifera from Erben Bank: Cushman Found. Foram. Research Contr., v. 3, no. 1, p. 18–20.

1952 The genotype of *Siphogenerina*: Cushman Found. Foram. Research Contr., v. 3, no. 1, p. 17–18.

—— SEPM field trip itinerary to Palos Verdes Hills and San Pedro: AAPG, SEPM, and SEG Guidebook, Joint Ann. Mtg.

—— Foraminiferal evidence as to the age of the Pacific Coast *Coralliochama* beds [abs.]: Geol. Soc. America Bull., v. 63, p. 1320.

1953 Ecology and paleoecology of some California Foraminifera, Part I: The frequency distribution of some Recent Foraminifera of California: Jour. Paleontology, v. 27, no. 1, p. 161–182; Part II: Foraminiferal evidence of subsidence rates in the Ventura Basin: Jour. Paleontology, v. 27, no. 2, p. 200–203.

1954 Aragonite tests among the Foraminifera: Jour. Sed. Petrology, v. 24, p. 60–61.

—— Geologic guide No. 4, Southwestern part of Los Angeles Basin: California Div. Mines Bull., v. 170, p. 1–4.

—— Distribution of some shallow-water Foraminifera in the Gulf of Mexico: U.S. Geol. Survey Prof. Paper 254-F, p. 125–141.

—— (and McGrain, Preston) Origin and development of caverns in the Beach Creek Limestone in Indiana: Am. Caver. Bull., v. 16, p. 65–70.

1955 Evidence of displaced Foraminifera in the Purisima Formation of the Half-moon Bay area, California: Cushman Found. Foram. Research Contr., v. 6, no. 2, p. 77–79.

—— Foraminiferal criteria for distinguishing between near-shore and off-shore bottom prominences in clastic areas of the continental shelf [abs.]: Geol. Soc. America Bull., v. 66, pt. 2, p. 1642.

—— Paleotemperatures of Pacific bottom waters and multiple hypotheses: Science, v. 123, p. 459–460.

1956 General relationships between Foraminifera and bathymetry [abs.]: Jour. Paleontology, v. 30, p. 1384.

—— Ecology of Foraminifera in northeastern Gulf of Mexico: U.S. Geol. Survey Prof. Paper 274-G, p. 179–204.

1957 (and Arnal, R. E.) Some new Tertiary and Recent Foraminifera from California and the eastern Pacific Ocean: Cushman Found. Foram. Research Contr., v. 8, pt. 2, p. 54–58.

—— (and Arnal, R. E.) Distribution of Recent Foraminifera off the west coast of Central America: Am. Assoc. Petroleum Geologists Bull., v. 41, p. 2037–2053.

1958 Dominant molluscan faunas of the San Pedro Basin, California: Jour. Paleontology, v. 32, p. 703–714.

1959 The geologic significance of coiling ratios in the foraminifer *Globigerina pachyderma* (Ehrenberg): Geol. Soc. America Bull., v. 70, no. 12, pt. 2, p. 1708.

1960 Planktonic foraminiferal criteria for paleoclimatic zonation: Sendai, Japan, Tohoku Univ. Sci. Repts., 2d ser. (Geology), Spec. Vol. 4, p. 1–8.

—— General correlation of foraminiferal structure with environment: Internat. Geol. Cong., 21st, Copenhagen 1960, Rept., pt. 22, p. 7–18.

—— Rafting of benthonic Foraminifera: Internat. Geol. Cong., 21st, Copenhagen, 1960, vol. of abstracts: p. 241.

—— The geologic significance of coiling ratios in the foraminifer *Globigerina pachyderma* (Ehrenberg): Jour. Paleontology, v. 34, p. 671–681.

—— (and Arnal, R. E.) Concepts of foraminiferal paleoecology: Am. Assoc. Petroleum Geologists Bull., v. 44, p. 1921–1932.

1961 Distribution of Foraminifera, Radiolaria, and diatoms in sediments of the Gulf of California: Micropaleontology, v. 7, p. 1–26.

—— Facies studies can reconstruct oil-forming environments: World Oil, p. 68–71.

1962 Memorial to Jesse James Galloway: Geol. Soc. America Bull., v. 73, p. 95–98.

—— Cenozoic foraminiferal zonation and basinal development for part of the Philippines [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 46, p. 260.

1963 Aquitanian planktonic Foraminifera from Erben Guyot: Science, v. 140, no. 3574, p. 1402–1403.

—— (and Kolpack, R.) Foraminiferal and sedimentological trends in the Tertiary section of Tecolote Tunnel, California: Micropaleontology, v. 9, p. 117–170.

—— Foraminiferal biofacies in sediments of the Gulf of Batabano, Cuba [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 47, no. 2, p. 349–350.

—— Cenozoic planktonic foraminiferal zonation and basinal development in Philippines: Am. Assoc. Petroleum Geologists Bull., v. 47, no. 9, p. 1733–1745.

—— Larger living Foraminifera of the continental borderland of southern California: Cushman Found. Foram. Research Contr., v. 14, no. 4, p. 121–126.

—— Dominant paralic Foraminifera of southern California and the Gulf of California: Cushman Found. Foram. Research Contr., v. 14, no. 4, p. 127–134.

—— Miocene-Pliocene boundary in the Philippines as related to late Tertiary stratigraphy of deep-sea sediments: Science, v. 142, no. 3597, p. 1290–1292.

1963 (and Echols, R. J.) Antarctic foraminiferal zonation [abs.]: XVI Internat. Cong. Zoology Proc., v. 1, p. 221.

1964 Cenozoic planktonic foraminiferal zonation: Micropaleontology, v. 10, no. 1, p. 1–17.

—— Foraminiferal trends associated with deep-water sands: San Pedro and Santa Monica Basins, southern California: Jour. Paleontology, v. 38, no. 1, p. 138–148.

—— The type of *Globigerina quadrilobata* d'Orbigny: Cushman Found. Foramin. Research Contr., v. 15, no. 1, p. 36–37.

—— The type of *Globorotalia crassata* (Cushman): Cushman Found. Foram. Research Contr., v. 15, no. 1, p. 35–36.

—— (and Ingle, J. C., and Resig, J. M.) Foraminiferal trends, Laguna Beach outfall area, California: Limnology and Oceanography, v. 9, p. 112–123.

—— (and Ingle, J. C., and Resig, J. M.) Foraminifera, Los Angeles County outfall area, California: Limnology and Oceanography, v. 9, p. 124–137.

—— (and Ingle, J. C., and Resig, J. M.) Facies trends, San Pedro Bay, California: Geol. Soc. America Bull., v. 75, p. 403–424.

—— (and Echols, R. J.) Antarctic foraminiferal zonation: Antarctic Research Series, Am. Geophysical Union, v. 1, p. 73–91.

—— (and Rodolfo, K. S.) Distribution of Foraminifera and sediments, Peru-Chile Trench area: Deep-Sea Research, v. 11, p. 817–837.

—— Foraminiferal biofacies in sediments of the Gulf of Batabano, Cuba, and their geologic significance: Am. Assoc. Petroleum Geologists Bull., v. 48, no. 10, p. 1666–1679.

1964 (and Arnal, R. E.) Middle Tertiary foraminiferal paleoecology, San Joaquin Valley, California [abs.]: Am. Assoc. Petrol. Geol. Bull., v. 48, p. 516.

1965 The pinger as a deep-water grab control: Undersea Technology, v. 6, no. 3, p. 36.

—— (and Ingle, J. C., and Resig, J. M.) Modification of foraminiferal distribution by the Orange County outfall, California: Washington, D.C., Ocean Science and Ocean Engineering, Trans. Joint Conf., marine Technology Soc. Jour. and Am. Soc. Limnology and Oceanography: p. 55–76.

—— (and Ingle, J. C., and Resig, J. M.) Foraminiferal trends, Hyperion outfall, California: Limnology and Oceanography, v. 10, p. 314–332.

—— (and Merriam, R. H.) Source of upper Cenozoic sediments in Colorado Delta region: Jour. Sed. Petrology, v. 35, no. 4, p. 911–916.

—— (and McNaughton, D. A.) San Pedro de Maturin diapir, Venezuela: Am. Assoc. Petroleum Geologists Bull., v. 49, no. 3, p. 334.

1966 Base of the Pleistocene in the Los Angeles Basin, California [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 50, no. 3, p. 604–605.

—— Faunal evidence of Miocene-to-Recent paleoclimatology in Antarctic [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 50, no. 3, p. 643–644.

—— Restriction of the *Orbulina* datum: Micropaleontology, v. 12, no. 1, p. 79–86.

—— Time-transgressive problems of the California Cenozoic [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 50, no. 3, p. 644.

—— Cretaceous planktonic foraminiferal zonation [abs.]: Geol. Soc. America, Abs. with Programs for 1966 (Ann. Mtg.), p. 9.

—— (and Chierici, M. A.) Depth-temperature evaluation of selected California and Mediterranean bathyal Foraminifera: Marine Geology, v. 4, no. 4, p. 259–271.

1967 (and Frerichs, W. E., and Vincent, E.) Origin, development, and geologic significance of *Neogloboquadrina* Bandy, Frerichs, and Vincent, gen. nov.: Cushman Found. Foram. Research Contr., v. 18, no. 4, p. 152–157.

—— Foraminiferal definition of the boundaries of the Pleistocene in southern California, *in* Progress in oceanography—Vol. 4, The Quaternary history of the ocean basins: London and New York, Pergamon Press, p. 27–49.

—— Cruise report, Research Vessel *Anton Bruun*, Cruise 17: Spec. Rept. 7, Marine Laboratory, Texas A&M Univ., Galveston, Tex., p. 1–16.

—— (and Ingle, J. C., and Frerichs, W. E.) Isomorphism in "*Sphaeroidinella*" and "*Sphaeroidinellopsis*": Micropaleontology, v. 13, no. 4, p. 483–488.

—— (and Wade, Mary E.) Miocene-Pliocene-Pleistocene boundaries in deep-water environments, *in* Progress in oceanography—Vol. 4, The Quaternary history of the ocean basins: London and New York, Pergamon Press, p. 51–66.

—— Cretaceous planktonic foraminiferal zonation: Micropaleontology, v. 13, no. 1, p. 1–31.

—— Cycles in Neogene paleo-oceanography and eustatic changes: Geol. Soc. America, Abs. for 1967, Spec. Paper 115, p. 463.

1967 Paleo-oceanographic variations and planktonic faunas near the Miocene-Pliocene boundary, California [abs.]: Geol. Soc. America, Programs Southeastern Section.

—— Paleontological guides to depositional environments [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 51, no. 3, p. 453.

—— (and Ingle, J. C.) Neogene planktonic events and radiometric scale, California [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 51, no. 3, p. 453–454.

—— Problems of Tertiary foraminiferal and radiolarian zonation, Circum-Pacific area, *in* Hatai, K., ed., Tertiary correlations and climatic changes in the Pacific—Pacific Sci. Cong., 11th, Tokyo, Japan, 1966, Symposium No. 25: Sendai, Sasaki Pub., p. 95–102.

—— Development of *Globigerina bulloides* in the California Miocene [abs.]: Geol. Soc. America Spec. Paper 115, p. 11–12.

1968 Paleoclimatology and Neogene planktonic foraminiferal zonation: Giornale Geol., ser. 2, v. 35, no. 2, p. 277–290.

—— Cycles in Neogene paleoceanography and eustatic changes: Palaeogeography, Palaeoclimatoogy, and Palaeoecology, v. 5, p. 63–75.

—— (and Vincent, E.) Relationships of orbulines to the *Globorotalia fohsi* lineage: Geol. Soc. America, Abs. with Programs (Ann. Mtg.), p. 17.

—— (and Arnal, R. E.) Middle Tertiary planktonic foraminiferal facies, San Joaquin Basin, California [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 52, no. 3, p. 518–519.

—— Planktonic foraminifera as indices of paleoceanography [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 52, no. 3, p. 559–560.

—— Neogene polar planktonic foraminiferal invasions of temperate regions [abs.]: Internat. Geol. Cong., 23d, Prague 1968, p. 269–270.

—— (and Vincent, E.) Review of Manuel de Micropaléontologie des Foraminifères by Neumann, M., 1967: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 4, p. 305–306; and Jour. Paleontology, v. 42, p. 610–611.

1969 (and Arnal, R. E.) Middle Tertiary Basin development, San Joaquin Valley, California: Geol. Soc. America Bull., v. 80, p. 783–820.

—— Relationships of Neogene planktonic foraminifera to paleoceanography and correlation, *in* Bronnimann, P., and Renz, H. H., eds.: Internat. Conf. Planktonic Microfossils, 1st, Geneva, 1967, Proc., v. 1, p. 46–57.

—— (and Casey, R. E.) Major late Cenozoic planktonic datum planes, Antarctic to the tropics: Antarctic Jour. U.S., v. 4, no. 5, p. 170–171.

—— (and Morin, R. W., and Wright, R. C.) Definition of the *Catapsydrax steinforthi* Zone in the Saucesian Stage, California: Nature, v. 222, p. 468–469.

—— The Calabrian stratotype, a correlative of the California Wheelerian Stage [abs.]: INQUA Cong., Paris, 7th, Résumés, sec. 6, p. 179.

1969 (and Morin, R. W., and Wright, R. C.) Identification of the *Catapsydrax steinforthi* Zone in the upper part of the lower Saucesian Stage, California: Am. Assoc. Petroleum Geologists Bull., v. 53, no. 3, p. 705.

—— (and Wright, R. C., and Yen, Meei-Meei) Planktonic foraminiferal indices common to the lower Pliocene of California and Italy: Am. Assoc. Petroleum Geologists Bull., v. 53, no. 2, p. 465–466.

—— (and Casey, R. E., and Wright, R. C.) The geologic significance of *Prunopyle titan* Campbell and Clark [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 53, no. 2, p. 467.

—— (and Wilcoxon, J. A.) Correlation of the middle Tertiary Stages of California with tropical planktonic zones [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 53, no. 2, p. 467–468.

—— (and Vincent, E., and Wright, R. C.) Chronologic relation-

ships of orbulines to the *Globorotalia fohsi* lineage: Revista Española de Micropaleontologia, v. 1, no. 2, p. 131–145.

—— (and Butler, E. A., and Wright, R. C.) Alaskan upper Miocene marine glacial deposits and the *Turborotalia pachyderma* datum plane: Science, v. 166, p. 607–609.

—— (and Casey, R. E., and Wright, R. C.) Climatic deterioration near the Brunhes-Matuyama boundary: INQUA Cong., Paris, 7th, Résumés Communications, sec. 2, p. 61–62.

1970 Bipolar synchroneity of late Cenozoic paleoclimatic cycles [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 54, no. 12, p. 2468.

—— Upper Cretaceous–Cenozoic paleobathymetric cycles, eastern Panama and northern Colombia: Gulf Coast Assoc. Geol. Socs. Trans., v. 20, p. 181–193.

—— Introduction, *in* Radiometric dating and paleontologic zonation: Geol. Soc. America Spec. Paper 124, p. 1–6.

—— (and Ingle, J. C., Jr.) Neogene planktonic events and radiometric scale, California: Geol. Soc. America Spec. Paper 124, p. 131–172.

—— (and Wilcoxon, J. A.) The Pliocene-Pleistocene boundary, Italy and California: Geol. Soc. America Bull., v. 81, p. 2939–2948.

—— (and Hornibrook, N. de B., and Scholfield, J. C.) Age relationships of the *Globigerinoides trilobus* zone, Muriwai Quarry, New Zealand: New Zealand Jour. Geology and Geophysics, v. 13, no. 4, p. 980–992.

—— (and Casey, R. E.) Late Cenozoic paleoclimatic cycles, Antarctic to the tropics: Antarctic Jour. U.S., v. 5 (Sept.–Oct.), p. 176–178.

—— (and Casey, R. E.) Quaternary paleoclimatic variations [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 54, no. 5, p. 835.

—— (and Casey, R. E., and Wright, R. C.) Late Neogene planktonic zonation, magnetic reversals, and radiometric dates, Antarctic to the tropics: Planktonic Conference, Roma, Abstracts of papers.

—— (and Wilcoxon, J. A.) The Pliocene-Pleistocene boundary, Italy and California: Geol. Soc. America Bull., v. 18, no. 10, p. 2939–2947.

1971 (and Casey, R. E., and Wright, R. C.) Late Neogene planktonic zonation, magnetic reversals, and radiometric dates, Antarctic to the tropics: Antarctic Research Series (Oceanology I), v. 15, p. 1–26.

—— (and Ingle, J. C., Jr., and Wright, R. C.) *Globorotaloides suteri* Bolli *relizensis* new subsp.: Jour. Foraminiferal Research, v. 1, no. 1, p. 15–16.

—— Time-transgressive aspects of some critical planktonic species [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 55, no. 2, p. 330.

—— Origin and development of *Globorotalia* (*Turborotalia*) *pachyderma* (Ehrenberg) [abs.]: Gulf Coast Assoc. Geol. Socs. Trans., v. 21, p. 433–444.

—— Neogene planktonic foraminiferal zones, the tropics and California: Geol. Soc. America, Abs. with Programs (Cordilleran Sec.), p. 78.

—— Recognition of upper Miocene Neogene Zone 18, experimental mohole, Guadalupe site: Nature, v. 233, no. 5320, p. 476–478.

—— (and Theyer, F.) Growth variation in *Globorotalia pachyderma* (Ehrenberg): Antarctic Jour. U.S., Sept.–Oct. issue, v. 6, no. 5, p. 172–174.

—— Le stratotype du Calabrien, sa corrélation avec l'étage Wheelerien de Californie [abs.]: Quaternaria, v. 15, p. 75.

—— Radiometric dates and planktonic foraminifera of the lower Miocene—A reply: New Zealand Jour. Geology and Geophysics, v. 14, p. 908–909.

—— Environmental controls for *Buliminella elegantissima* (d'Orbigny), a neritic foraminifer: Univ. Southern Calif., Univ. Press, Abstracts, Second Coastal and Shallow Water Research Conf., Oct. 1971, p. 18.

—— Review of The micropaleontology of the oceans, Funnell, B. M., and Riedel, W. R., eds., Cambridge University Press: American Scientist, Nov.–Dec. 1971, v. 59, no. 6, p. 758.

1972 Time-transgressive aspects of the late Neogene Wheelerian-Hallian boundary, southern California: Revue de Micropaléontologie, v. 14, no. 5, p. 73–77.

—— A review of the calibration of deep-sea cores based upon species variation, productivity, and $^{16}O/^{18}O$ ratios of planktonic foraminifera—including sedimentation rates and climatic inferences, *in* Bishop, W. W., and Miller, J. A., eds., Calibration of hominoid evolution: Scottish Academic Press, p. 37–61.

—— The Plio-Pleistocene boundary, Europe and California, and the paleomagnetic scale: Moscow, Internat. Colloquium on Problem "The boundary between the Neogene and Quaternary," Collection of Papers I, p. 15–62.

—— Neogene planktonic foraminiferal zones, California, and some geologic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 12, p. 131–150.

—— Environmental significance of variations in *Globigerina bulloides* d, Orbigny [abs.]: Internat. Geol. Cong. Montreal, 24th Session, Abstracts volume, p. 214.

—— Messinian deep-water evaporite deposition and the Miocene-Pliocene boundary, Pasquasia-Capodarso sections, Sicily: Internat. Geol. Cong. Montreal, 24th Session, Abstracts volume, p. 533.

—— Origin and development of *Globorotalia* (*Turborotalia*) *pachyderma* (Ehrenberg): Micropaleontology, v. 18, no. 3, p. 294–318.

—— Concepts of micropaleontology applied to petroleum geology [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 56, no. 3, p. 602.

—— Late Paleogene-Neogene planktonic biostratigraphy and its geologic implications, California, *in* Stinemeyer, E. G., ed., Pacific Coast Miocene Biostratigraphic Symposium Proc., Pacific Section SEPM, March 9–10, Bakersfield, Calif.: p. 37–51.

—— Upper Paleogene planktonic correlations, Santa Barbara area, California, *in* Guidebook, Pacific Sections, AAPG-SEPM, Spring Field Trip, June 2, 1972, Central Santa Ynez Mountains, Santa Barbara Co., Calif.: p. 55–58.

—— Variations in *Globigerina bulloides* d'Orbigny as indices of water masses: Antarctic Jour. U.S., v. 7, no. 5, Sept.–Oct. issue, p. 194–195.

—— Biostratigraphic and paleomagnetic studies of *Eltanin* samples, 1971–72: Antarctic Jour. U.S., v. 7, no. 5, Sept.–Oct. issue, p. 193–194.

—— (and Casey, R. E., and Theyer, F.) Planktonic events, upper Gilbert-Gauss magnetic epochs [abs.]: Geol. Soc. America, Abstracts, v. 4, no. 7, p. 442–443.

—— Critical problems of the Quaternary: Miami, Fla., Am. Quaternary Assoc., 2d Conf., Abs., p. 1–2.

—— Major Quaternary palaeoceanographic cycles: Antarctic to the tropics: Antarctic Geology and Geophysics, Oslo Univ. Forlaget, Internat. Union Geological Sci., Series B, no. 1, Adie, R. J. (ed.), p. 739–744.

—— Review of Manual of planktonic Foraminifera by Postuma,

J. A., 1971: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 12, p. 296–297.

—— (and Lindenberg, H. G., and Vincent, E.) History of research, Indian Ocean Foraminifera: Jour. Marine Biology Assoc. India, v. 13, no. 1, p. 86–105.

—— (and Doyle, L. J.) Southern California borderland; Baja California: Its tectonic and environmental development: Geol. Soc. America Bull., v. 83, p. 3785–3794.

1973 (and Vincent, E.) Review of Contribution à l'étude des Foraminifères Paléogènes du Bassin de Paris by LeCalvez, Y., 1970: Jour. Paleontology, v. 47, p. 811–812.

—— (and Marincovich, L.) Rates of late Cenozoic uplift, Baldwin Hills, Los Angeles, California: Science, v. 181, p. 653–654.

—— (and Casey, R. E.) Reflector horizons and paleobathymetric history, eastern Panama: Geol. Soc. America Bull., v. 84, p. 3081–3086.

—— (and Casey, R. E.) Paleotemperature characteristics, Matuyama-Brunhes sequence in the southern ocean [abs.]: INQUA Cong., 9th, Christchurch, Abstracts, p. 10–11.

—— Chronology and paleoenvironmental trends, Late Miocene-Early Pliocene, western Mediterranean: *in* Messinian events in the Mediterranean, Koninklijke Nederlandse Akademie Van Wetenschappen, Amsterdam, p. 21–25.

—— Planktonic biostratigraphy, southern ocean deep-sea cores: Antarctic Jour. U.S., v. 8, no. 5, Sept.–Oct. issue, p. 286.

1975 Messinian evaporite deposition and the Miocene/Pliocene boundary, Pasquasia-Capodarso sections, Sicily: *in* Late Neogene epochs boundaries, Saito, T., and Burckle, L., eds., Micropaleontology Press, Am. Mus. Nat. History, p. 49–63.

BENTHONIC FORAMINIFERAL ECOLOGY
and PALEOECOLOGY

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 17–39, 1980

TRENDS IN THE DISTRIBUTION OF RECENT FORAMINIFERA IN SAN FRANCISCO BAY

R. E. ARNAL[1], P. J. QUINTERNO[1], T. J. CONOMOS[1], AND RALPH GRAM[2]

ABSTRACT

Much of the bathymetry of the southern part of San Francisco Bay reflects the drainage pattern of late Pleistocene streams. Holocene estuarine silt and clay cover most of the bay floor; relict eolian and deltaic sand occurs along the eastern shore; sandy patches are present in the main channel owing to higher tidal current velocities. Organic content is high along the western shore, where tidal flats are extensive, and in the slough at the mouth of Coyote Creek where wastewaters discharge.

Thirty-one species of benthonic foraminifera were identified in surficial sediments of San Francisco Bay estuary; of these, 20 species were stained red by rose Bengal and are considered as live. Water depth, sediment textural characteristics, salinity, organic matter, sediment pH, and biological competition were considered as factors that might affect distribution of foraminifera. Four ecologic zones based on observed trends in the distribution and abundance of several species correlate well with some environmental factors. Four groups based on the Q-mode analysis of frequency counts of foraminiferal assemblages are reasonably similar to the four ecologic zones. These zones, showing restricted depth ranges, are: Inner Coastal Zone, where *Elphidium incertum obscurum* and *Trochammina inflata* are prominent; Outer Coastal Zone, dominated by *Ammonia beccarii tepida* and *Elphidium incertum*; Deep Bay Zone, where *Elphidiella hannai, Elphidium incertum clavatum, Hopkinsina pacifica,* and *Bolivina* spp. appear in abundance; and Deep Channel Zone, where *Elphidiella hannai* is most abundant. In the Inner Coastal Zone, salinity due to large fluctuations is a limiting factor for many species. Substrate textural characteristics are primary determinants of the distribution of agglutinated foraminifers. The percentage of organic matter in the sediment correlates well with the abundance of *Elphidium incertum obscurum,* a ubiquitous species in San Francisco Bay. Sediment pH is not critical. Biologic competition can be estimated by comparing the percentage of a species with the number of species present in the assemblage, as shown for *Ammonia beccarii tepida* and *Elphidiella hannai.*

INTRODUCTION

A study of the surficial sediments, benthic foraminifera, and selected water properties of the San Francisco Bay estuary was initiated several years ago by the Department of Geology, San Jose State University. Five advanced research projects, each with a different emphasis or covering different geographic areas of the San Francisco Bay estuary, have been completed to this time (Conomos, 1963; Reese, 1965; Gram, 1966; Quinterno, 1968; Locke, 1971). The results of this research augment the limited knowledge of the sediment and foraminiferal characteristics of estuaries and lagoons of the Pacific Coast. In addition, they permit the determination of the relation between foraminifera and various environmental factors. Such basic data are important for future environmental studies, as they suggest parameters that may be used to separate natural variations in the distribution of foraminifera from those variations caused by man-induced pollutants.

---

[1] U.S. Geological Survey, 345 Middlefield Road, Menlo Park, California 94025.

[2] Department of Geology, San Jose State University, San Jose, California 95192.

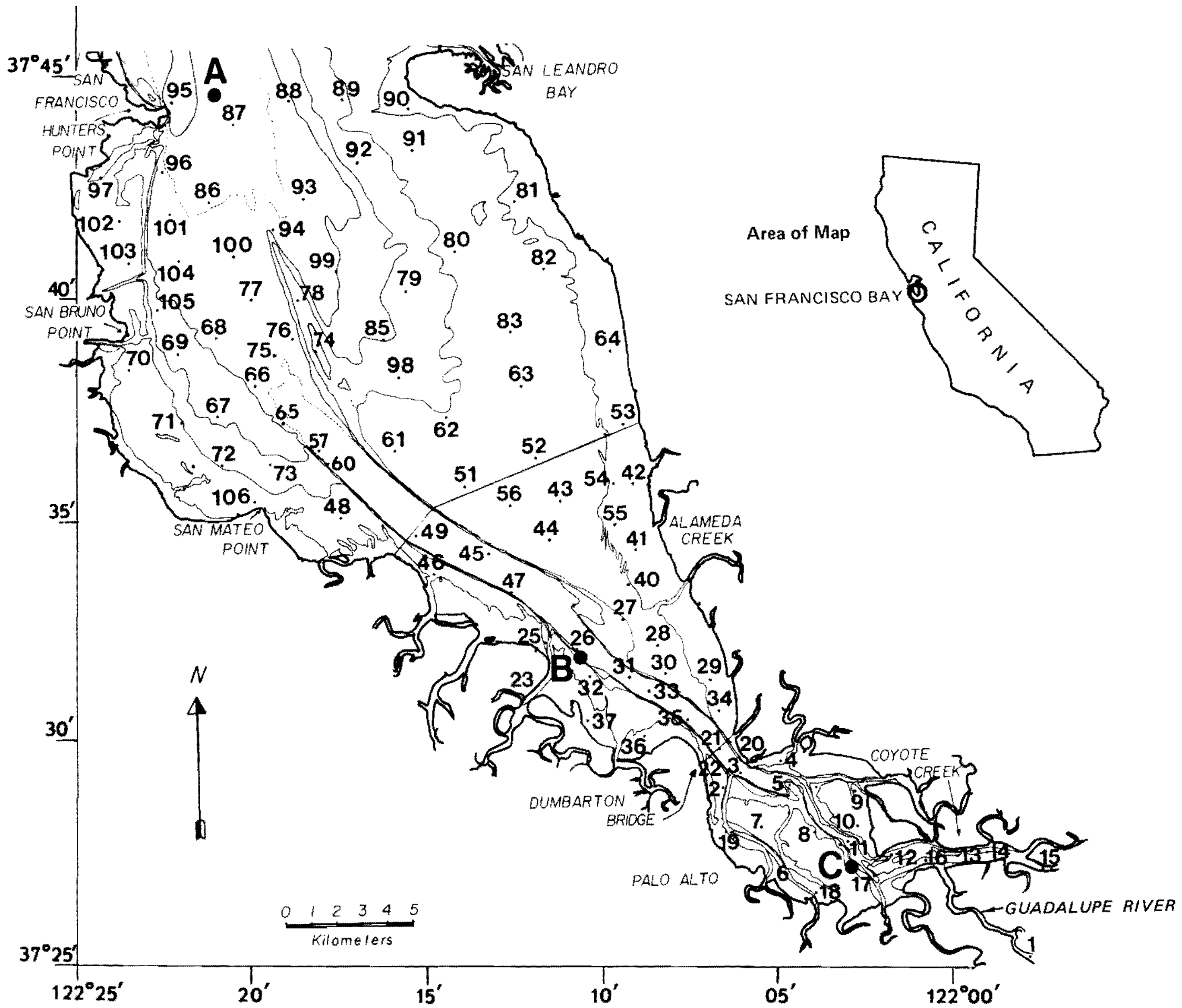


FIGURE 1
Location of stations.

This paper, compiled from the studies of Quinterno (1968), Conomos (1963), and Gram (1966), presents the sedimentologic characteristics and selected water properties of the southern part of San Francisco Bay (Fig. 1) and relates the distribution and abundance of benthic foraminifers to these parameters.

Sumner and others (1914) and Miller and others (1928) were the first to describe the chemical and physical characteristics of the water masses. Storrs and others (1963, 1965, 1968) much later conducted long-term studies of physical, chemical, and biological aspects of the waters and sediments relevant to sanitary-engineering problems. McCulloch and others (1970) have presented preliminary results of water-chemistry studies. Folger (1972) has summarized graphically the sediment studies of Conomos (1963) and Gram (1966).

No detailed studies of foraminifera have been published. Preliminary information has been presented by McDonald and Diediker (1930), Arnal and Conomos (1962), and Arnal and others (1970). More extensive

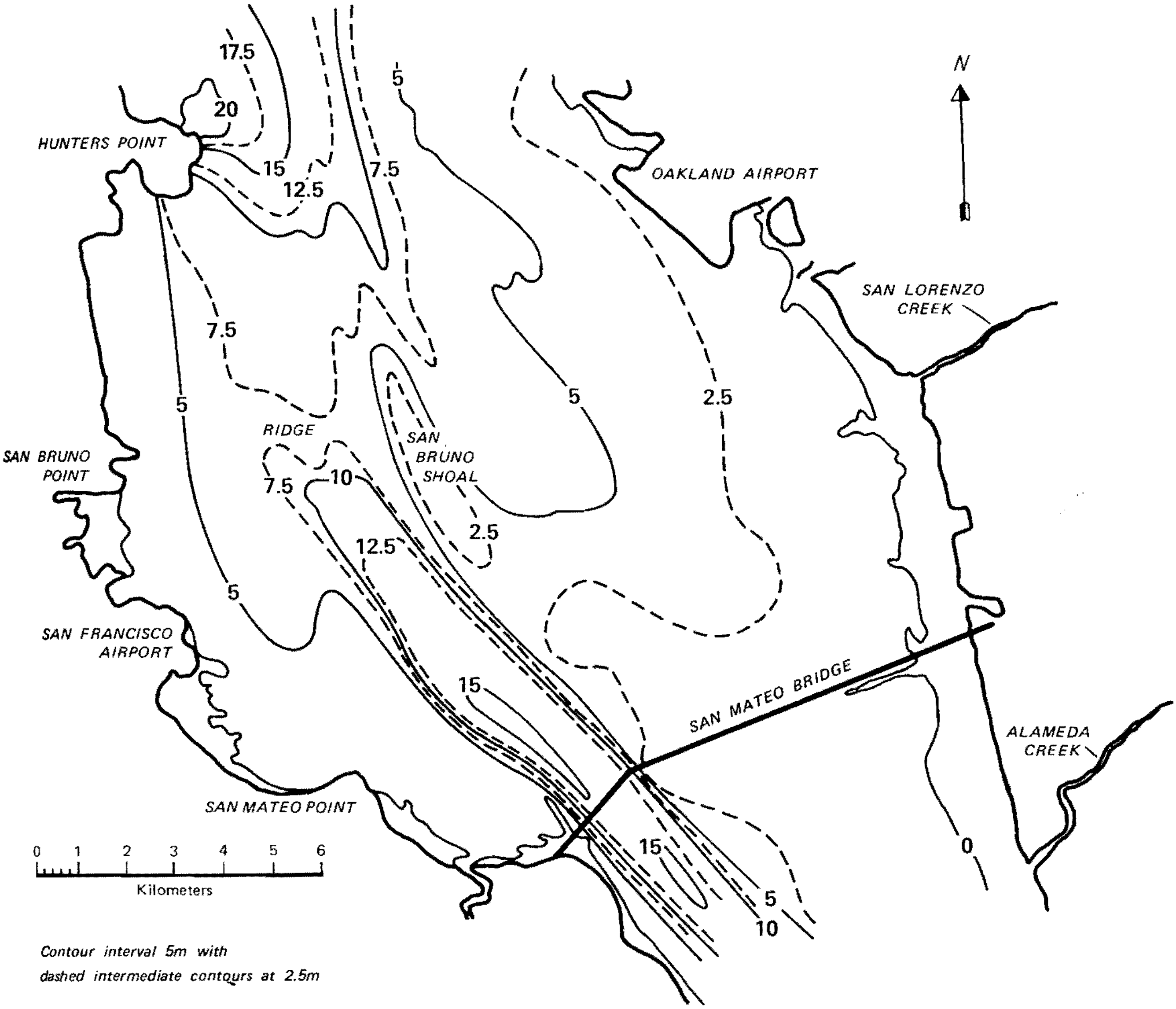


FIGURE 2
Detailed bathymetry north of San Mateo Bridge.

studies of foraminifera found in surficial sediments have been conducted by Quinterno (1968) in the study area and by Locke (1971) in San Pablo Bay.

We thank W. H. Raub and L. H. Brubaker of the technical staff at San Jose State University for their assistance in the field and laboratory; Brian Atwater, U.S. Geological Survey, and C. H. Stevens, Department of Geology, San Jose State University, for their advice and manuscript reviews. We are grateful for the laboratory, library, and computer facilities provided us by San Jose State University, the U.S. Geological Survey, and Scripps Institution of Oceanography.

AREAL DESCRIPTION

Southern San Francisco Bay occupies a late Cenozoic structural valley between the Diablo Range on the east and the Santa Cruz Mountains on the west. Poorly consolidated sediments, ranging in thickness from 0 to 300 m or more (Hazelwood, 1976), partly fill the trough and overlie late Mesozoic basement rocks.

Alternating marine and nonmarine facies in these deposits record glacio-eustatic changes in sea level during the Quaternary Period (Louderback, 1951; Atwater, in press). Nonmarine conditions prevailed

TABLE 1

Typical water temperature and salinity measurements in southern San Francisco Bay.[a]

SUMMER (July through October 1969–72)

Parameter	Station A	Station B	Station C
Salinity (‰)			
Range	(25.4–32.2)	(22.0–32.4)	(19.5–30.8)
Median	31.0	30.5	27.5
Temperature (°C)			
Range	(16.1–20.2)	(15.7–23.1)	(19.0–24.5)
Median	17.9	20.2	20.7

WINTER (January through April 1969–73)

Parameter	Station A	Station B	Station C
Salinity (‰)			
Range	(6.9–27.5)	(13.0–26.6)	(9.3–24.9)
Median	24.0	19.2	16.0
Temperature (°C)			
Range	(8.7–14.3)	(8.5–19.2)	(8.3–16.6)
Median	12.3	13.5	13.5

[a] Unpublished U.S. Geological Survey data; sampling depth approximately two meters; see Figure 1 for location of stations.

throughout the study area as recently as 10,000 years ago. Subsequent changes in sea level, due largely to the melting of Wisconsinan glaciers, caused sea water to enter the Golden Gate, creating a growing bay that had reached the site of the Dumbarton Bridge by 6,500 years ago (Atwater, Hedel, and Helley, 1977).

The San Francisco Bay estuary is characterized by large expanses of marshes, tidal flats, shoals, and narrow deep channels extending longitudinally through the broad depression. Seventy percent of the area below mean low water is shallower than 5.5 m and 80 percent is shallower than 9 m (Sumner and others, 1914). Much of the submarine topography appears to reflect the shape of the late Pleistocene (Wisconsinan) land surface that has been buried by the bay and its sediment. The general morphology of the original stream beds has not been obliterated and suggests that perhaps the Guadalupe River occupied a distinct channel separated from the channel of Alameda Creek and San Lorenzo Creek by San Bruno Shoal (Fig. 2).

Precipitation is highly seasonal. Almost 90 percent of the annual precipitation occurs during the period November through April (Rantz, 1971). The relief of the drainage basin has a strong local influence on the amount of rainfall. Mean annual precipitation ranges from 25 cm in low-lying valley areas to 200 cm in mountain areas.

The tides are mixed and predominantly semi-diurnal, ranging from 1.7 m at the Golden Gate to 2.7 m at the south end of the study area (U.S. Coast and Geodetic Survey, 1973). Waves are generated in response to high winds and the long fetch. The observed frequency of wave heights of 0.5 to 1 m is at least 50 percent.

Discharge from the Sacramento-San Joaquin Rivers dilutes Pacific Ocean water entering the estuary and largely controls the salinity of the water in the study area. Local streams and wastewater flows have only limited effects (McCulloch and others, 1970). Typical near-surface salinity values at three main channel stations (Fig. 1) are listed in Table 1. Winter salinities (median) range from 16 to 24‰ and reflect the high river runoff; salinity stratification results in vertical differences of as much as 10‰. Summer salinities are somewhat higher, ranging from 28 to 31‰. Although evaporation removes more than a meter of water per year, its effect on the salinity is noticeable only during the summer of years with exceptionally low freshwater discharge.

Water temperatures measured by Conomos (1963) and Gram (1966) at the time of sediment collection varied from 6.5°C (winter) to 25.2°C (summer); within a given day, however, spatial differences rarely exceeded 3°C.

Tidal currents, commonly exceeding 100 cm/sec, resuspend and transport bottom sediments. Nontidal circulation, generated by water-density differences and wind, is generally less than 5 cm/sec; together with tidal mixing, it is important in flushing the south bay (Conomos and others, 1971). Its role in transporting sediment in the south bay is unknown.

METHODS

SHIPBOARD ACTIVITIES

Nearly 100 sampling stations, generally 2 to 3 km apart, were established (Fig. 1). Positioning by triangulation and dead reckoning was generally accurate to better than 0.25 km. The routine sampling procedure at each station consisted of:

1. Measurement of water turbidity with a Secchi disc and water depth with a sounding line;
2. Collection of surface water at most stations with an additional near-bottom sample when the water depth exceeded 4 m;
3. Sampling of the upper 5 to 10 cm of undisturbed sediment with a Peterson dredge;
4. Measurement of temperature, pH, and Eh of both water and sediment; and

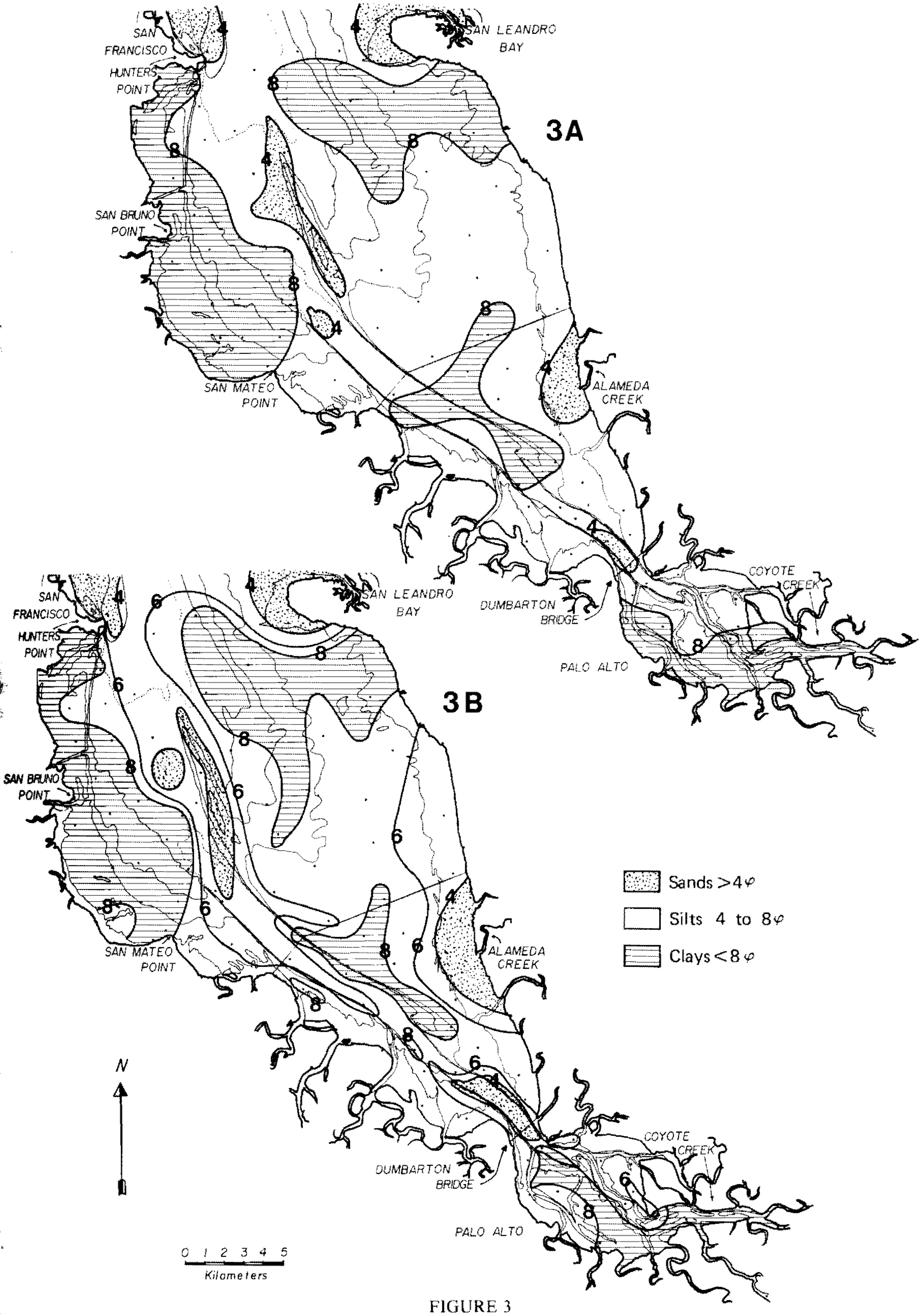


FIGURE 3

A. Distribution of sediment mean size. B. Distribution of sediment median diameter.

TABLE 2

Average annual sediment inflow to San Francisco Bay estuary.[a]

Drainage basin	Drainage area (km²)	Sediment inflow[b] (10⁶ metric tons/year)
Central Valley	117,700	4.56
Suisun Bay	1,500	0.17
San Pablo Bay	2,500	0.32
San Francisco Bay (total)	4,400	0.27
(study area)	(3,400)	(0.25)
Tulare Basin and Goose Lake[c]	36,400	—
TOTAL	162,500	5.32

[a] Data from Porterfield and others (1961).

[b] 1909–1959 records adjusted to 1957–1959 conditions measured by Porterfield and others (1961).

[c] Interior drainage, not contributing to estuary.

5. Splitting the sediment sample in two representative parts—one for sediment studies, the other, treated with an organic dye (rose Bengal), for studies of foraminifera.

LABORATORY TECHNIQUES

Sediment textural analysis was performed by pipette and settling tube methods. The data from each sample were plotted as cumulative curves using the standard phi-unit scale, and the comprehensive statistical parameters of Trask (1932) and Folk and Ward (1957) were applied to these data using a programmable calculator.

The organic-carbon content (OCC) was determined by the Allison (1935) technique, and this value then converted to organic-matter content by multiplying the OCC by 1.7 as recommended by Trask (1932).

The foraminifera were separated from a known amount of dried sediment by flotation in carbon tetrachloride. After being dried on filter paper, the total mass was divided with a microsplitter until an optimum number of specimens was obtained for counting.

SEDIMENT

SOURCES AND DISPOSITION

The drainage area of streams tributary to the San Francisco Bay estuary is more than 162,000 km², or about 40 percent of the surface area of California. The Sacramento and San Joaquin Rivers contribute 86 percent of the alluvial sediment (Table 2). Small ephemeral streams tributary to the study area contribute about 5 percent of the total; of these, Alameda Creek is the dominant source, contributing almost half this amount.

Ninety-four percent of the riverborne sediment enters as suspended load; 95 percent by volume is silt- and clay-size (Schultz, 1965). The sediment is constantly resuspended, transported, and redeposited because of the shallowness of the estuary, the large size and prevelance of wind-induced waves, and the strong tidal currents. This constant reworking of the surficial sediments prohibits meaningful short-term measurements.

Some of the suspended sediment contributed by the Sacramento and San Joaquin Rivers is transported seaward through the Golden Gate. The rest of the sediment-laden water is moved by tidal currents into the study area, where sediment is eventually deposited. Sedimentation rates in the post-Wisconsinan San Francisco Bay estuary have probably varied greatly in time and space. Long-term rates in the central parts of the estuary range from 100 to 200 cm/1,000 years (Kvenvolden, 1962). In the south bay, average rates based on radiocarbon dates range from 30 to 200 cm/1,000 years (Story and others, 1965; Atwater and others, 1977).

TEXTURAL CHARACTERISTICS

Size

The particle size of the surficial sediments of southern San Francisco Bay, expressed as mean diameter, ranges from 4 to 64 μm (8 to 4 phi), silt or silty clay (Fig. 3A) by Folk and Ward (1957) classification. Clay (>8 phi) is generally restricted to shallow areas, sand (<4 phi) to the main channel and the mouth of Alameda Creek.

Although median diameter is by far the most commonly used sediment-size parameter, it does not represent well the size distribution for asymmetrical or bimodal sediments (Folk, 1968). Comparison of Trask median diameters (Fig. 3B) with Folk and Ward mean size (Fig. 3A) shows that the sand, silt, and clay are similar in areal extent with the exception of the area south of Dumbarton Bridge, where size distribution in several samples is bimodal. This bimodality is caused by: (1) strong tidal currents to 90 cm/sec that winnow away fine-grained sediments at the narrow straits beneath the Dumbarton Bridge; (2) discharge from several streams that contribute coarser sediments; and (3) marsh vegetation that traps fine particles, especially east of Palo Alto (Fig. 3A).

Sorting

Most of the sediments are very poorly or extremely poorly sorted (Fig. 4A). One exception is the sandy

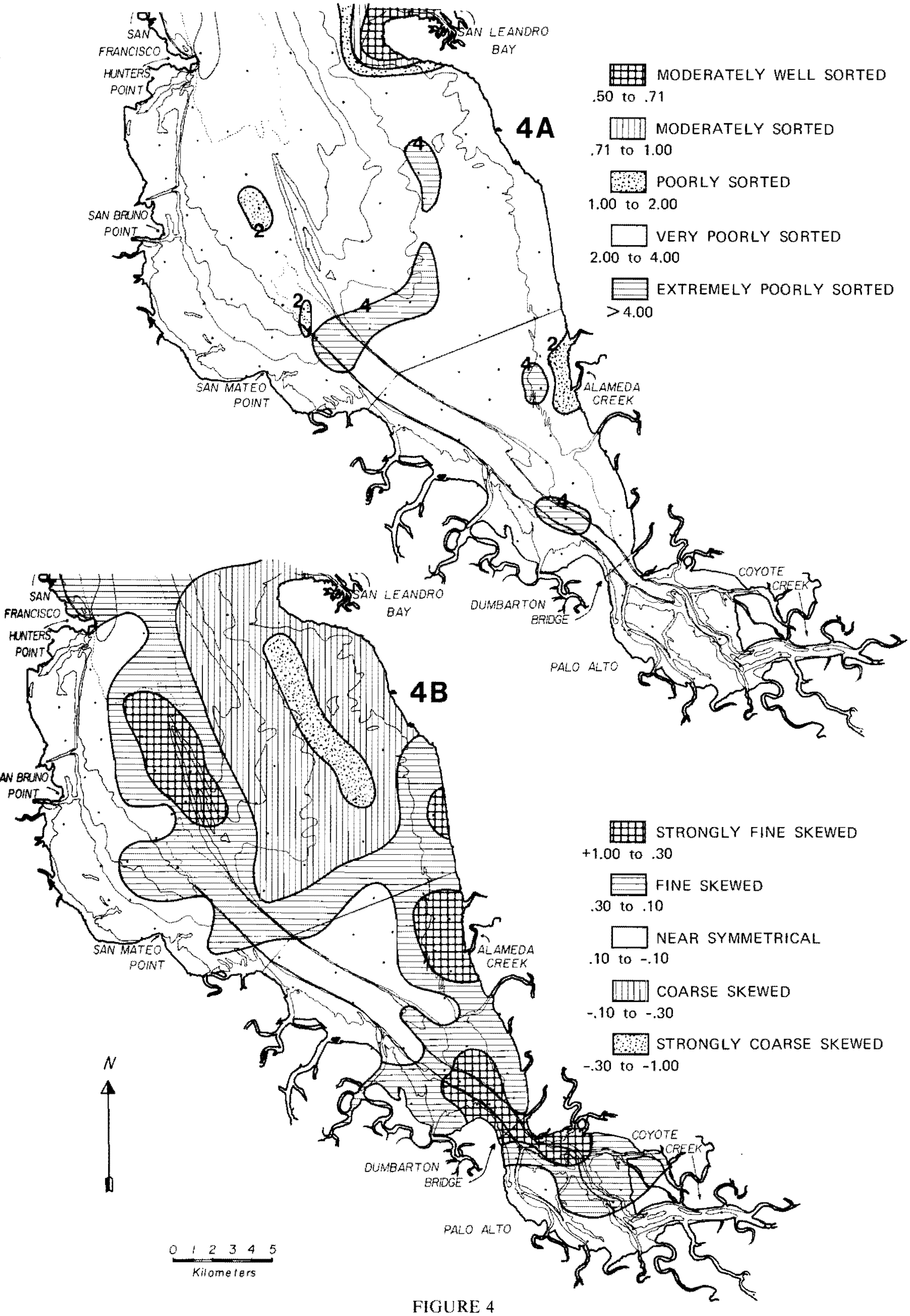


FIGURE 4
A. Distribution of sediment sorting. B. Distribution of sediment skewness.

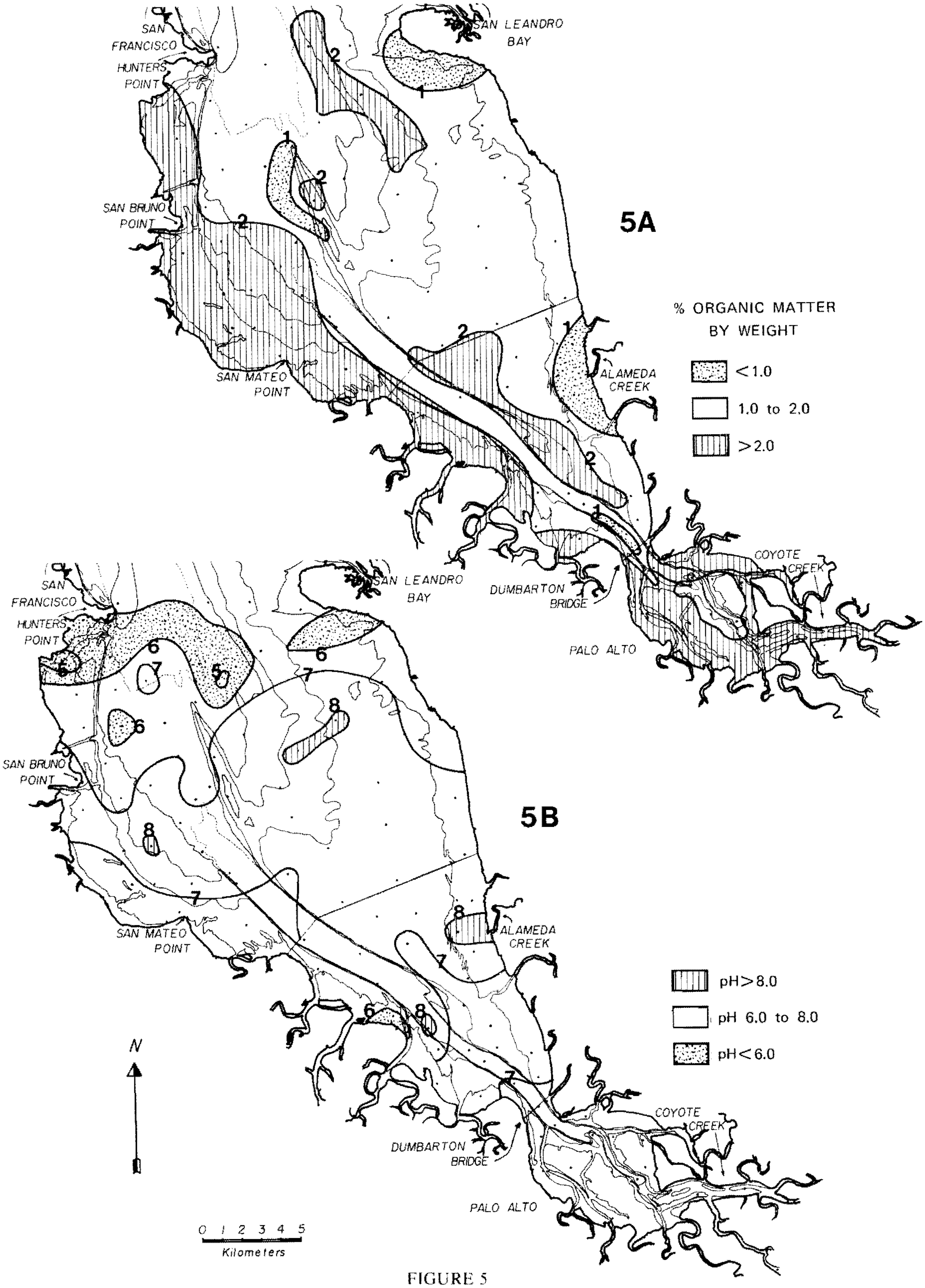


FIGURE 5

A. Sediment organic matter content. B. Sediment pH.

patch near San Leandro Bay where bottom sediments grade westward from moderately well sorted to very poorly sorted. These sediments, which contain minor admixtures of fine sand and silt particles, are either reworked or man-moved sand originally mined from the Merritt Sand, believed by Trask and Rolston (1951) to be of eolian origin. The median diameter of the sand (2.2 phi) is well within the normal size range for eolian sands.

The river sand deposited at the mouth of Alameda Creek and the sand of the ridge between San Bruno Point and San Bruno Shoal (Fig. 2) are better sorted than the average sediment of the study area.

Skewness

Sediment on the west side of the study area is mostly clay finer than 4 μm or 8 phi (Fig. 3) and has nearly nil skewness (Fig. 4B). Apparently only one process, settling in calm waters, is responsible for the accumulation of particles. Three large areas showing strongly fine-skewed particle size distributions (Fig. 4B) generally coincide with areas of coarse-grained sediments of fluvial origin (Fig. 3). This relation is in agreement with Folk (1966), who reported that a dominant coarse-grained sediment population and subordinate fine-grained population create a positive skewness (Fig. 4B). The size-distribution curves of samples from the east half of the study area north of San Mateo Bridge show the reverse situation, having a dominant fine-grained sediment with negative skewness.

CHEMICAL CHARACTERISTICS

Organic-matter Content

Coarse-grained sediments contain less than 1 percent organic matter, whereas finer grained sediments have 2 to 3 percent (Figs. 3, 5). Highest concentrations (>4 percent) are found in the slough at the mouth of Coyote Creek and in the adjacent Alviso Slough, areas characterized by fine-grained sediments and also close to large wastewater effluents and marshlands. Pestrong (1965) reported even higher organic-content percentages in his study of tidal marshes.

Hydrogen-ion Concentration (pH)

The pH of the upper 5 to 10 cm of undisturbed sediment ranges from 4.6 at station 90 to 8.2 at station 55 (Fig. 5B). Values between 5.0 and 7.0 characterize a zone in the northern part of the study area and another zone located approximately midway between the San Mateo and Dumbarton Bridges. Immediately northwest and southeast of the bridges, the pH values are more alkaline, ranging from 7.0 to 8.2; silt and some sand predominate in these areas (Figs. 3A, B). Higher pH values are also found in the southern part of the South Bay.

TABLE 3

Species of Foraminifera present in the study area.

_Ammonia beccarii tepida_*
_Bolivina striatula_*
_Bolivina vaughani_*
_Bulimina marginata_*
Bulimina sp.*
_Buliminella elegantissima_*
Discorbis sp.*
Elphidiella hannai
Elphidium advenum
_Elphidium crispum_*
Elphidium gunteri
_Elphidium incertum_*
_Elphidium incertum clavatum_*
_Elphidium incertum obscurum_*
_Elphidium magellanicum_*
Fissurina sp.
Globigerina bulloides
_Hopkinsina pacifica_*
Jadammina polystoma
Lagena costata
_Miliammina fusca_*
_Nonionella japonica_*
_Quinqueloculina bellatula_*
Quinqueloculina cultrata
Quinqueloculina seminulum jugosa
Reophax nanus
Spirobolivina sp.*
Textularia earlandi
_Trochammina inflata_*
Trochammina macrescens
Uvigerina sp.*
Virgulina sp.

* Live species.

FORAMINIFERA

The distribution of foraminifera is controlled by several interrelated factors whose significance can be determined by comparing the geographic distribution of various elements of the foraminiferal population with the distribution of ecologic parameters. Favorable factors are expected to show a direct correlation with the abundance of a given species, whereas limiting factors are expected to show an inverse correlation. Previous work (i.e., Bradshaw, 1961, 1968; Arnold, 1953; Phleger, 1965, 1967, 1970; Bandy and Arnal, 1960) has shown that water depth, salinity, sediment size, food, sediment sorting, organic-matter content, water and sediment temperature, sediment pH, and biologic competition are among the most important factors affecting the abundance of foraminifera.

DISTRIBUTION AND ABUNDANCE

A count of foraminifera was made of a representative fraction of each sample that had an estimate of at least 100 specimens present. Thirty-one species of benthonic foraminifera were identified; of these, 20 species were stained red by the organic dye rose Bengal and are assumed to have been living at the time of collection (Table 3). *Globigerina bulloides*, the only

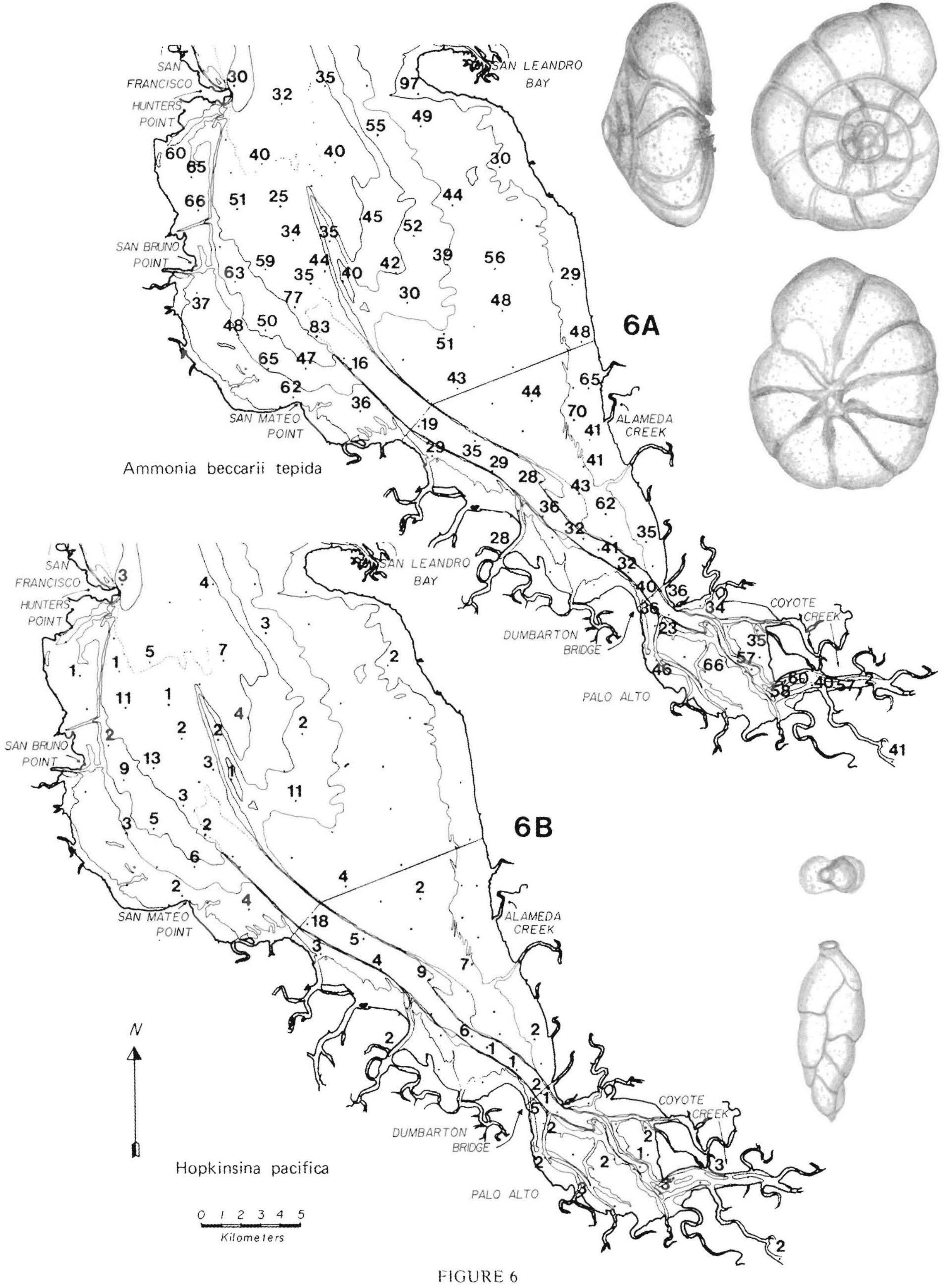


FIGURE 6

A. Distribution of *Ammonia beccarii tepida*. B. Distribution of *Hopkinsina pacifica*.

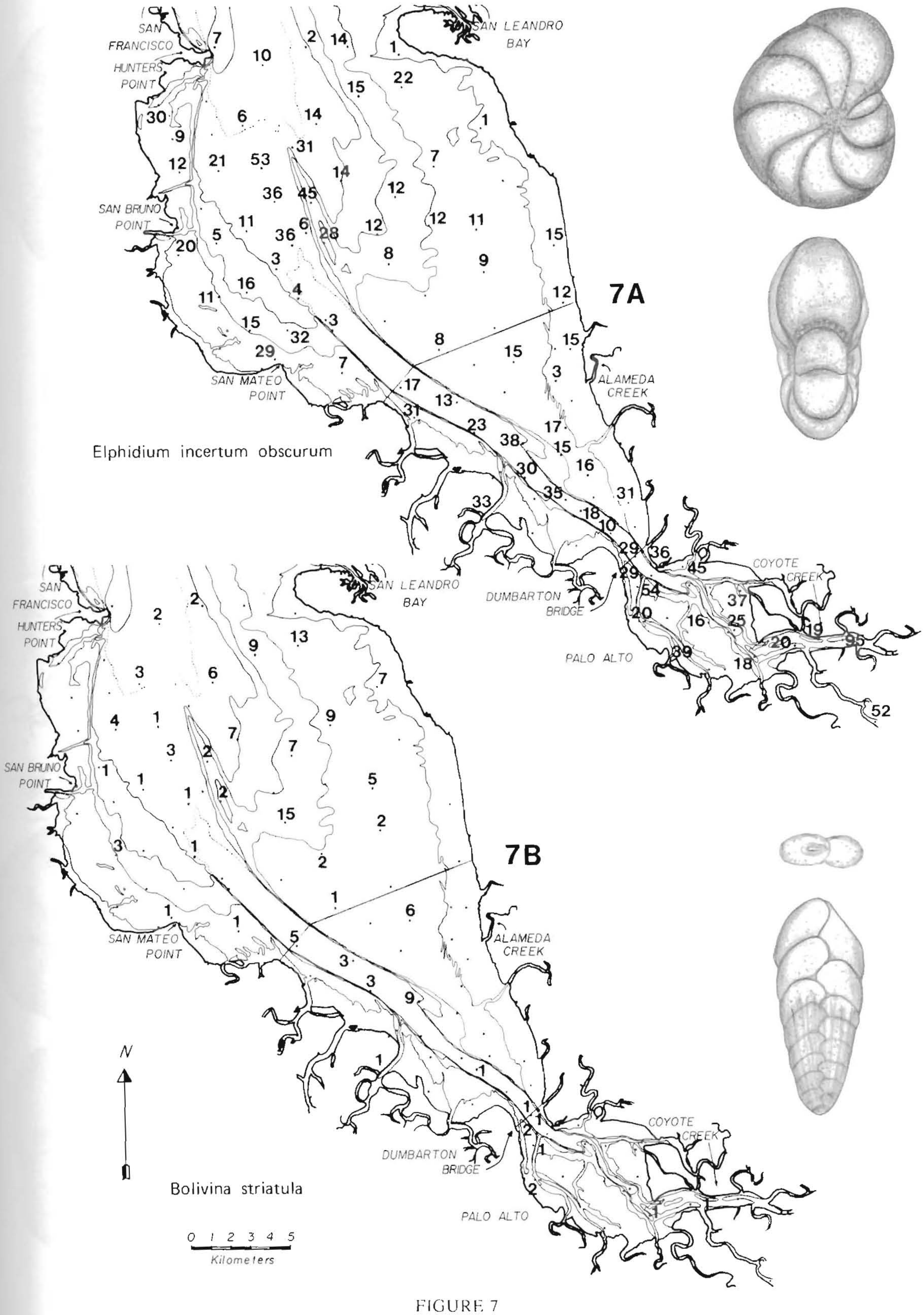


FIGURE 7

A. Distribution of *Elphidium incertum obscurum*. B. Distribution of *Bolivina striatula*.

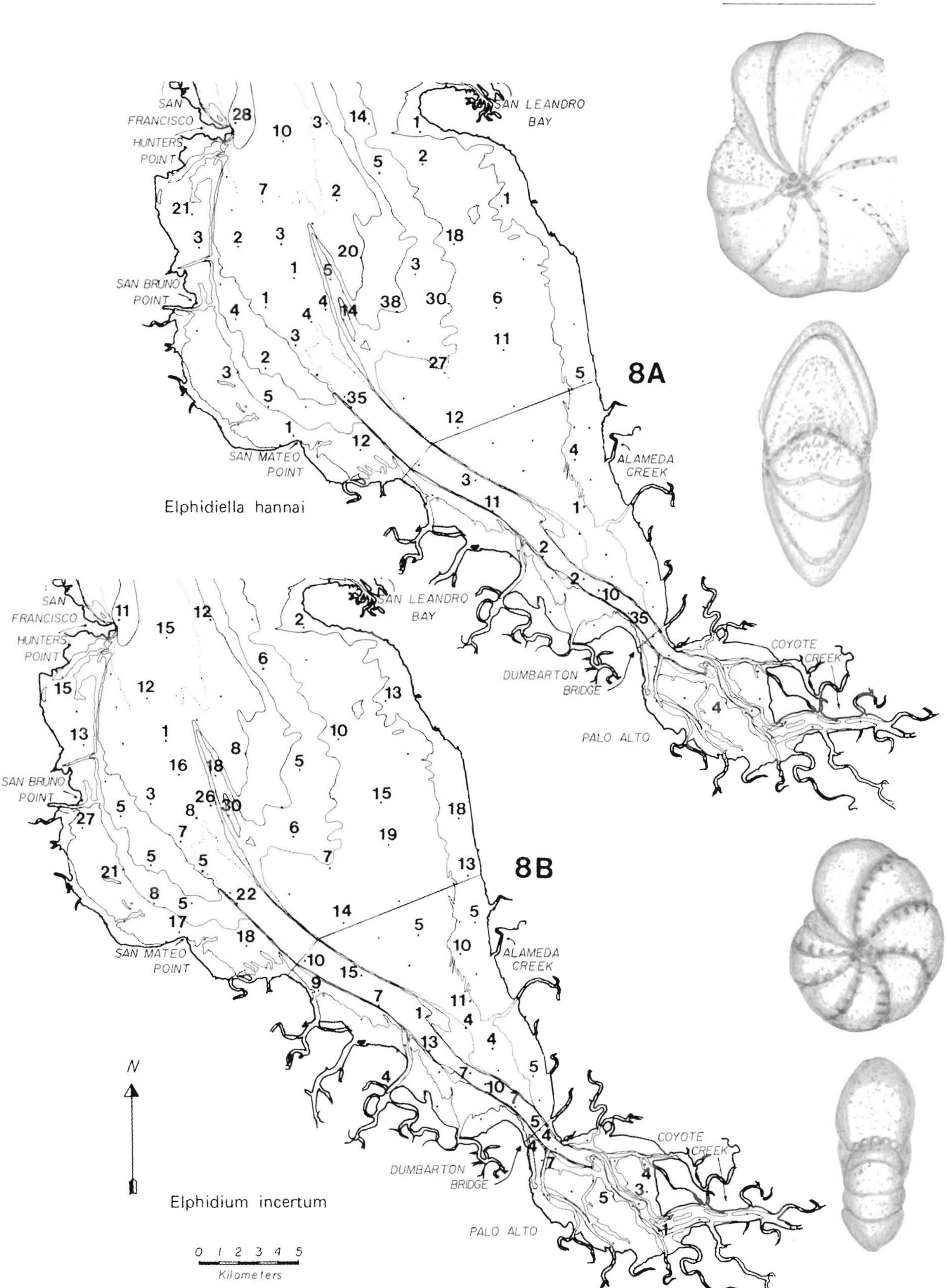


FIGURE 8

A. Distribution of *Elphidiella hannai*. B. Distribution of *Elphidium incertum*.

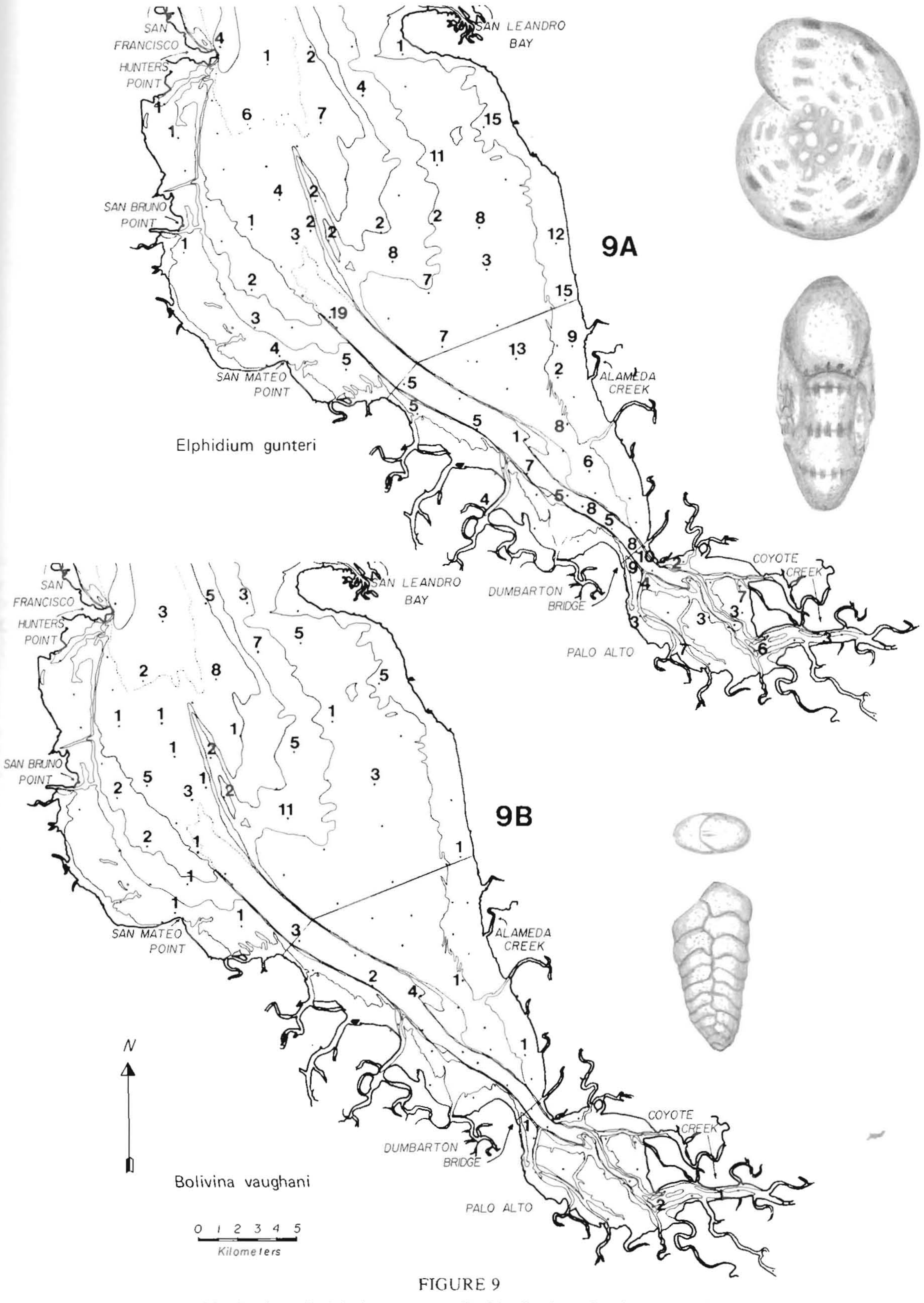


FIGURE 9

A. Distribution of *Elphidium gunteri*. B. Distribution of *Bolivina vaughani*.

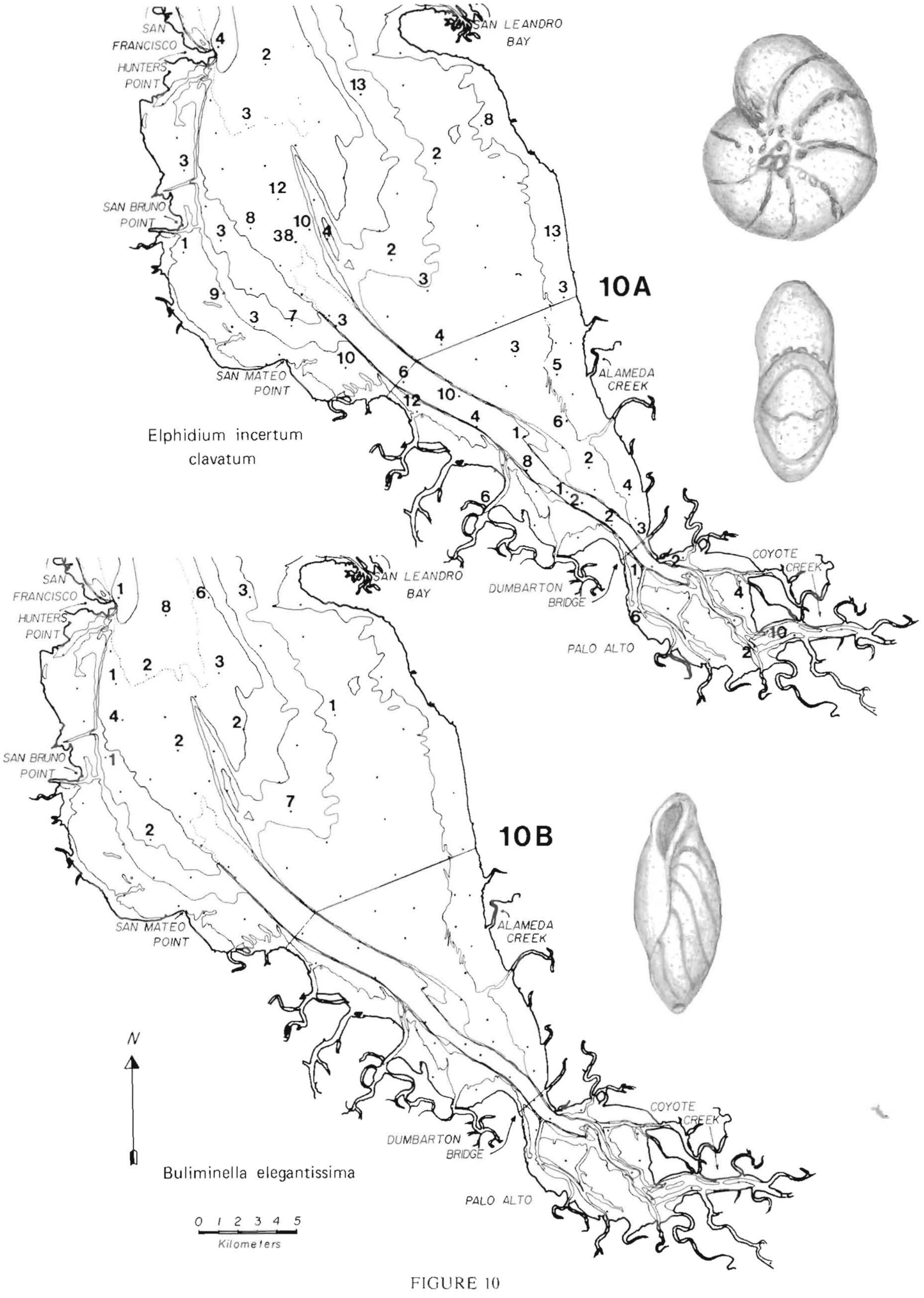


FIGURE 10

A. Distribution of *Elphidium incertum clavatum*. B. Distribution of *Buliminella elegantissima*.

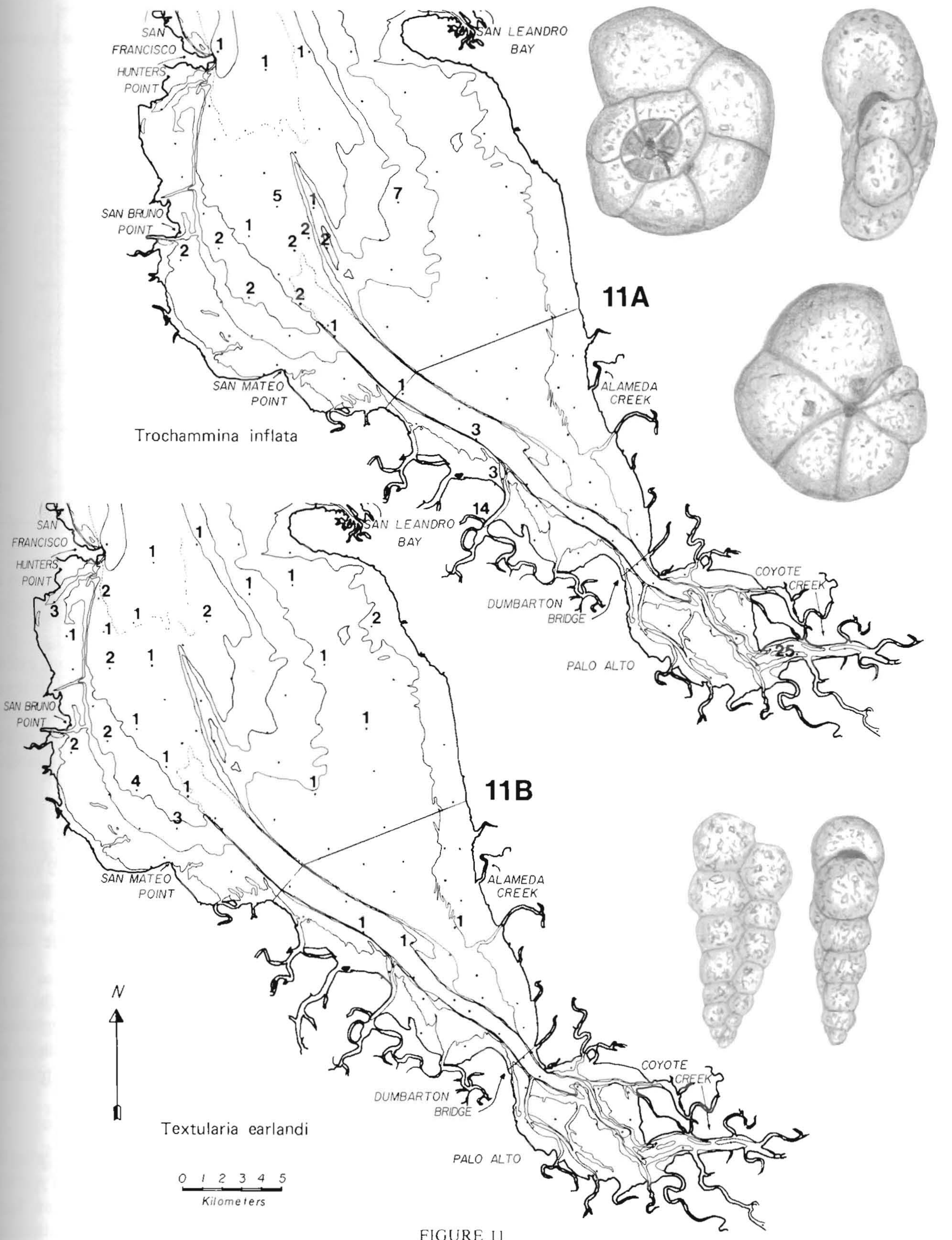


FIGURE 11

A. Distribution of *Trochammina inflata*. B. Distribution of *Textularia earlandi*.

TABLE 4

Foraminiferal ecologic zones based on the relative abundance of species.

Dominant species	Zone I Inner coastal	 II Outer coastal	 III Deep bay	 IV Deep channel
Ammonia beccarii tepida	32–46[a]	45–54	25–45	25–30
Elphidium incertum obscurum	22–40	5–18	5–22	5–22
Elphidium incertum	7–10	9–14	7–21	10–13
Elphidiella hannai	0–3	3–10	2–12	12–28
Elphidium gunteri	2–9	2–7	2–9	0–9
Elphidium incertum clavatum	3–4	2–4	3–8	3–4
Hopkinsina pacifica	1–3	1–4	5–10	3–7
Bolivina striatula	x	0–4	2–5	0–4
Bolivina vaughani		2–3	0–6	
Buliminella elegantissima		x	0–3	x
Trochammina inflata	0–25	x	0–3	x
Textularia earlandi			0–3	x
Depth ranges (m)	0–2	2–8	8–15	12–22

[a] Percentage of total specimens averaged for stations having similar depths.

x equals 2 percent or less.

TABLE 5

Percentage occurrence of foraminiferal populations at four stations selected by Q-mode analysis

	Station number 14	 68	 99	 60
Ammonia beccarii tepida	18	51	44	18
Elphidium incertum obscurum	67	1	14	2
Elphidium incertum	13	31		25
Elphidiella hannai		1	22	42
Elphidium gunteri		1		10
Hopkinsina pacifica		5	3	<1
Bolivina striatula	1	2	6	<1
Bolivina vaughani			1	
Buliminella elegantissima			2	
Trochammina inflata		2	2	1
Textularia earlandi		1	1	
Bulimina sp.		1		
Quinqueloculina bellatula			1	
Quinqueloculina seminulum jugosa				<1
Trochammina macrescens			1	
Nonionella japonica			1	
Jadammina polystoma		1	2	<1
Reophax nanus				<1
Spirobolivina sp.		1		

planktonic species present, was very rare and was apparently transported into the study area from the adjacent ocean.

The geographic distribution of the 12 most abundant species was plotted as percentage of total specimens counted at each station. Drawings of a typical specimen of each of these species accompany the illustrations showing geographic distribution (Figs. 6–11). *Ammonia beccarii tepida* and *Elphidium incertum obscurum* occur at all stations with percentages ranging from 18 to 96 and 1 to 67 respectively (Figs. 6A, 7A). *Hopkinsina pacifica* (Fig. 6B), *Elphidium incertum* (Fig. 8B), *E. gunteri* (Fig. 9A), *Elphidiella hannai* (Fig. 8A), and *Elphidium incertum clavatum* (Fig. 10A) occur at most stations. Although their abundance may approach 40 percent, the average is 5 percent. *Bolivina striatula*, *B. vaughani*, *Buliminella elegantissima*, and the agglutinated species *Trochammina inflata* and *Textularia earlandi* (Fig. 11) are abundant but scattered in distribution.

ENVIRONMENTAL FACTORS

Water Depth

The depth zonation of foraminifera is evident on a graph of abundance values averaged from several stations having similar depth regardless of geographic position (Fig. 12). Although sharp boundaries do not exist, faunal changes with water depth are readily apparent. Four ecologic zones (Table 4) have been established, chiefly on the basis of these faunal changes:

Zone I: Inner Coastal

Water depth ranges from 0 to 2 m. This zone extends 1 to 4 km seaward from the intertidal zone. It is generally characterized by few species but many individuals. The genus *Trochammina* represents 25 percent of the fauna in high marsh areas south of Dumbarton Bridge.

Zone II: Outer Coastal

Water depth ranges from 2 to 8 m. The zone is as much as 10 km wide, extending from about 2 km from the shoreline to the central part of the bay. The abundance of species (nearly twice that of Zone I) and large numbers of individuals indicate a favorable habitat.

Zone III: Deep Bay

This zone comprises the central part of the bay in water depth ranging from 8 to 15 m. Agglutinated forms and species of *Bolivina* occur in significant percentages. The greatest number of genera is present in this zone.

Zone IV: Deep Channel

Water depth ranges from 12 to 22 m, indicating that oceanic water is present most of the year. Typical estuarine forms are present in small percentages. Agglutinated forms are present whenever the substrate contains some silt-size particles.

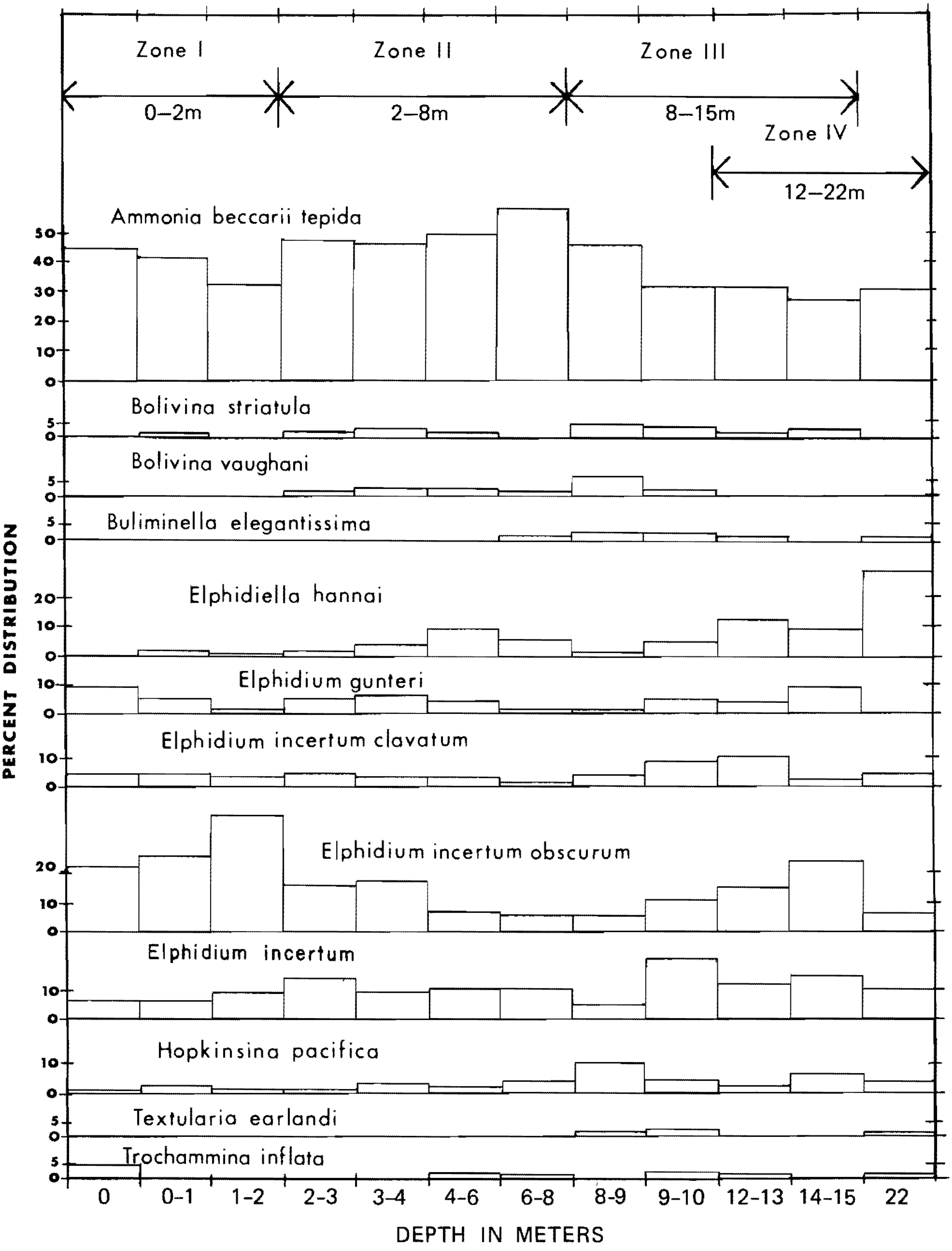


FIGURE 12

Relation between species and water depth.

A Q-mode analysis, using a program of Imbrie (1963), was made of the results of the frequency counts of foraminiferal populations. Coefficients of proportional similarity were first computed by comparing the frequency count of each station with those of all other stations. Eigen values were then computed by postulating that eight undetermined stations would account for 100 percent of the compositional variation. Examination of the results on the table of Eigen values showed that nearly 100 percent of the compositional variation could be accounted for with only four representative stations, identified as stations 99, 68, 14, and 60 in the rotated matrix and oblique matrix part of the program (Table 5).

On the basis of similarity coefficients, 10 stations are most similar to station 14; most of these are located south of San Mateo Bridge. The most abundant species is *Elphidium incertum obscurum*; *Ammonia beccarii tepida* is next in abundance. The average depth at these stations is 3.3 m. Stations of this type correlate best with stations used to define Zone I (Table 4).

Station 68 has 10 stations showing good similarity; all are located near the San Mateo Bridge. In samples assigned to type station 68, *A. beccarii tepida* is most abundant and *E. incertum* is second in abundance. The average depth at these stations is 4.0 m and compares well with the average depth for Zone II (Table 4).

Forty-one stations are most similar to station 99 and are located mainly in the north half of the bay. *Ammonia beccarii tepida* is the most abundant species at stations assigned to type 99. *Elphidiella hannai* is second in abundance and *Elphidium incertum obscurum* third. Stations of this type are characterized by moderate but significant numbers of *Hopkinsina pacifica, Bolivina striatula,* and *B. vaughani*. Percentages of significant species at these stations compare well with those used in defining Zone III (Table 4). The average depth at these stations is 5.0 m.

Station 60 has three similar channel stations at which *Elphidiella hannai* is the most abundant species. The average depth at these stations is 10.8 m. Compare Figure 12, Table 4 and Table 5.

To relate the cumulative abundance of species to their lateral distribution, two intersecting profiles were constructed (Fig. 13). The east-west profile extends from station 97 to station 53 (Fig. 1) and covers a distance of 23 km; the north-south profile is 17 km long and extends from station 106 to station 90. These profiles were selected to include wide variations in current velocities and water depth as well as major differences in sediment textural characteristics.

Ammonia beccarii tepida is most abundant in shallow water and decreases in percentage with increasing depth along the east-west profile (Fig. 13). In contrast, *Elphidium incertum obscurum* is most abundant at depths of 8 to 10 m. Percentages for *Elphidiella hannai* are higher at intermediate depths (4 to 5 m) and decrease in both shallower and deeper water along this profile. This peak shows on Figure 12 in Zone II on the distribution plot for *E. hannai*. Species of *Bolivina* and *Trochammina* exist in small percentages at intermediate water depths but do not occur at all stations. Specimens of *Hopkinsina pacifica* appear to be limited to the west half of the profile, that part most exposed to flushing with oceanic water.

Similar or more clearly defined trends are apparent on the north-south profile (Fig. 13). The decrease in abundance of *Ammonia beccarii tepida* with increasing water depth is similar with the exception of station 65, where there is a marked percentage increase with increasing depth. This station is located on a steep channel slope and has a very small number of species, a situation that may indicate a lack of interfaunal competition. The notably high percentage of *A. beccarii tepida* at station 90 is associated with a small number of species. As with the east-west profile, *Elphidium incertum obscurum* and *Elphidiella hannai* occur predominantly at intermediate depths. *Hopkinsina pacifica* is limited to the east half of the profile, an area readily accessible to recently exchanged ocean water. This distribution implies that *H. pacifica,* though found in the estuarine environment, prefers typical marine conditions.

Salinity

Bradshaw (1961) showed that certain foraminifera have a remarkable tolerance for large salinity changes; lethal salinities are below 2‰ for *Ammonia beccarii tepida* and 13‰ for *Bolivina vaughani.* Both species live in the study area and are good representatives of typical estuarine and shallow marine assemblages, respectively.

Estuarine species (i.e., species of *Elphidium, Elphidiella hannai,* and *A. beccarii tepida,* Table 4) are reported to occur generally in areas where salinity differs significantly from that of the open ocean. For these species, salinity variations in the study area are well within tolerable limits. Species with high frequency percentages in Zones III and IV are more typical of shallow marine environments and are relatively sensitive to salinity changes. Salinity undoubtedly affects the distribution of *Buliminella elegantissima* (Fig. 10B), *Hopkinsina pacifica* (Fig. 6B), and perhaps that of *Bolivina vaughani* (Fig. 9B).

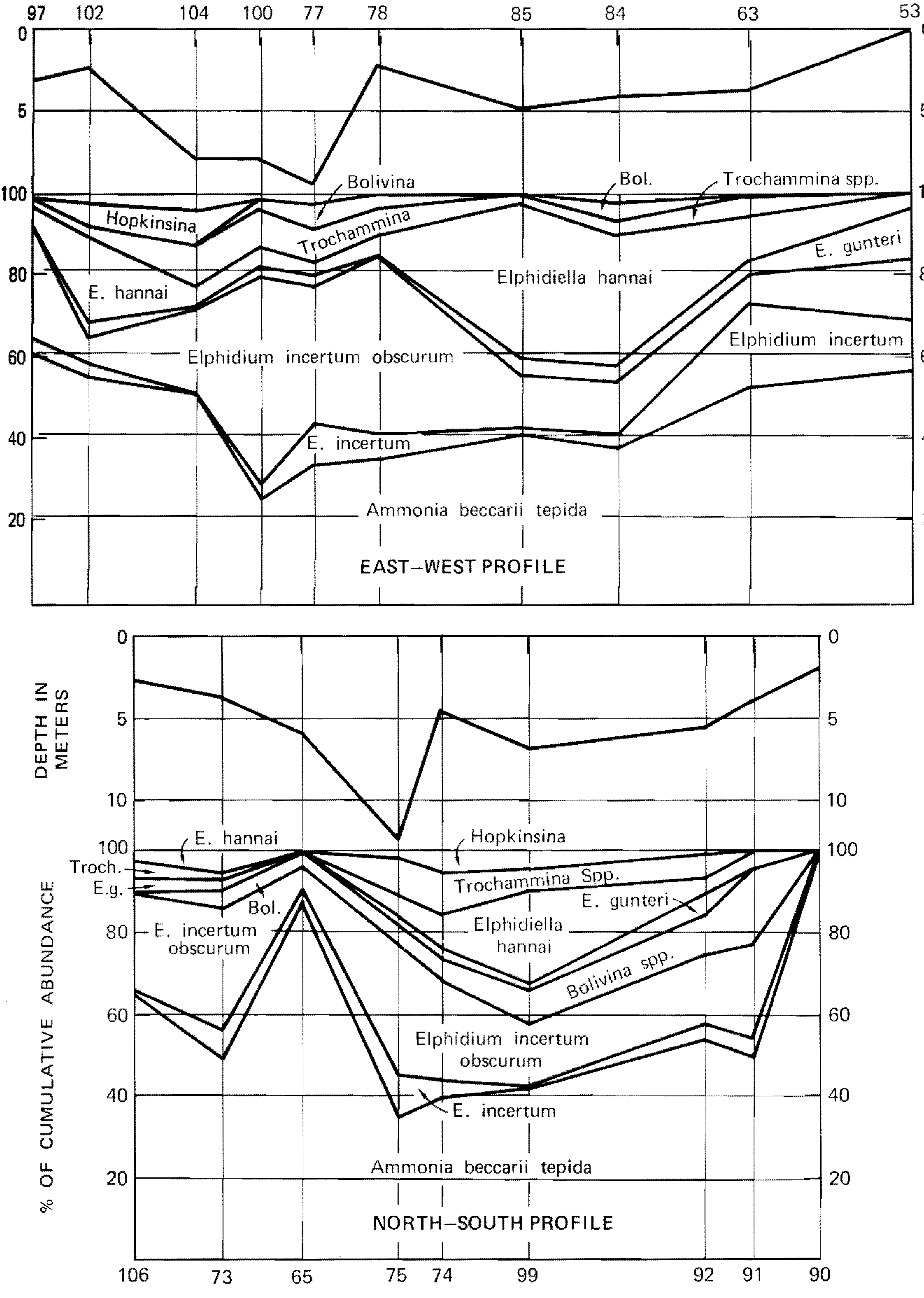


FIGURE 13
East-west and north-south profiles.

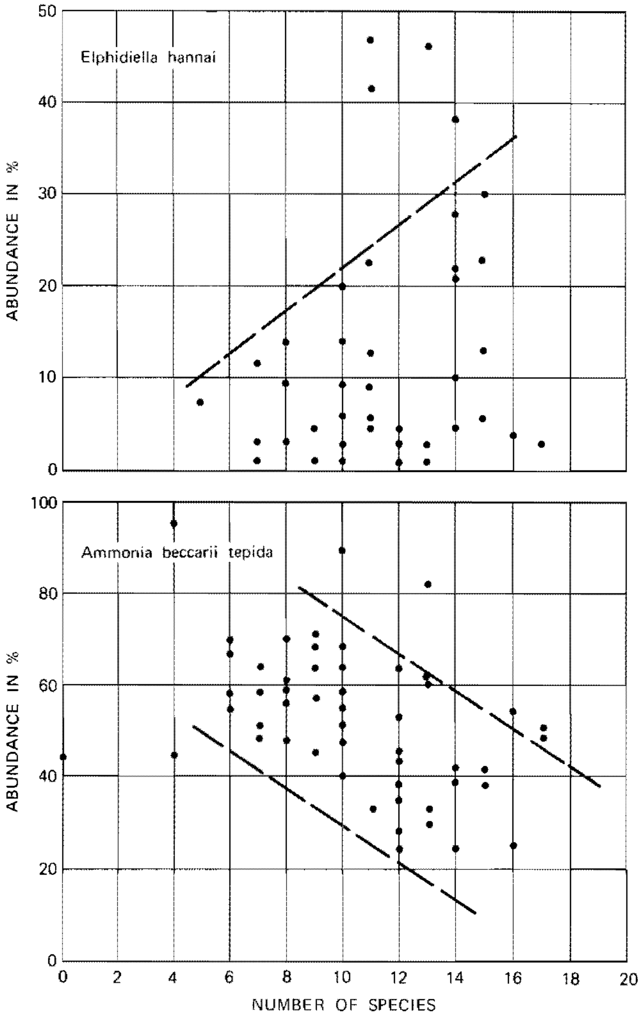


FIGURE 14

Abundance of *Elphidiella hannai* and *Ammonia beccarii tepida* relative to number of species.

Substrate

The high percentage (typically 20 percent) of *Elphidiella hannai* (Fig. 8A) in Zone IV may be related to the occurrence of coarse-grained sediments. The test of this form is larger and thicker than most others and apparently remains as a lag deposit along with coarse-grained sediments. Smaller and lighter forms are carried away with finer grained sediment particles by strong tidal currents.

Agglutinated foraminifera are restricted to areas where there is material suitable for building their tests. Owing to their small size, usually less than 1 mm, the optimum material is in the silt-size range (4 to 64 μm), although occasionally a fragment of fine sand may be used. At the 12 stations where the frequency of *Textularia earlandi* is > 1 percent, two stations are in sand, seven are in silty clay, and two are in sand-silt-clay mixtures (compare Fig. 11B and Fig. 4). The frequent occurrence of this species in finer sediments may be explained by the ability of agglutinated foraminifers to concentrate from the available sediment coarser particles to build their tests. Moreover, if the preferred silt-size particles are not available, the test will be constructed of smaller particles (Salma, 1954). Sediment size is apparently a limiting factor for the distribution of agglutinated foraminifers only in areas where well-sorted fine-skewed clay predominates (Fig. 4B).

Since agglutinated foraminifers are capable of concentrating the optimum sediment size for building their tests, coarse-grained sediments that are fine-skewed or fine-grained sediments that are coarse-skewed are acceptable substrates (compare Fig. 4A and Figs. 11A and 11B).

Organic Matter

The abundance of *Elphidium incertum obscurum* correlates well with the distribution of organic matter with the lowest frequencies where organic matter is least (Figs. 5A and 7A). At stations 33 and 35, the organic matter content is 1.3 and 0.9 percent, respectively, and the abundance of *E. incertum obscurum* is relatively low, frequencies being 18 and 10 percent, respectively. Near Alameda Creek, organic matter ranges from 0.4 to 1.8 percent and frequencies of *E. incertum obscurum* range from 3 to 15 percent (Fig. 7A). North of San Mateo Bridge, the greatest abundance of *E. incertum obscurum* occurs west and south of San Bruno Shoal in an area where the organic-matter content generally is 2 percent or more (Fig. 5A).

Sediment pH

Dissolution of foraminiferal tests occurs at pH values below 7.0 (Arnal, 1961). A short exposure to waters of pH as low as 2.0 is not necessarily lethal. Bradshaw (1961) has shown that a living foraminifer may survive partial dissolution of its test and that regeneration of the test occurs when pH values again become alkaline. Quinterno (1968) reported some etching of foraminiferal tests in the study area. She did not find any sample completely devoid of tests however; this result indicates that low pH values found at some stations are only temporary. The pH does not appear to be a limiting parameter for benthonic foraminifera in the study area (Fig. 5B), as the

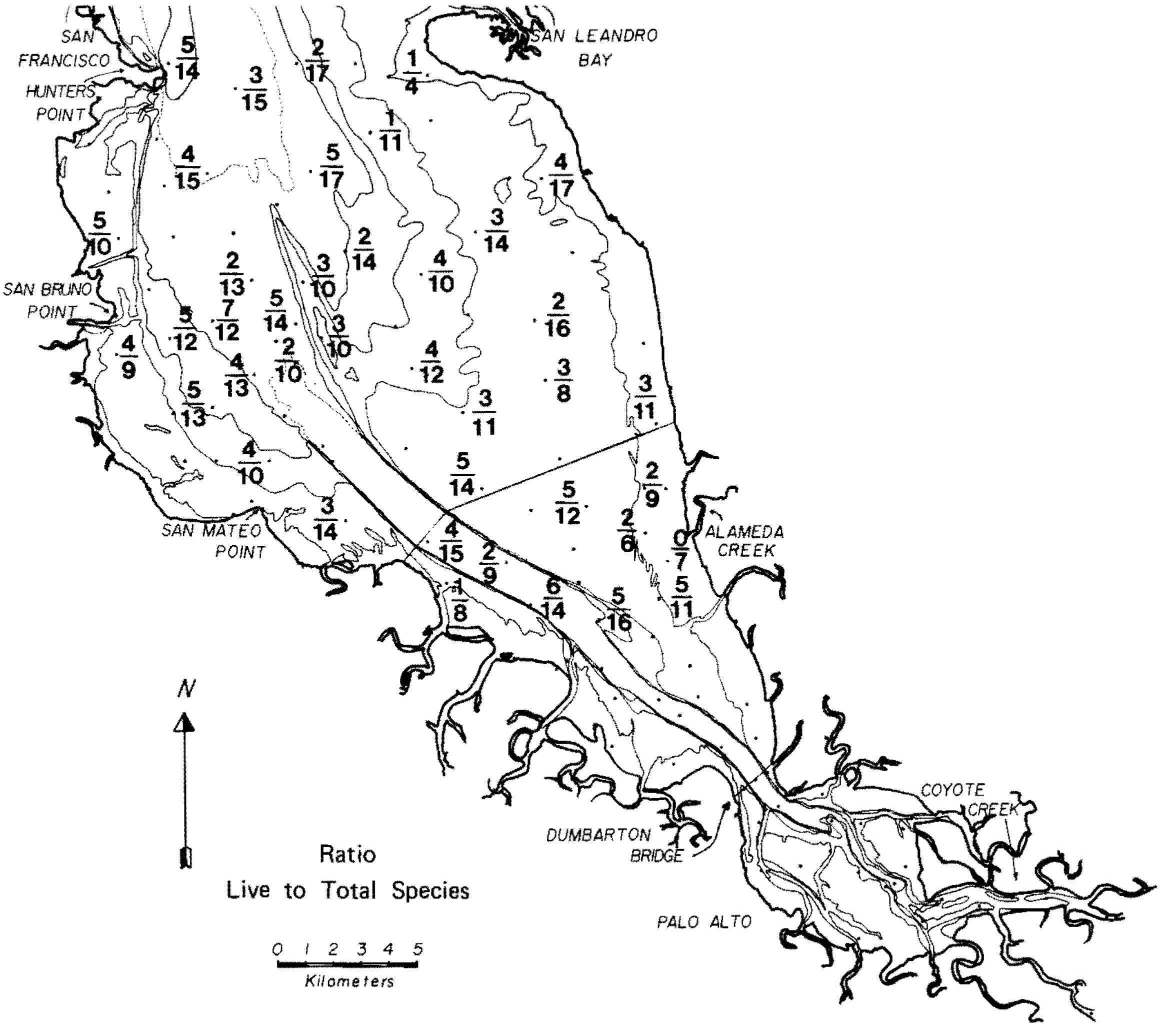


FIGURE 15
Number of live species and total number of species.

range of values recorded vary well within the tolerable limits reported in the literature (Bradshaw, 1961).

Biologic Competition

Biologic competition is difficult to evaluate and its effect is largely unknown. One simple method to obtain a gross estimate is to compare the abundance of a given species with change in diversity of a population as expressed by the number of species present. If a species increases in frequency as the number of species increases, that species might be a good competitor; conversely, if the frequency decreases with greater number of species, a poor competitor might be detected.

To test this method, plots of the percentage abundance of a dominant species relative to the increasing number of species per station were made using *Elphidiella hannai* and *Ammonia beccarii tepida* (Fig. 14). The plots indicate that *E. hannai*, because of the direct correlation, may be considered a good competitor, whereas *A. beccarii tepida*, which shows an inverse correlation, is a poor competitor. *Ammonia beccarii tepida* has a remarkable tolerance to large variations in several physical parameters and apparently uses this tolerance to colonize certain habitats rather than compete with other species where living conditions are more homogeneous. This is well exemplified at both ends of the east-west profile discussed and at stations 65 and 90 of the north-south profile (Fig. 13).

SPECIES DIVERSITY

The number of species per sample gives an adequate approximation of species diversity for this type of study (Phleger, 1965). The total number of species as well as live species increases when the environmental conditions are more typically marine (Fig. 15). More notable, however, is the increase in number of live species from marsh areas toward the deep channels.

CONCLUSIONS

In this study, we have described the general distribution of sedimentary characteristics with respect to selected water properties for southern San Francisco Bay. We determined the distribution and abundance of the main species of the foraminiferal population and found that they correlate well with depth and several other environmental factors. For example, salinity, when fluctuations are large, may be a limiting factor; distribution of agglutinated foraminifera is closely related to substrate texture; biologic competition affects the distribution of *Ammonia beccarii tepida* and *Elphidiella hannai*; and a high organic content in the sediment correlates well with high percentages of *Elphidium incertum obscurum*. The four zones that were established on the basis of observed trends and those defined by Q-mode analysis are reasonably similar in view of the great environmental complexity of the study area. Because several factors are interrelated, it is often difficult to select among several possibilities the limiting factor responsible for an observed relation.

Additional work is needed for a better understanding of foraminiferal distributions, particularly on the sand ridge between San Bruno Shoal and San Bruno Point and in the high marsh zones south of Dumbarton Bridge. This work will greatly facilitate a study of the foraminiferal population of the rest of the San Francisco Bay estuary.

REFERENCES

ALLISON, L. E., 1935, Organic carbon by reduction of acid: Soil Science, v. 40, p. 311–320.

ARNAL, R. E., 1961, Limnology, sedimentation and microorganisms of the Salton Sea, California: Geol. Soc. America Bull., v. 72, p. 427–478.

ARNAL, R. E., and CONOMOS, T. J., 1962, Sedimentary and foraminiferal aspects of southern San Francisco Bay: Geol. Soc. America Spec. Paper 73, Abs. for 1962, p. 21–22.

ARNAL, R. E., QUINTERNO, P. J., CONOMOS, T. J., and GRAM, RALPH, 1970, Environmental factors affecting Foraminifera in South San Francisco Bay: Geol. Soc. America Abs. with Programs, v. 2, p. 67–68.

ARNOLD, Z. M., 1953, An introduction to the study of movement and dispersal in *Allogromia laticollaris*: Cushman Found. Foram. Research Contr., v. 4, pt. 1, p. 15–21.

ATWATER, BRIAN, in press, Ancient processes at the site of southern San Francisco Bay—movement of the crust and changes in sea levels, *in* Conomos, T. J., ed., San Francisco Bay, the urbanized estuary: Am. Assoc. Adv. Sci.

ATWATER, BRIAN, HEDEL, C. W., and HELLEY, E. J., 1977, Late Quaternary depositional history, Holocene sea-level changes, and vertical crustal movement, southern San Francisco Bay, California: U.S. Geol. Survey Prof. Paper 1014, 15 p.

BANDY, O. L., and ARNAL, R. E., 1960, Concepts of foraminiferal paleoecology: Am. Assoc. Petroleum Geologists Bull., v. 44, p. 1921–1932.

BRADSHAW, J. S., 1961, Laboratory experiments on the ecology of Foraminifera: Cushman Found. Foram. Research Contr., v. 12, p. 87–106.

———, 1968, Environmental parameters and marsh Foraminifera: Limnology and Oceanography, v. 13, p. 26–38.

CONOMOS, T. J., 1963, Geologic aspects of the Recent sediments of south San Francisco Bay: San Jose State Univ., San Jose, Calif., Master's thesis, 118 p.

CONOMOS, T. J., MCCULLOCH, D. S., PETERSON, D. H., and CARLSON, P. R., 1971, Drift of surface and near-bottom waters of the San Francisco Bay system; March 1970 through April 1971: U.S. Geol. Survey Open-file map.

FOLGER, D. W., 1972, Characteristics of estuarine sediments of the United States: U.S. Geol. Survey Prof. Paper 742, 94 p.

FOLK, R. L., 1966, A review of grain-size parameters: Sedimentology, v. 6, p. 73–93.

———, 1968, Petrology of sedimentary rocks: Hemphill's Drawer M, University Station, Austin, Texas, 170 p.

FOLK, R. L., and WARD, W. C., 1957, Brazos River Bar; A study in the significance of grain size parameters: Jour. Sed. Petrology, v. 27, p. 3–26.

GRAM, RALPH, 1966, The marine geology of the Recent sediments of central San Francisco Bay: San Jose State Univ., San Jose, Calif., Master's thesis, 132 p.

HAZELWOOD, R. M., 1976, Contour map and interpretive cross sections showing depth and configuration of bedrock surface, South San Francisco Bay region, California: U.S. Geol. Survey Misc. Field Studies Map MF-796, scale 1:62,500.

IMBRIE, JOHN, 1963, Factor and vector analysis programs for analyzing geologic data: Northwestern Univ., Evanston, Ill., Tech. Rept. no. 6 of ONR Task no. 389-135, Contract Nonr 1228(26), Office of Naval Research, Geography Branch, 60 p.

KVENVOLDEN, K. A., 1962, Normal paraffin hydrocarbons in sediments from San Francisco Bay, California: Am. Assoc. Petroleum Geologists Bull., v. 46, p. 1643–1652.

LOCKE, J. L., 1971, Sedimentation and foraminiferal aspects of the Recent sediments of San Pablo Bay: San Jose State Univ., San Jose, Calif., Master's thesis, 100 p.

LOUDERBACK, G. D., 1951, Geologic history of San Francisco Bay, *in* Geologic Guidebook, San Francisco Bay Counties: California Div. Mines Bull. 154, p. 75–94.

MCCULLOCH, D. S., PETERSON, D. H., CARLSON, P. R., and CONOMOS, T. J., 1970, Some effects of fresh-water inflow on the flushing of South San Francisco Bay. A preliminary report: U.S. Geol. Survey Circ. 637A, p. A1–A27.

MCDONALD, J. A., and DIEDIKER, P. L., 1930, A preliminary report on the Foraminifera of San Francisco Bay, California: Micropaleontology Bull., v. 2, p. 33–37.

MILLER, R. C., RAMAGE, W. D., and LAZIER, E. L., 1928, A study of physical and chemical conditions in San Francisco Bay especially in relation to the tides: California Univ. Pubs. Zoology, v. 31, p. 201–267.

PESTRONG, RAYMOND, 1965, The development of drainage patterns on tidal marshes: Stanford Univ. Pub. Geol. Sciences, v. 10, no. 2, p. 1–87.

PHLEGER, F. B., 1965, Ecology and distribution of Recent Foraminifera: Johns Hopkins Press, Baltimore, 297 p.

———, 1967, Marsh foraminiferal patterns, Pacific Coast of North America: Ann. Inst. Biol. Univ. Nat. Auton, Mexico 38, Ser. Cienc. del May y Limnol., v. 1, p. 11–38.

———, 1970, Foraminiferal populations and marine marsh processes: Limnology and Oceanography, v. 15, p. 522–534.

PORTERFIELD, G., HAWLEY, N. L., and DUNNAM, C. A., 1961, Fluvial sediments transported by streams tributary to the San Francisco Bay area: U.S. Army Corps of Engineers, San Francisco District, California, 70 p.

QUINTERNO, P. J., 1968, Distribution of Recent Foraminifera in Central and South San Francisco Bay: San Jose State Univ., San Jose, Calif., Master's thesis, 83 p.

RANTZ, S. E., 1971, Precipitation-depth-duration-frequency relations for the San Francisco Bay region, California, and isohyetal map of San Francisco Bay region, California, showing mean annual precipitations: U.S. Geol. Survey Open-file Report, 5 p., 1 map, 1:500,000.

REESE, J. E., 1965, Sedimentation of the Suisun Bay Complex: San Jose State Univ., San Jose, Calif., Master's thesis, 109 p.

SALMA, D. C., 1954, Arenaceous tests in Foraminifera—an experiment: The Micropaleontologist, v. 8, p. 29–30.

SCHULTZ, E. A., 1965, San Francisco Bay dredge spoil disposal: U.S. Army Engineer District, San Francisco, Calif., 47 p.

STORRS, P. N., PEARSON, E. A., and SELLECK, R. E., 1968, Final Report Vol. 5—Summary of physical, chemical and biological water and sediment data, A comprehensive study of San Francisco Bay, Univ. Calif. (Berkeley), SERL Rept. No. 67-2, Sanitary Eng. Research Lab.

STORRS, P. N., SELLECK, R. E., and PEARSON, E. A., 1963, A comprehensive study of San Francisco Bay, 1961–62: Univ. Calif. (Berkeley), SERL Rept. No. 63-3.

———, 1965, A comprehensive study of San Francisco Bay, 1963–64, Univ. of Calif. (Berkeley), SERL Rept. No. 65-1, Sanitary Eng. Research Lab.

STORY, J. A., WESSELS, V. E., and WOLFE, J. A., 1965, Radiocarbon dating of Recent sediments of San Francisco Bay, California (abs.): Geol. Soc. America, 18th Annual Meeting, Rocky Mountain Section (Colorado State Univ., Fort Collins, Colo., May 13–15, 1965), Program, p. 51.

SUMNER, F. B., LOUDERBACK, G. D., SCHMIDT, W. L., and JOHNSON, E. C., 1914, A report upon the physical conditions in San Francisco Bay, based upon the operations of the United States steamer *Albatross* during the years 1912 and 1913: California Univ. Pub. Zoology, v. 14, p. 1–198.

TRASK, P. D., 1932, Origin and environment of source sediments of petroleum: Houston, Texas, Gulf Publ. Co., 97 p.

TRASK, P. D., and ROLSTON, J. W., 1951, Engineering geology of San Francisco Bay: Geol. Soc. America Bull., v. 62, p. 1074–1110.

UNITED STATES COAST AND GEODETIC SURVEY, 1973, Tide tables, west coast, North and South America: U.S. Printing Office, Washington, D.C.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 40–58, 1980

DISTRIBUTION PATTERNS OF INTERTIDAL AND SHALLOW-WATER FORAMINIFERA OF THE TROPICAL PACIFIC OCEAN

Robert H. Lessard
Earth Science Division, New Mexico Highlands University

ABSTRACT

Intertidal and shallow-water sediment samples from the tropical Pacific Ocean were studied and a quantitative analysis made of the foraminifera and other constituents. The results indicate that many species of the intertidal and shallow-water foraminifera have been transported great distances across the Pacific Ocean. Seven methods of dispersal are analyzed. The distribution pattern of *Baculogypsina* and *Tinoporus* seems to be best explained by the transportation of their zygotic stages by ocean currents. The fluctuation in populations of *Baculogypsina* and *Tinoporus* is similar to the fluctuations in populations of many other marine invertebrates.

INTRODUCTION

General Statement

This investigation was initiated to gain a more comprehensive understanding of the distribution of the intertidal and shallow-water foraminifera of the tropical Pacific Islands. Although the islands occupy but a fraction of the total area in the Pacific, they are so sparsely distributed, separated by such great depths, bathed by such a wide variety of currents, and under the influence of such uniform physical conditions, that an ideal situation exists for the study of the distribution of their foraminiferal faunas and to advance hypotheses to explain this distribution pattern.

The samples used in the study were obtained from several different sources including scientific workers and persons living on or traveling through the islands. In the majority of instances the samples are beach sands. There is usually only one or two from each island but there may be more. For example, an extensive collection of samples was obtained from the shallow waters surrounding Johnston Island (lat 16°45′N., long 169°30′W.).

Area of Investigation

A total of 170 samples from the islands of the tropical Pacific Ocean (Fig. 1) were examined. The majority are from the northern hemisphere and represent a section with Ishigaki-shima (lat 24°25′N., long 124°15′E.) and the Hawaiian Islands (lat 20°N., long 156°W.) acting as the western and eastern extremities, respectively. Even though the number of samples from the southern hemisphere is low, they are part of a section which extends the length of the Island of Bali (lat 8°45′S., long 115°E.) as the western boundary and Raroia Atoll (lat 16°15′S., long 142°30′W.) as the eastern boundary.

Most of the localities are shown in Figure 1, with the exception of New Caledonia and Raroia Atoll. Two samples were collected from New Caledonia (Stations 167–168) which is located at lat 22°30′00.0″S. and long 166°30′00.0″E. and one sample from Raroia Atoll (Station 170) at lat 16°04′12.0″S. and long 142°15′00.0″W. Maps of islands from which more than four samples were collected are shown in Figure 2.

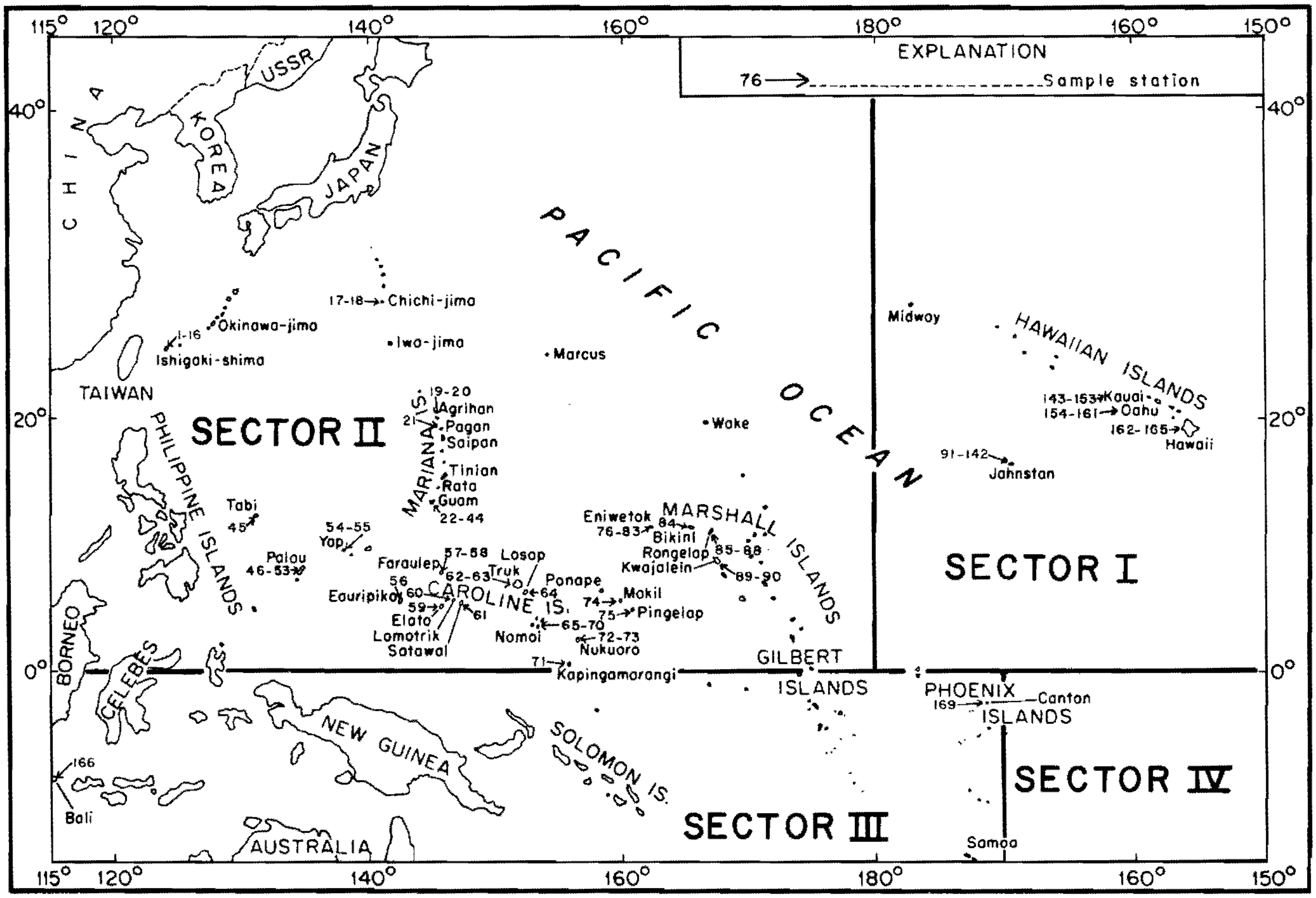


FIGURE 1

Map showing locations of sample stations in the tropical Pacific Ocean and the four sectors into which the ocean is divided.

ACKNOWLEDGMENTS

The author wishes to express his gratitude to all the individuals who supplied the samples which made this study possible. They include Wendell Gayman, Kenneth O. Emery, Robert Given, and Orville L. Bandy. Further acknowledgment is due Dr. Bandy for initially suggesting that an analysis of these samples be undertaken and for making a critical evaluation of both the foraminiferal identification and the manuscript. Finally, the author wishes to thank Dr. Richard H. Merriam and Dr. Donn S. Gorsline for suggestions and criticism of the manuscript.

PREVIOUS WORK

Numerous papers have been written on the foraminifera of the tropical Pacific Islands. Most of them are concerned with a taxonomic description of the fauna but there has been some attempt to correlate these analyses with ecological data. Cushman, Todd, and Post (1954), Graham and Militante (1959), and Todd and Low (1960) have excellent bibliographies of this topic and area as part of their publications. A similar repetition seems unnecessary.

Papers which were extensively used (other than taxonomic works) in the formulation of this study are Cushman, Todd, and Post (1954) with their study of the Recent foraminifera of the Marshall Islands, Graham and Militante (1959) who investigated Recent Philippine Island foraminifera, Todd (1960) with an extensive discussion on the distribution of *Baculogypsina* and *Tinoporus* (*Calcarina*), and again Todd (1961) with a paper dealing with the foraminifera from Onotoa Atoll. The nature of their contributions is discussed in the sections that follow. More recently, Resig (1969) investigated the Pleistocene, shallow-water microfauna of Oahu (Hawaiian Islands). There are certain similarities existing between the Oahu fauna and that described in this study.

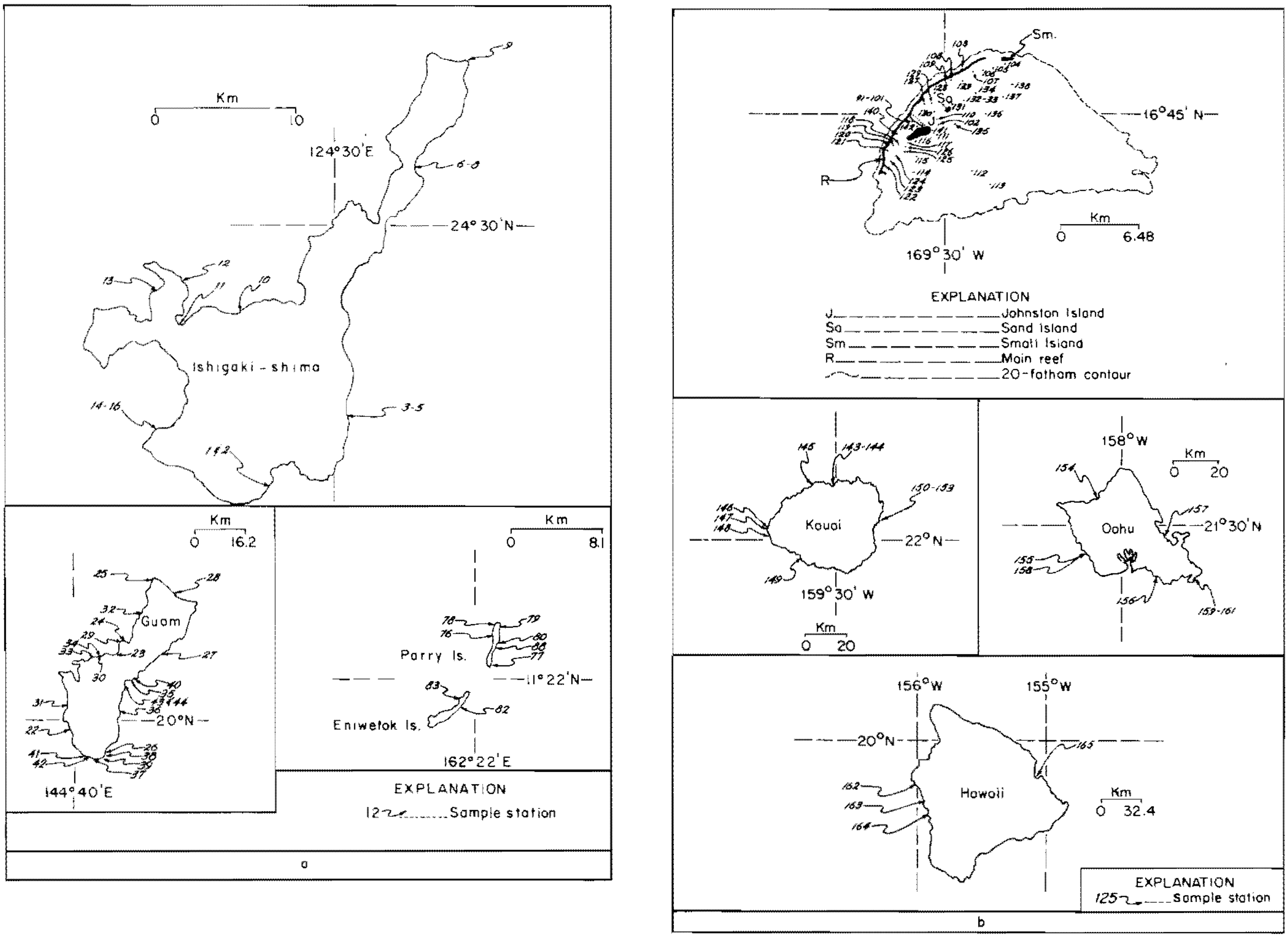


FIGURE 2

Maps of islands from which more than four samples were collected.

Method of Study

The majority of samples were collected prior to the initiation of the study and by persons other than the author. They were not preserved in alcohol so that live-dead ratios could be determined. In most cases the physical and biological conditions existing at the collection sites were not recorded.

In the laboratory the samples were treated and examined in the following manner. A representative portion of each sample was poured into a beaker of CCl_4. This resulted in the lighter fraction (including the smaller foraminiferal tests) floating to the top of the liquid and the heavier falling to the bottom. The former was collected by filtration and then both fractions were dried. Each fraction was then examined under a binocular microscope and counts made of the foraminiferal tests, ostracod valves, gastropod and pelecypod protoconchs, echinoid spines, alcyonarian spicules, recognizable coral and calcareous algae fragments, incertae sedis, and calcareous, igneous, and metamorphic grains. The remainder of the original sample was then examined to determine if any of the major elements which had not been observed in the split could be found therein. The results of the statistical analysis are presented in figures and a table.

OCEANOGRAPHY

Detailed physical oceanographic data for each of the individual islands and atolls are unavailable. However, data for the Pacific surface waters surrounding the islands have been gathered by different cruises and synthesized and interpreted by qualified workers such as Sverdrup, Johnson, and Fleming (1942) and the editors of the Morskoi Atlas (1953).

Tropical Pacific islands do not as a rule have a marked influence on the shallow-water masses that surround them. However, oceanic waters have a major control over the physical characteristics of the shallow island waters. Bikini lagoon illustrates this phenomenon. Johnson (1949) reported that the difference between the lagoonal and oceanic waters is negligible. When measured, the salinity and temperature of the lagoonal water were only 0.1 percent and .08°C higher (respectively) than oceanic waters. This indicates a constant flushing of the lagoonal waters by oceanic waters, a phenomenon known and utilized by many islanders to dispose of their waste. Graham and Militante (1957) and Emery (1956) have reported similar conditions in the shallow waters surrounding the Philippine Islands and Johnston Island.

One of the most diagnostic features of the tropical Pacific Ocean is the uniformity of the physical characteristics of the oceanic surface waters in the areas away from the major continents. The continuity of this phenomenon maintains itself to depths of as little as 10 to 15 m or as great as 100 m (Sverdrup, Johnson, and Fleming, 1942). This fact coupled with the phenomenon of continual oceanic flushing discussed above allows us to apply the oceanographic conditions discussed and illustrated in the following sections to the shallow island waters (in the appropriate geographic locations) and subsequently to the foraminifera which inhabit them.

There is very little annual variation in the surface water temperatures of the tropical Pacific (Fig. 3a, b). In fact, in some areas near the equator there is none. The greatest variation occurs in the latitudes of the Hawaiian Islands where the temperature reaches 26°C in the summer and drops to 23°C in the winter. However, considering the area as a whole, the annual temperature range is from 23°C to 28°C, which is relatively small compared to some other oceanic areas.

Salinity values are exceedingly stable throughout the year except in the vicinity of the continents and large islands where surface runoff of rainwater dilutes oceanic waters. This results in a lowering of the salinity values and the consequent exclusion of some marine organisms from the area. The largest salinity value, directly affecting tropical island foraminifera, is 35‰ in the vicinity of the equator and the lowest is between 33 and 34‰ in the higher latitudes.

The lowest oxygen values occur in the vicinity of the equator. They gradually increase in the higher latitudes until they reach a maximum in Arctic waters. The values most consistently encountered between latitudes 20°N. and 20°S. are in the range of from 4.2 to 4.9 ml/L (Cromwell and Austin, 1954).

The most southerly of the currents which influence the shallow-water tropical foraminifera is the South Equatorial Current (Fig. 4a, b). Although it is more extensively developed south of the equator, it extends as far as 5°N. lat (Sverdrup, Johnson, and Fleming, 1942), ending abruptly against the Equatorial Countercurrent. Its direction of flow varies annually (Fig. 4a, b). During the summer months the current flows in a west-southwesterly direction but in the winter months, due to a strong western wind, the current is pushed southwestward. In fact, immediately below the equator and between longitudes 140°E. and 170°W. there is an almost complete reversal of current flow to an east-southeasterly direction. The summer flow allows water from the eastern islands to flow past the western islands while the winter flow permits the exact opposite to occur as far east as long 170°W. Thus, a thorough admixture results.

The Equatorial Countercurrent (Fig. 4a, b) is described by Sverdrup, Johnson, and Fleming (1942). It is found in the northern hemisphere, flows eastward, is relatively thin and is almost always present. Due to two convergences and two divergences between the equator and the northern boundary of the Countercurrent, there is a spiralling rather than a direct eastward flow of Countercurrent water. If an observer were standing on the current looking toward the Americas, the direction of flow would be to the right carrying northern surface water in a southern direction. However, the north-south velocity is only ⅕ of its east-west component. A characteristic result of the divergences, which occur in the region of the equator and at the northern boundary of the Countercurrent, is to bring nutrients to the region, thus increasing its productivity. One of the main benefits of the Equatorial Countercurrent is that it carries its water masses through the Caroline Islands into the Marshall Islands.

The North Equatorial Current flows from east to west and like the Equatorial Countercurrent it possesses a spiral motion due to a convergence and divergence within its main body (Sverdrup, Johnson, and Fleming, 1942). It carries water from the Hawaiian Islands to Johnston Island which is in turn brought to the Marshall and Mariana Islands. Near the Asiatic continent the majority of the water travels northwestward (its volume increasing with the addition of Kuroshio Countercurrent water) and terminates at the

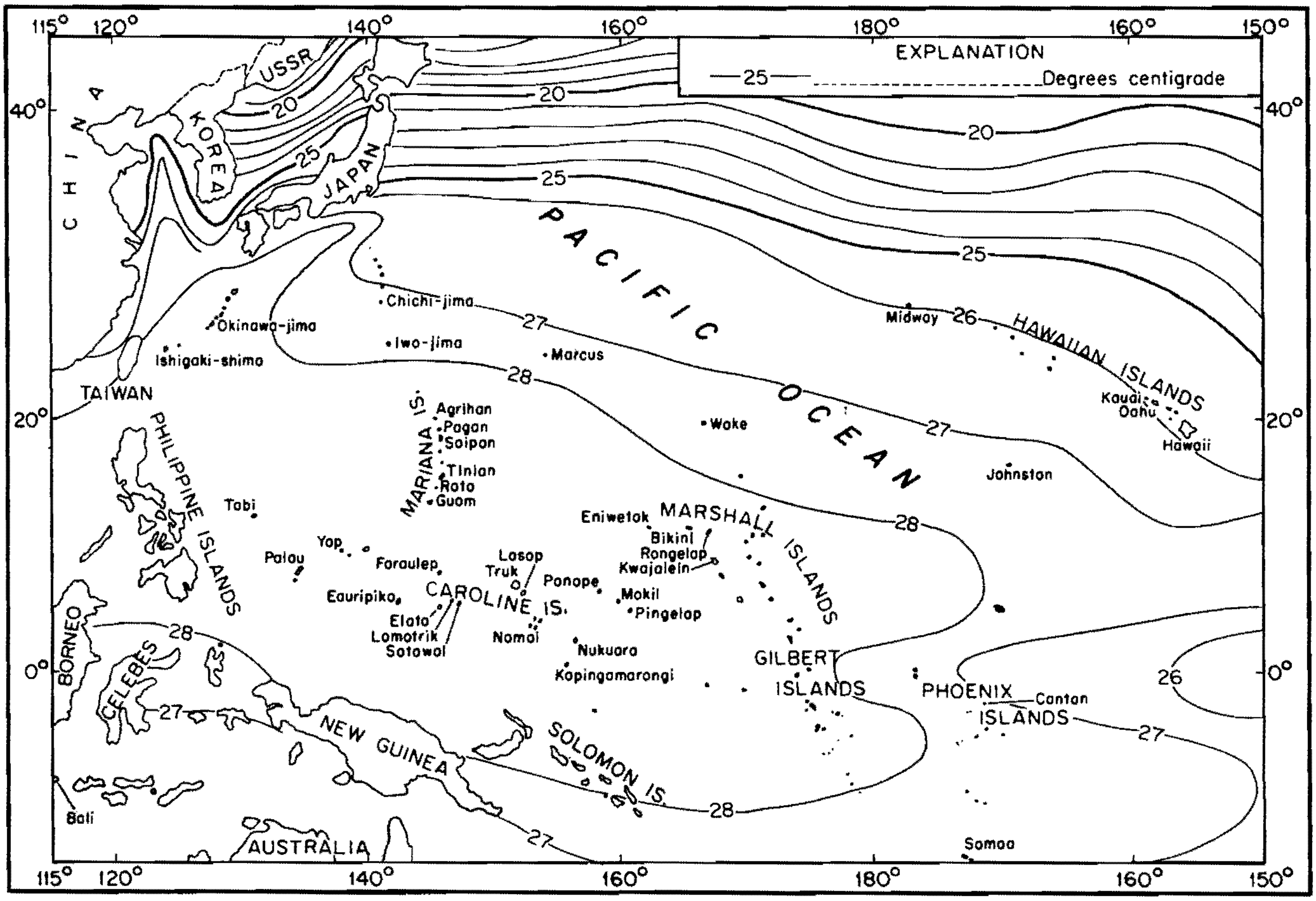


FIGURE 3

Surface temperatures of the tropical Pacific Ocean in the summer (a) and winter (b). After *Morskoi Atlas* (1953, Vol. II, pl. 17).

southern extremity of Formosa. Some of the water travels southward passing the Philippines and other southern islands.

The North Equatorial Current continues northeastward from Formosa as the Kuroshio Current, carrying North Equatorial water as far as lat 35°N. (Sverdrup, Johnson, and Fleming, 1942). Its velocity increases considerably and the current parallels the Kuroshio Countercurrent which lies to the east. Ishigaki-shima, as well as other Japanese Islands, are bathed by this current.

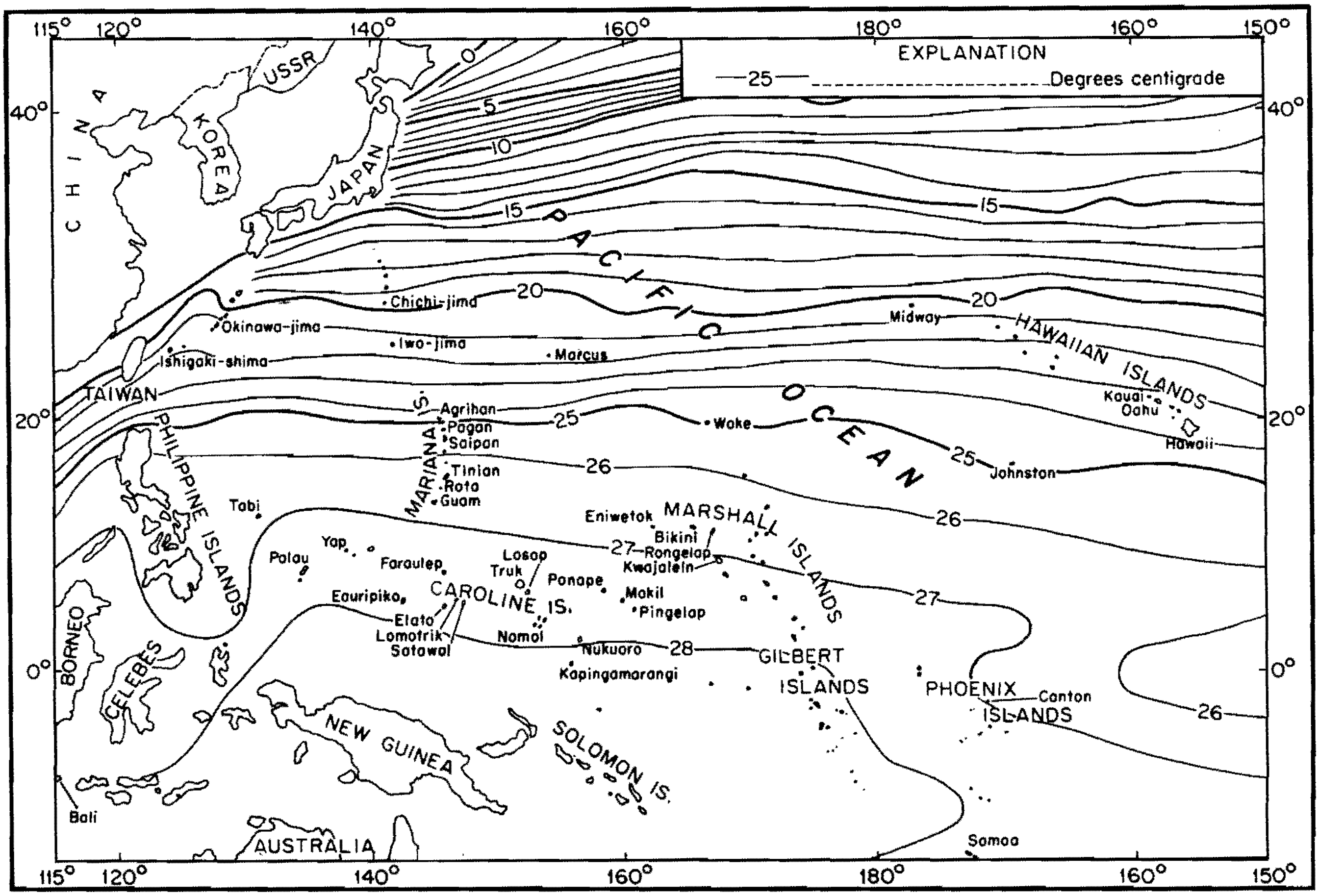
The waters of the Kuroshio continue their long journey eastward as the Kuroshio Extension. Some of this water turns south and southeastward and is known as the Kuroshio Countercurrent but most of it travels as far as long 170°E. There are no islands along the route occupied by the Kuroshio Extension.

The eastward extension of the Kuroshio Extension is the North Pacific Current. It continues as far east as long 150°W. and its waters eventually reach the Hawaiian Islands, but as part of the North Equatorial Current.

Division of the Tropical Pacific into Sectors

The tropical Pacific is divided into four sectors (Fig. 1) for convenience of discussion using as criteria certain pertinent physical and biological features.

The western and southern boundaries of Sector I are the 180° meridian and the equator respectively. It is unique because of the great distances between islands and the westerly current flow which bars some current dispersed organisms from migrating to the Hawaiian Islands and Johnston Island directly from the more southerly tropical islands. Sector II is bound-



ed on the east by the 180° meridian and to the south by the equator. It is characterized by the relatively short distances between individual islands and the several currents which provide a rapid and wide dispersal of current carried organisms. The eastern and the northern boundaries of Sector III are long 170°W. and the equator. It is also characterized by short distances between islands and admixture of the water mass by the current to insure rapid and wide dispersal of marine organisms. Sector IV is bounded on the west by long 170°W. and on the north by the equator. It is segregated from Sector III by the continual west-southwest flow of the South Equatorial Current whereas an almost complete reversal of this current occurs in Sector III. The monodirectional flow appears to act as a barrier to the dispersal of certain marine organisms from Sectors II and III.

FAUNAL ANALYSIS

GENERAL STATEMENT

The homogeneity of the intertidal and shallow-water foraminiferal fauna of the tropical Pacific is one of the most striking results which has been resolved from the faunal analysis (Table 1). Equally significant is the restriction of particular elements of the fauna to certain sectors in the Pacific.

The samples used in this study are divided into two types, intertidal and shallow water. The intertidal samples are dominated by the larger foraminifera including various species of *Tinoporus*, *Baculogypsina sphaerulata*, *Amphistegina lessonii*, *Marginopora vertebralis*, and *Heterostegina depressa*. Smaller foraminifera usually are present but are not significant in a numerical sense. The majority of the shallow-water

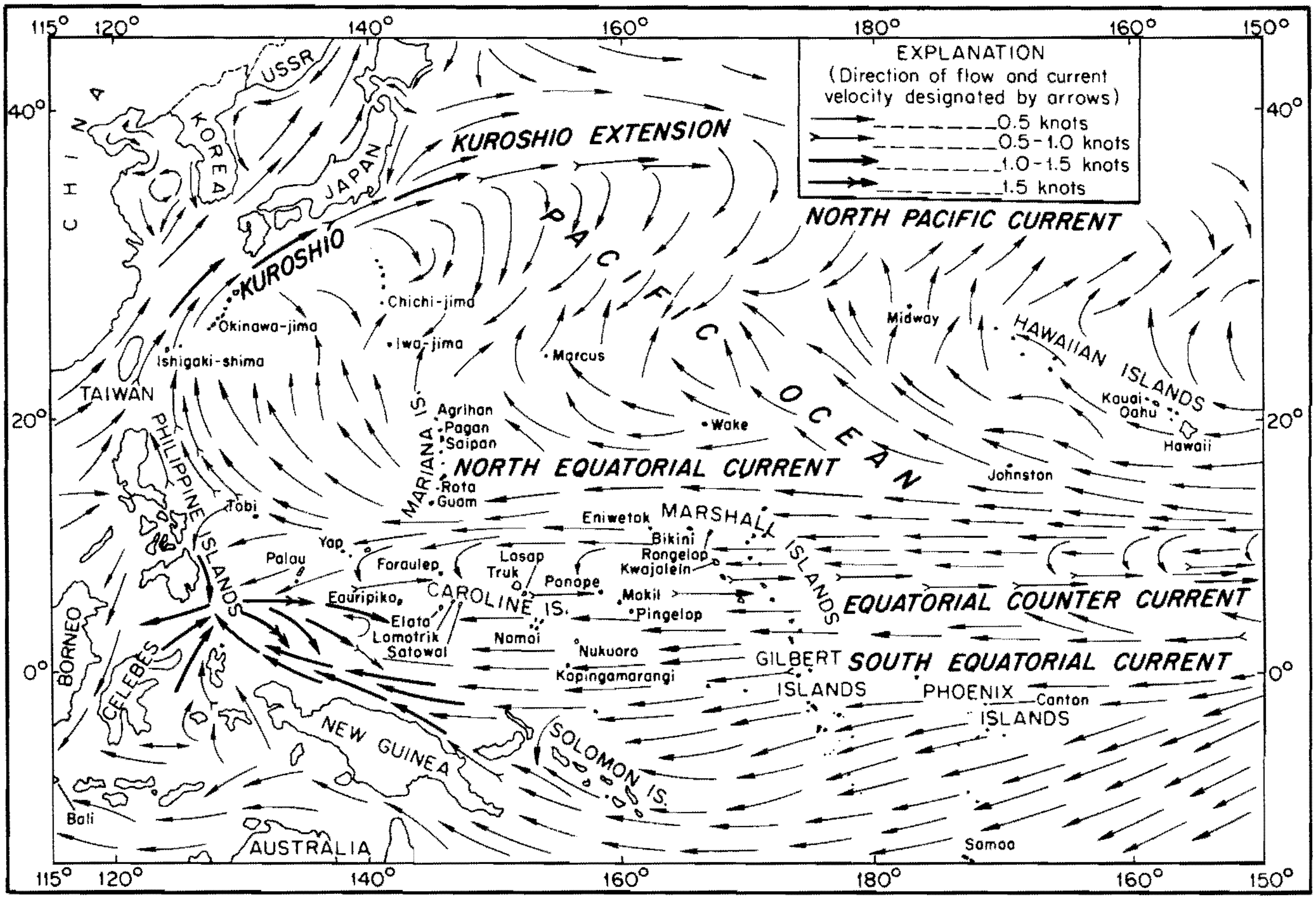


FIGURE 4

Surface currents of the tropical Pacific Ocean in the summer (a) and winter (b). After *Morskoi Atlas* (1953, Vol. II, pl. 31).

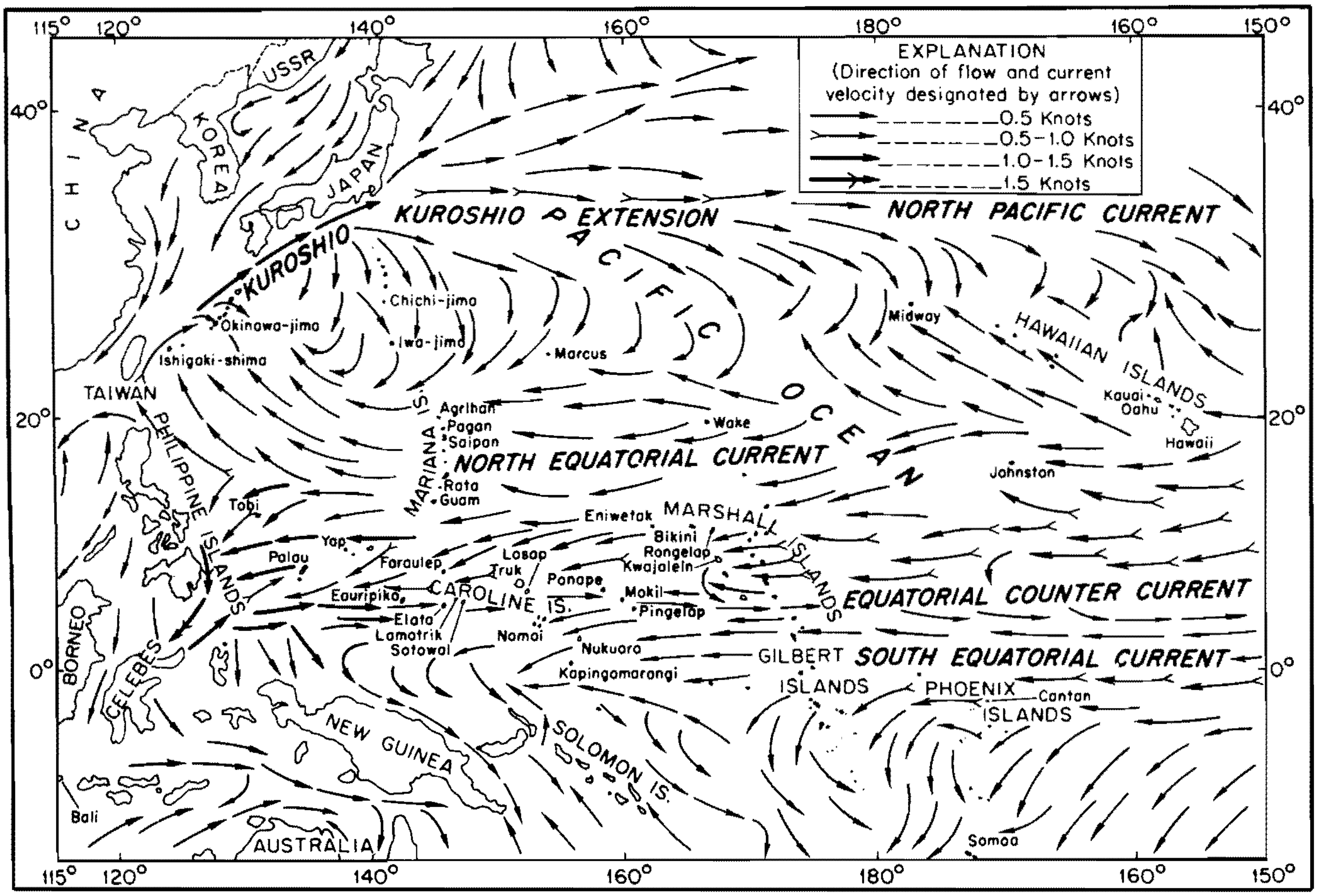
samples are from Johnston Island. In most of these the smaller foraminifera (Table 1) dominate the fauna. Discussions of the quantitative and qualitative analyses of all the samples are presented in separate sections.

The general physical conditions to which the foraminifera are exposed are discussed in the oceanography section. Information regarding yearly diurnal conditions is not available but it seems probable that the foraminifera must be able to withstand extreme fluctuations due to their proximity to atmospheric conditions.

Chapman (1900), Cushman, Todd, and Post (1954), Graham and Militante (1959), Todd (1960, 1961) discuss where the foraminifera are thought to live within the shallow-water column surrounding the island. For example, Chapman (1900) found that *Baculogypsina* and *Tinoporus* prefer living on the reef rather than in the lagoon. Todd (1960) expanded this by showing that they also live in the bottom sediments next to the reefs and less frequently in the intertidal region. Todd (1961) and Graham and Militante (1959) discussed the geographical preferences shown by other species in the shallow-water areas.

An analysis was made of the physical appearance of the foraminiferal tests. A major percentage of the larger skeletons exhibits varying degrees of erosion. However, only a very small percentage of the smaller tests shows evidence of wear.

The planktonic species are an unimportant part of the foraminiferal fauna. Even though they are abundant in the deep oceanic water surrounding the islands, their tests are only rarely deposited in shallow or intertidal water. The highest frequency of occur-

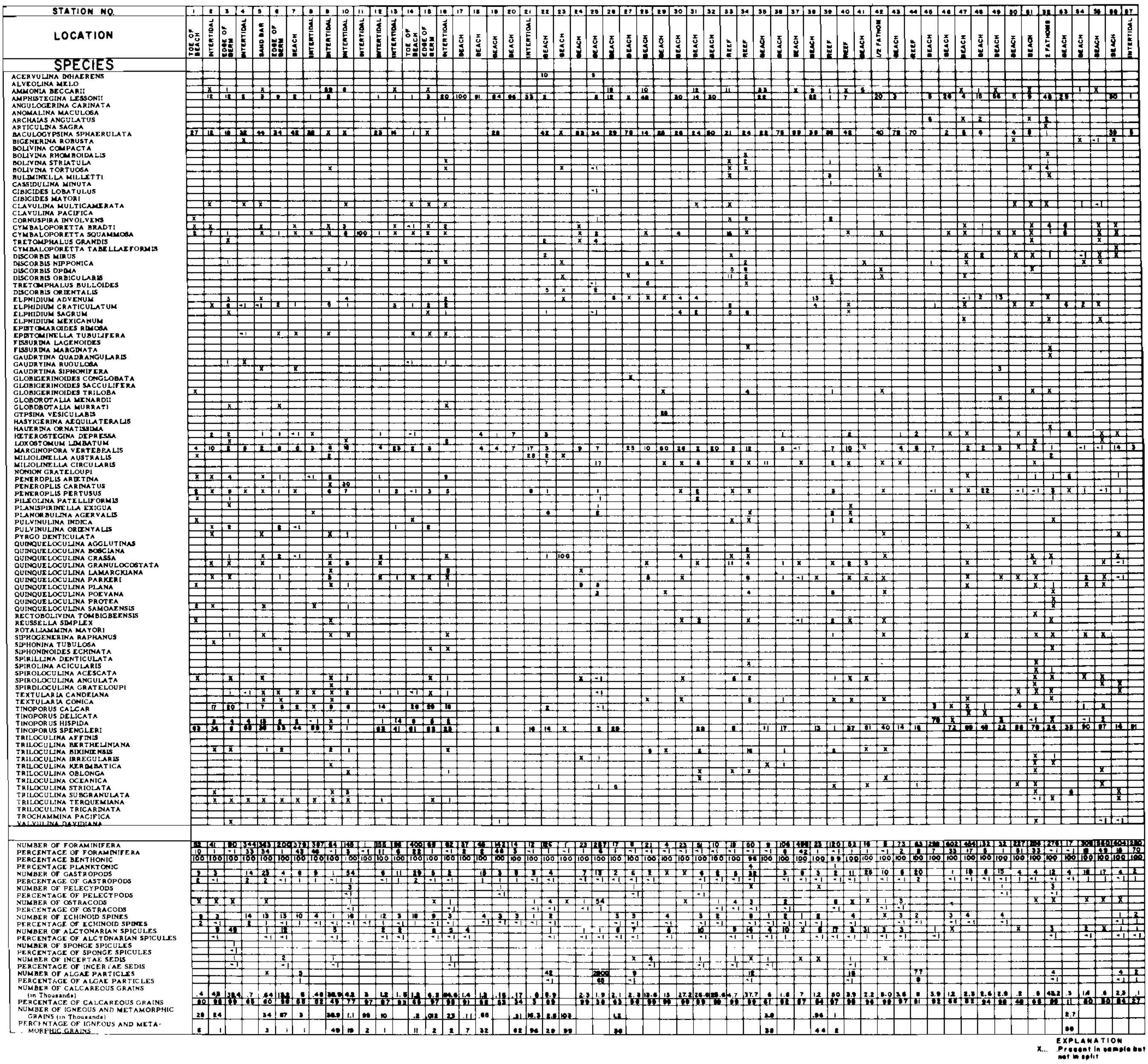


rence of the planktonics is in the shallow water surrounding Johnston Island and the lowest is in the beach sands of various islands.

EURYTOPIC RANGES OF BENTHONIC TROPICAL FORAMINIFERA

An investigation of Table 1 reveals that 67 percent (70 species) of the 105 benthonic foraminifera listed are distributed throughout Sectors I and II, while 30 percent (32 species) are common to Sectors I, II, and III, 14 percent (15 species) to Sectors I, II, and IV, and 10 percent (11 species) to Sectors I, II, III, and IV. [The low percentages of the last three combinations in comparison to the first is probably due to the paucity of samples (a total of five) from Sectors III and IV.] The major significance of these statistics is the fact that many shallow-water foraminifers of the tropical Pacific Ocean have been capable (and possibly still are) of migrating across great stretches of water with depths exceeding 4,000 meters. The principal question is how this migration was (is) accomplished.

Seven known methods of island hopping are available to these eurytopic (wide-ranging) shallow-water benthonic foraminifera. Although none of them has been observed in operation in the tropical Pacific, they are presented in order to act as a foundation for future investigations in this area. They are: (1) transportation of the zygotic stage of the foraminifera by ocean currents; (2) rafting of grown or immature individuals on marine algae or other material capable of floating; (3) distribution of the microspheric or megalospheric stages by currents; (4) transport of individuals which



STATION NO.

LOCATION

SPECIES

ACERVULINA INHAERENS
ALVEOLINA MELO
AMMONIA BECCARII
AMPHISTEGINA LESSONII
ANGULOGERINA CARINATA
ANOMALINA MACULOSA
ARCHAIAS ANGULATUS
ARTICULINA SAGRA
BACULOGYPSINA SPHAERULATA
BIGENERINA ROBUSTA
BOLIVINA COMPACTA
BOLIVINA RHOMBOIDALIS
BOLIVINA STRIATULA
BOLIVINA TORTUOSA
BULIMINELLA MILLETTI
CASSIDULINA MINUTA
CIBICIDES LOBATULUS
CIBICIDES MAYORI
CLAVULINA MULTICAMERATA
CLAVULINA PACIFICA
CORNUSPIRA INVOLVENS
CYMBALOPORETTA BRADTI
CYMBALOPORETTA SQUAMMOSA
TRETOMPHALUS GRANDIS
CYMBALOPORETTA TABELLAEFORMIS
DISCORBIS MIRUS
DISCORBIS NIPPONICA
DISCORBIS OPIMA
DISCORBIS ORBICULARIS
TRETOMPHALUS BULLOIDES
DISCORBIS ORIENTALIS
ELPHIDIUM ADVENUM
ELPHIDIUM CRATICULATUM
ELPHIDIUM SAGRUM
ELPHIDIUM MEXICANUM
EPISTOMAROIDES RIMOSA
EPISTOMINELLA TUBULIFERA
FISSURINA LAGENOIDES
FISSURINA MARGINATA
GAUDRYINA QUADRANGULARIS
GAUDRYINA RUGULOSA
GAUDRYINA SIPHONIFERA
GLOBIGERINOIDES CONGLOBATA
GLOBIGERINOIDES SACCULIFERA
GLOBIGERINOIDES TRILOBA
GLOBOROTALIA MENARDII
GLOBOROTALIA MURRATI
GYPSINA VESICULARIS
HASTIGERINA AEQUILATERALIS
HAUERINA ORNATISSIMA
HETEROSTEGINA DEPRESSA
LOXOSTOMUM LIMBATUM
MARGINOPORA VERTEBRALIS
MILIOLINELLA AUSTRALIS
MILIOLINELLA CIRCULARIS
NONION GRATELOUPI
PENEROPLIS ARIETINA
PENEROPLIS CARINATUS
PENEROPLIS PERTUSUS
PILEOLINA PATELLIFORMIS
PLANISPIRINELLA EXIGUA
PLANORBULINA AGERVALIS
PULVINULINA INDICA
PULVINULINA ORIENTALIS
PYRGO DENTICULATA
QUINQUELOCULINA AGGLUTINAS
QUINQUELOCULINA BOSCIANA
QUINQUELOCULINA CRASSA
QUINQUELOCULINA GRANULOCOSTATA
QUINQUELOCULINA LAMARCKIANA
QUINQUELOCULINA PARKERI
QUINQUELOCULINA PLANA
QUINQUELOCULINA POEYANA
QUINQUELOCULINA PROTEA
QUINQUELOCULINA SAMOAENSIS
RECTOBOLIVINA TOMBIGBEENSIS
REUSSELLA SIMPLEX
ROTALIAMMINA MAYORI
SIPHOGENERINA RAPHANUS
SIPHONINA TUBULOSA
SIPHONINOIDES ECHINATA
SPIRILLINA DENTICULATA
SPIROLINA ACICULARIS
SPIROLOCULINA ACESCATA
SPIROLOCULINA ANGULATA
SPIROLOCULINA GRATELOUPI
TEXTULARIA CANDEIANA
TEXTULARIA CONICA
TINOPORUS CALCAR
TINOPORUS DELICATA
TINOPORUS HISPIDA
TINOPORUS SPENGLERI
TRILOCULINA AFFINIS
TRILOCULINA BERTHELINIANA
TRILOCULINA BIKINIENSIS
TRILOCULINA IRREGULARIS
TRILOCULINA KERIMBATICA
TRILOCULINA OBLONGA
TRILOCULINA OCEANICA
TRILOCULINA STRIOLATA
TRILOCULINA SUBGRANULATA
TRILOCULINA TERQUEMIANA
TRILOCULINA TRICARINATA
TROCHAMMINA PACIFICA
VALVULINA DAVIDIANA

NUMBER OF FORAMINIFERA
PERCENTAGE OF FORAMINIFERA
PERCENTAGE BENTHONIC
PERCENTAGE PLANKTONIC
NUMBER OF GASTROPODS
PERCENTAGE OF GASTROPODS
NUMBER OF PELECYPODS
PERCENTAGE OF PELECYPODS
NUMBER OF OSTRACODS
PERCENTAGE OF OSTRACODS
NUMBER OF ECHINOID SPINES
PERCENTAGE OF ECHINOID SPINES
NUMBER OF ALCYONARIAN SPICULES
PERCENTAGE OF ALCYONARIAN SPICULES
NUMBER OF SPONGE SPICULES
PERCENTAGE OF SPONGE SPICULES
NUMBER OF INCERTAE SEDIS
PERCENTAGE OF INCERTAE SEDIS
NUMBER OF ALGAE PARTICLES
PERCENTAGE OF ALGAE PARTICLES
NUMBER OF CALCAREOUS GRAINS (in Thousands)
PERCENTAGE OF CALCAREOUS GRAINS
NUMBER OF IGNEOUS AND METAMORPHIC GRAINS (in Thousands)
PERCENTAGE OF IGNEOUS AND METAMORPHIC GRAINS

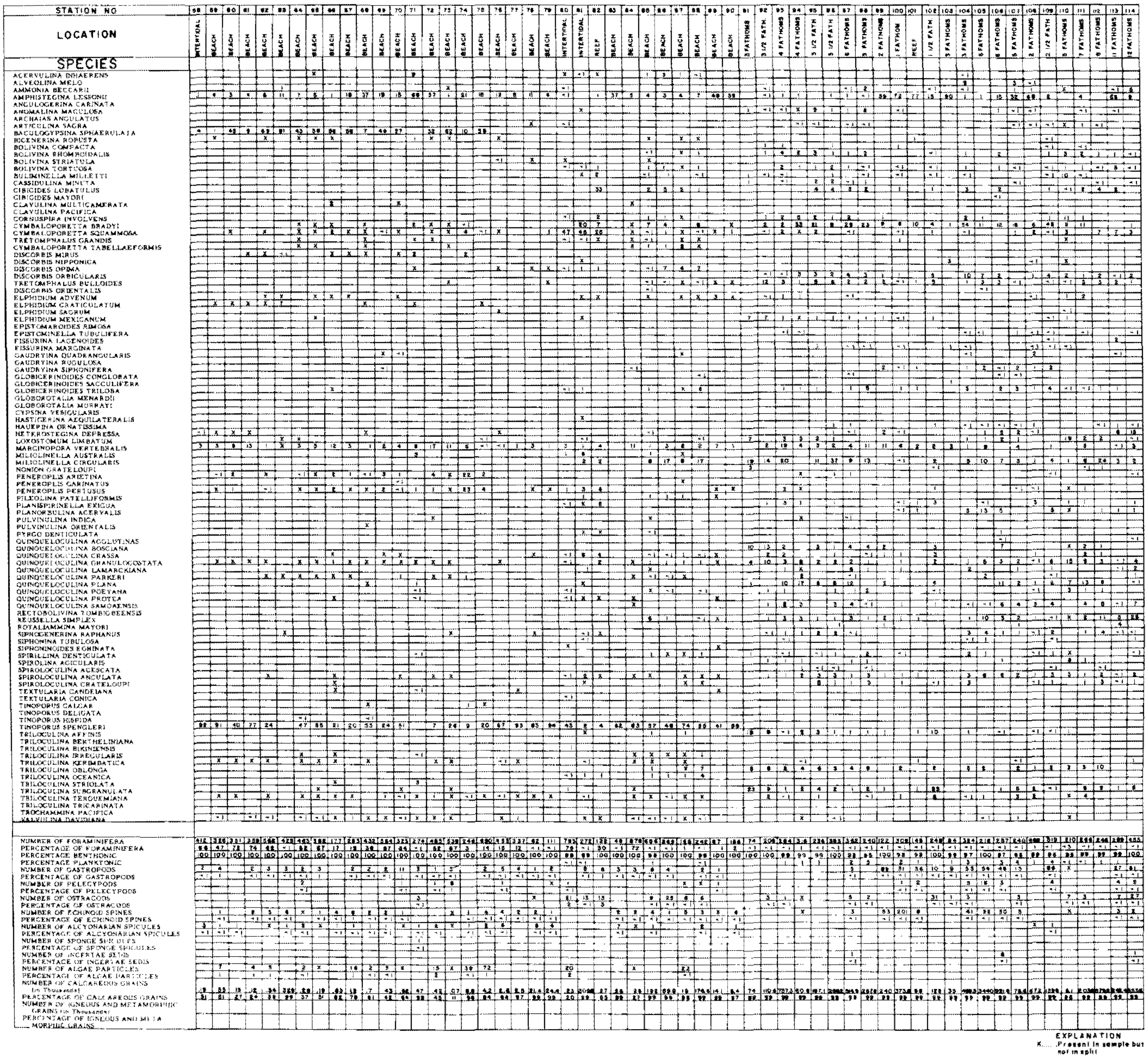
EXPLANATION
X... Present in sample but not in split

have become attached to the feet or bodies of birds; (5) transportation either in the digestive tract or on the dermal surface of shore fishes; (6) vehicular transportation by man; and (7) crawling over the ocean floor.

Transportation of the Zygotic Stage of the Foraminifera by Ocean Currents

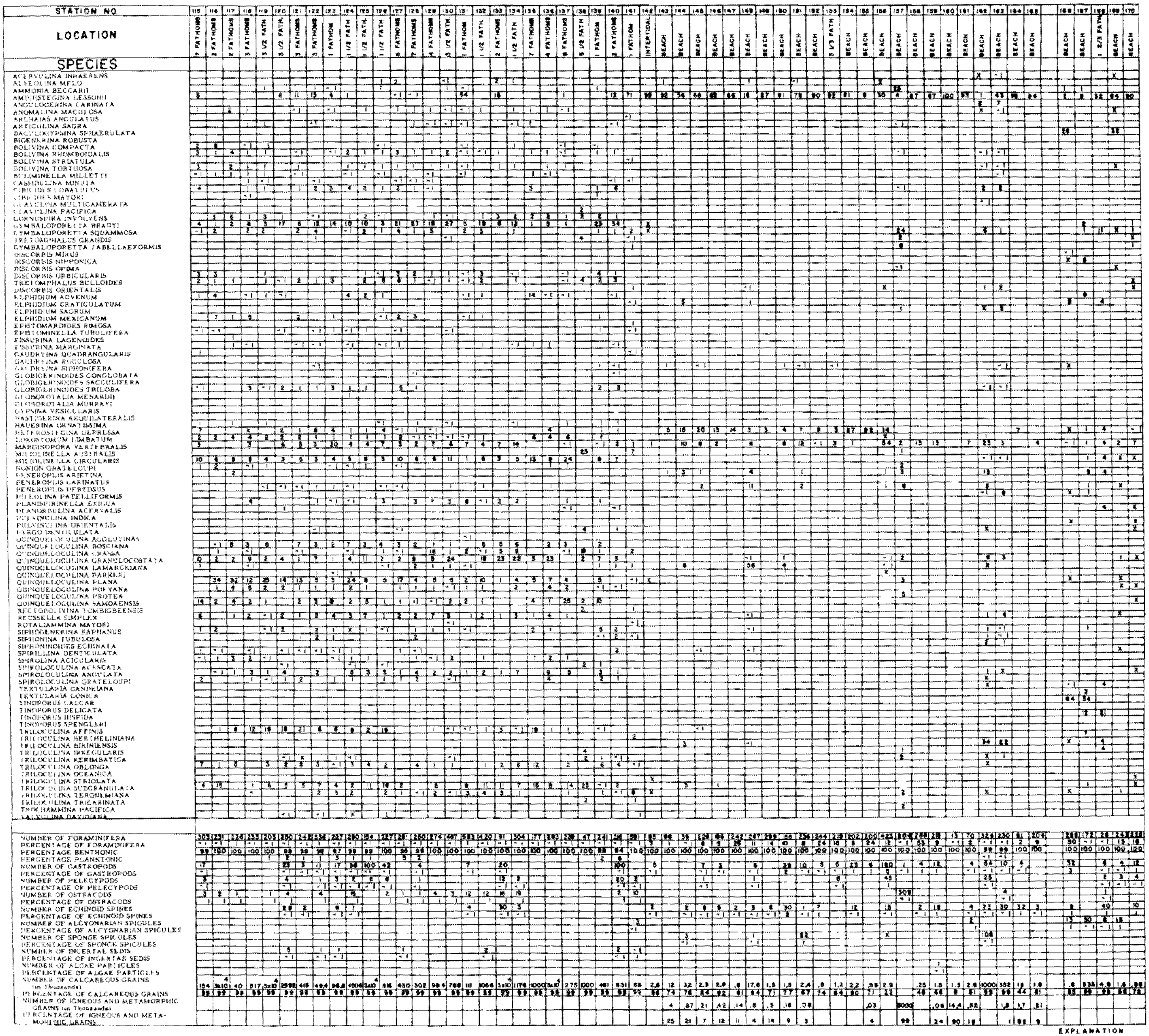
The most direct and uncomplicated method of dispersion is that of the zygotic stage by ocean currents. There have been many objections raised against this method and they are probably best summarized in a single statement by Myers and Cole (1957): "There is no true pelagic stage known in the life cycle of most of the benthonic foraminifera." However, an almost diametrically opposed statement appears in the same article. It is: "The life cycles of relatively few of the foraminifera are completely known."

Facts which tend to support the hypothesis that the zygotic stage of foraminifera may be transported by ocean currents are numerous. Thorson (1957), in a general reference to the level botton communities,



EXPLANATION
X.....Present in sample but not in split

states that in the tropics 85 to 90 percent of the invertebrate species have a long pelagic life, while only ⅔ of the invertebrate species in cold temperate seas have pelagic larvae, a figure which decreases to zero in Arctic and Antarctic coastal waters. Although this statement does not apply directly to foraminifera, it is worth taking into consideration, for it has been established that the majority of foraminifera (in which the life cycle is known) possess flagellate gametes and subsequently flagellate zygotes while the ameboid gamete is rare (Glaessner, 1947). The flagellate zygote could possibly act as the pelagic larval stage. The length of time between the formation of the zygote and the development of the microspheric stage is unknown in the majority of the benthonic species. Although it is comparatively short in the few species for which it has been studied, these are perhaps not typical of tropical Pacific foraminifera. If and when they are determined under laboratory conditions certain factors might extend this period beyond its normal length. For instance, it might be necessary for a flagellate zygote, which has been swept from its parental island home



EXPLANATION
X. Present in sample but not in split

into the deep open ocean, to find shallow water before it can continue its development into a microspheric stage, a condition which may require several days if not weeks. If, after a certain time, it does not find a shallow-water column, offering optimum conditions for development, it will perish. This condition for development of the pelagic larvae is experienced by polychaete larvae and it should be determined if tropical Pacific shallow-water foraminifera are similarly characterized. In addition, temperature changes might be influential in extending the larvae stage for possible lengthy distribution periods in certain parts of the tropical Pacific area. This explanation assumes that the origin of a portion of the species involved was in other than Sector I. If the species originally had to and still must migrate into Sector I to maintain the population, it would seemingly have to travel by way of the Kuroshio Extension and the North Pacific Current to reach the Hawaiian Islands, a trip which would normally require approximately 180 days. Its direct migration from any other area in the tropical Pacific seems to be barred by the westerly flowing North Equatorial Current unless the direction of flow of the major current systems has changed in the recent geologic past.

Figure 3a, b reveals that during the winter months temperatures are considerably lower than in the summer in the vicinity of the Kuroshio Extension and North Pacific Current. It is possible that the lowering of the temperature of the zygotic, pelagic stage, instead of being lethal, would slow down its metabolic processes sufficiently to lengthen the life expectancy of that particular stage of development and permit wider distribution.

However, it seems self-evident that the only way to prove or disprove the ability of the zygote of benthonic foraminifera to be carried by currents is to: (1) study the life history of these animals in controlled experiments, noting in particular the characteristics of the zygote, and (2) examine the phytoplankton of the water masses of the currents leading to and away from the islands in order to determine if the zygotes are part of the plankton population.

Rafting of Benthonic Foraminifera by Marine Algae or Other Floating Objects

The association between marine plants and foraminifera has been recognized for a considerable length of time. Myers (1943) noted that if the *Tretomphalus* stage of *Discorbis* should become attached to marine algae it could be rafted by currents considerable distances outside of its geographical range. Brönniman (1949) recorded numerous species of benthonic foraminifera (several of which are living in the Pacific) attached to marine plants (the eelgrass, *Thalassia testudinum*) in Atlantic tropical waters. Bandy (1960) found living foraminifera on kelp growing off the coast of California and suggested rafting of algae as a means of dispersal. Lessard (1960, unpublished paper) discovered 53 species of foraminifera (both fossil and Recent) together with representatives of eight other animal phyla being rafted by *Macrocystis* off the southern California coast. In this instance, all the foraminifera were part of arenaceous worm colonies, *Phragmatopoma californica*, and no effort was made to determine if any of the individuals were alive.

On the basis of the data which were available prior to 1957, Myers and Cole (1957) stated that the principal means of dispersal of shallow-water foraminifera is by floating weeds (marine plants). However, there has been no study made of the number of species of shallow-water tropical Pacific foraminifera capable of being rafted. In other words, how many species actually live a part of their life on the plants, and of these, how many remain on it after it has detached itself from the shallow substratum? These questions can only be answered by direct observation.

A favorable aspect of rafting as a method of dispersion is the eurytopic distribution of marine algae in the area as shown by Okamura (1932). In discussing the distribution of marine algae in Pacific waters, Okamura divided the ocean into several areas for convenience of discussion. They include Japan, Australia, the Malay Archipelago and Polynesia (the tropical Pacific between latitudes 20°S. and 20°N. including the Hawaiian Islands). It was discovered that the Polynesian area contains 657 species of which only 194 are peculiar. Of the remaining 463 species, 324 are found in the Malay Archipelago, 209 in Japan, 205 in the Indian Ocean, and 164 in the West Indies. The actual distribution of many of these species is due to the transplantation of the entire or parts of the thallus (body) which has been detached from the substratum and is carried away, perhaps with foraminiferal passengers, by the major currents. An example of marine algae whose thallus is commonly found floating in warm waters is *Sargassum* (Fuller and Oswald, 1958). Okamura (1932) lists 27 species of *Sargassum* common to Australia, Polynesia, the Malay Archipelago, and Japan. An extensive investigation of the foraminiferal-algal relationship would, no doubt, help to ascertain the role of marine algae in the distribution of benthonic foraminifera.

In addition to marine plants, other modes of rafting are available. Land vegetation, pumice, coral and, more recently, man-made items have been observed floating in the ocean. Foraminifera attached to any of these objects could surmount the great oceanic depths.

The currents, which act as the transportation media for the majority of species of marine plants, would carry the plants and other floating objects along the same general paths as the pelagic foraminiferal zygotes.

Distribution of Microspheric or Megalospheric Stages by Currents

Myers and Cole (1957) stated that it is possible for juveniles or even adult specimens of a small species (of benthonic foraminifera) to be carried considerable distances by normal currents. J. M. Resig and L. Lidz (personal communication), working independently, found specimens of *Bolivina* in plankton tows off the coast of southern California. However, if this were a common phenomenon among foraminifera, one would expect to find numerous tests of shallow-water foraminifera in deep-water planktonic oozes taken at considerable distances from the coast. Such occurrences are the exception rather than the rule.

Dispersal by Attachment to the Bodies of Birds

Allee and Schmidt (1951) reported that freshwater eggs and animal forms in a dormant state can be distributed by adhering to the bodies of birds. Headlee (1961, unpublished paper) found several foraminifera in the mud adhering to the feet of numerous ducks shot by hunters in the Salton Sea area. The foraminiferal species are different from those normally found in the lake and were being transported by the birds during their migratory flights. No attempt was made to determine live-dead ratios.

There are many eurytopic species of birds in the tropical Pacific. An excellent example is the distribution pattern of the storm petrels (*Tubinares*) which are found throughout the tropical Pacific area during the nonmating season. The question as to whether or not these or other wide-ranging birds can effectively transport live foraminifera can only be answered by direct observation in the field. If they are proven capable of accomplishing this phenomenon, foraminifera can be said to be passively distributed independent of the oceanic current system.

Transportation Inside or Outside the Bodies of Fishes

Shore fishes are widely distributed in the tropical Pacific and may possibly carry foraminifera from one locality to another. Two observations have led to this conclusion. Meyers (1939) reported that the same species of shore fishes could be found from one end of the Indo-Pacific realm to the other. Todd (1961) reported 62 species of foraminifera in the gut and stomach contents of 10 different species of shore fishes, which were swallowed while eating coral, marine algae, and/or organic matter on the substratum.

It is not known if foraminifera can pass through the digestive system of these fish without being lethally attacked by their digestive enzymes which include hydrochloric acid. This could be determined by examining their waste products. If the foraminifera can either survive this hazardous journey or attach to the fish's dermal surface while the latter is eating or resting, then perhaps the fish can act as an effective agent of foraminiferal distribution. During a migrational period or severe storm, fish travel to foreign islands where their foraminiferal passengers could be dropped. This method of distribution is also independent of the existing currents.

Vehicular Distribution by Man

Shallow-water tropical foraminifera accidentally brought aboard canoes, boats, ships, or planes by man or his domestic animals could be transported from island to island. However, if it can be shown that those foraminifers lived on the islands before the appearance of man, then the hypothesis must be discarded.

Dispersal by Crawling Over the Ocean Floor

The supposition that shallow-water benthonic foraminifera migrate over the bottom substrate in the tropical Pacific does not seem plausible for the following reasons. An examination of a bathymetric map of the area under investigation reveals that in order for these foraminifera to travel between islands over the bottom, they would have to be physiologically adapted to survive in oceanic depths of 4,000 meters or more in conditions entirely different than those existing in their normal habitat. An immediate effect on the calcareous foraminifera could be the dissolution of their tests (Revelle and Fairbridge, 1957). There would also be a large drop in temperatures to values ranging from 4° to −10°C (Sverdrup, Johnson, and Fleming, 1942). This alone could be a lethal factor. Finally, it would take a foraminifer approximately 5,400,000 days to crawl from the Hawaiian Islands to Johnston Island (without taking into consideration any type of slope) at the rate of 1 cm per hour (an average figure)!

FLUCTUATIONS IN THE POPULATION AND DISTRIBUTION OF *BACULOGYPSINA* AND *TINOPORUS*

Todd (1960) has noted the restricted geographic distribution of *Baculogypsina* and *Tinoporus* in the tropical Pacific Ocean. *Baculogypsina* extends as far east as the Phoenix Islands while *Tinoporus* has not been found further west than the Gilbert and Ellice Islands (the same results were noted in the present faunal analysis). Todd, in the same paper, observed that the occurrence of these genera is sporadic both in Recent and fossil sediments. At the present time, within their stenotopic (limited) range, representatives of one genus may occur in the shallow waters of an atoll or island with the total exclusion of representatives of the other genus. If they are living together, representatives of the one genus may be either dominant, equal, or scarce in numerical relationship to the other. Todd (1960) gives the following examples.

Tinoporus and not *Baculogypsina* now lives on the reefs of both Bikini and Eniwetok in the Marshall Islands. It is also found in the upper portion of certain cores from these atolls. However, *Baculogypsina* is only found below the *Tinoporus* occurrence in the cores. On Onotoa Atoll both species are now living on the reefs while *Tinoporus* is found exclusive of *Baculogypsina* in shallow pits in the same area. Todd (1960) cited several other similar examples.

Todd made no attempt to explain the existing stenotopic range or the sporadic Recent and fossil occurrences but implied that a solution might be found by studying additional samples. Although it was not possible to obtain a large quantity of new samples, certain hypotheses are advanced to explain these phenomena using available biological and oceanographical data. The present overall distribution will be dealt with first.

It is evident from the present distribution of *Tinoporus* and *Baculogypsina* that they are experiencing difficulty in extending their geographical range. Their exclusion from Sectors I and IV indicates that both distance and current flow are important factors in controlling their distribution. These in addition to other factors permit us to eliminate certain methods of dispersal previously discussed.

Migration over the ocean floor is eliminated because of the great depths and pressures involved. The presence of the foraminifera in Miocene sediments precludes the possibility of vehicular transportation by man. The fact that they are present in Sector III and absent from Sector IV indicates that they are incapable of migrating over short distances against unfavorable currents, and therefore the hypotheses of countercurrent distribution by fishes and birds seem to be implausible explanations. Their large size and absence from deep sea oozes partially invalidates the hypothesis that either the microspheric or megalospheric test and animal are being carried by currents. The method cannot be entirely discounted because severe storms might provide the required energy for such a dispersal. However, the question remains as to why the same storms do not cause a migration from Sector III to IV. The rafting of these foraminifera by marine algae or other floating objects has in its favor the sporadic distribution of these animals which would be expected from such a method. But it also raises the question as to why they cannot be rafted to Sectors I and IV. The remaining means of dispersal, transportation by currents of the zygotic stage, overcomes most of the objections which have been advanced by the other methods. Therefore, it will be discussed in detail.

It is assumed, because of the irregular distribution, that the zygotic stages of species of these genera are relatively short and/or in a delicate natural balance with their environment. These conditions can easily result in their destruction and the prevention of wide dispersion. A comprehensive re-examination of the existing oceanic current system coupled with this factor serves to show that they are barring the distribution of these genera.

Their exclusion from the Hawaiian Islands and Johnston Island is explained by the fact that in order for the zygotic stage to reach these islands they would have to be transported, starting from the Ryukyu-retto Islands, by the Kuroshio, Kuroshio Extension, North Pacific Current and North Equatorial Current, a total distance of from 4,000 to 4,800 miles. Their direct migration from the Sector II to Sector I is barred by the westward-flowing North Equatorial Current.

It would seem that it would be relatively easy for *Tinoporus* and *Baculogypsina* to migrate from Sector III to Sector IV, for the distances are relatively short. However, the existing current system must again be taken into consideration. These eastern Pacific islands are perennially under the influence of the west-southwest-flowing South Equatorial Current. Its direction of flow creates an effective barrier to the eastward distribution of the genera and as in the case of the population of Sector I the distances involved for the migration of the zygotic stage would be too lengthy. Their presence in Sector III is due to the fact, as previously explained, that in the winter months the direction of flow of the South Equatorial Current between long 140°E. and 170°E. is erratic due to a westerly wind and at times an almost complete reversal of flow occurs, allowing an eastern migration of the fauna and flora. However, in Sector IV the only effect of the increase in wind velocity is to cause the South Equatorial Current to move in a more southwesterly direction. An additional explanation for their presence in Sector III is their proximity to the Caroline and Marshall Islands (Sector II). The spiral motion of the water masses in the vicinity of the equator might aid in a rapid dispersal across the hemispheric boundary. Barring the introduction of some uncalculated factor, it can be said with some certainty that unless there is a major change in the surface circulatory system of the tropical Pacific Ocean or transportation by man, it appears that *Tinoporus* and *Baculogypsina* will remain confined to the western tropical Pacific Ocean. However, the problem of their irregular distribution in the existing stenotopic range must be solved.

Fluctuations in the populations of invertebrates and even vertebrates is not an unusual occurrence in nature. Coe (1957) described several macro-marine invertebrates whose fluctuations are very similar to those experienced by *Tinoporus* and *Baculogypsina*. Coe explains that:

> ". . . the greatest ranges of fluctuations occur in restricted bodies of water, such as tide pools, lagoons, bays, and estuaries, for there are the greatest variations in environmental conditions, including enemies, temperature, salinity, organic matter, and oxygen supply."

An analogous and very illustrative example of fluctuation in populations was given in his discussion on resurgent populations. The "bean clam," *Donax*, at La Jolla experienced the following population explosion and decline between the years 1949–1953. In 1949 only one individual per square meter could be found living along the beach. In 1950, the sediment along the coast, in a zone 2–5 meters wide, contained somewhere in excess of 20,000 individuals per square meter. This entire population of living individuals had died by 1953. However, a whole new population could be found on a beach two miles away. The same species experienced a similar history, in the same locality in 1894–1895, 1909–1910, 1913–1915, 1931–1932, 1934, and 1937–1938.

An explanation of the causal effect of a fluctuation in the population of a macro-invertebrate such as *Donax* or of micro-invertebrates such as *Tinoporus* and *Baculogypsina* would necessitate possessing an understanding of the intricate physiological connection between the animals and their environments and especially a comprehension of the delicate parameters which might upset this balance. In the case of *Tinoporus* and *Baculogypsina*, such information does not exist.

Unfortunately, a survey of the literature indicates that very little has been written concerning the life history of individual foraminiferal species although that dealing with the morphological characteristics of the test is vast. This imbalance results in the perpetuation of a mass of incorrect interpretations as to the reasons for the behavior patterns of foraminifera and will continue to do so until it is corrected.

The irregularity of distribution of *Tinoporus* and *Baculogypsina*, in all probability, will not be explained by studying additional samples as suggested by Todd but instead by a complete investigation of the life history of these animals.

SUMMARY AND CONCLUSIONS

Intertidal and shallow-water sediment samples located along two major sections, were studied from the islands of the tropical Pacific Ocean. The first section, in the northern hemisphere, extends from Ishigaki-shima to the Hawaiian Islands and the second, in the southern hemisphere, extends from Bali to Raroia Atoll. Current systems, distances between islands, and faunal distribution patterns permit a division of the Pacific into four sectors (Fig. 1).

The homogeneity of certain elements of the intertidal and shallow-water foraminiferal fauna of the tropical Pacific as well as the restrictive distribution of others are significant characteristics of the study area. Sixty-seven percent of the benthonic species listed in Table 1 are distributed throughout Sectors I and II while 30 percent are common to Sectors I, II, and III, 14 percent to Sectors I, II, and IV, and 10 percent to Sectors I, II, III, and IV. The low percentages of the last three combinations in comparison to the first is probably due to the paucity of samples (a total of five) from Sectors III and IV. Seven processes of dispersal are discussed to explain the eurytopic distribution exhibited by the benthonic foraminifera.

The foraminifera probably are dispersed by several processes. Future controlled experiments and direct field observations will enable foraminiferal students to enumerate them.

The fact that the methods of dispersal are not well known does not negate the observation that these species have eurytopic distributions making these animals potential index foraminifera of widely separated shallow-water deposits.

A hypothesis is advanced to explain the restricted distribution of *Tinoporus* (*Calcarina*) and *Baculogypsina*. It is based on the supposition that these genera possess a short-lived zygotic pelagic stage and that they are in a delicate balance with their environment. The irregular distribution of the genera in their existing stenotopic range is partially contended with by reviewing the phenomenon of fluctuations in the populations of invertebrates.

TAXONOMY

Two major taxonomic problems have come to the attention of the author during the course of this investigation. The first deals with the taxonomic status of *Calcarina* and *Tinoporus* and the second with the relationship between *Discorbis*, *Tretomphalus*, and *Cymbaloporetta*.

The validity of the generic names *Calcarina* and *Tinoporus* has been a source of debate for many years. The author disposes of the question in the following manner. When d'Orbigny erected the genus *Calcarina* in 1826 he included *Calcarina spengleri* (Gmelin) and

Calcarina calcar, plus several other species. The argument that *Calcarina calcar* is the type species by rule of absolute tautonymy is incorrect for two reasons. First, the word *calcar* is not identical to *Calcarina* and therefore is not tautonymic. Second, *C. calcar* was not properly erected in that it was not accompanied by either a description or figure. Therefore, Parker and Jones (1859), who designated *Calcarina spengleri* as the type species, are justified in this action, for they are the first revisors. However, *Calcarina* is the junior subjective synonym of *Tinoporus* for the following reasons:

Tinoporus was erected by Denys de Montfort in 1808. The genoholotype was *Tinoporus baculatus* Denys de Montfort. An examination of type figures reveals that *T. baculatus* is synonymous with *Nautilus spengleri* Gmelin 1791. Therefore, *Tinoporus spengleri* becomes the genoholotype of *Tinoporus*. This results in both *Tinoporus* and *Calcarina* having *spengleri* as their genoholotype. Due to the fact that *Tinoporus* was erected first (1808 as compared to 1826), *Calcarina* becomes the junior subjective synonym of *Tinoporus*. Structural differences in test observed by earlier workers and used to differentiate these genera were more probably due to an alternation of generation than a differentiation in evolution.

Myers (1943) has observed that there is a close relationship between the *Discorbis*, *Tretomphalus*, and *Cymbaloporetta* groups. This relationship might lead, in the future, to the complete absorption of the latter two by the former. However, until the complete morphological cycle is understood for all the involved species in all environments there seems to be no justification for putting genera and species in synonymy with each other.

Direct observations of tests indicate that *Tretomphalus grandis* is the pelagic stage of the megalospheric *Cymbaloporetta squammosa*. *Cymbaloporetta bradyi* and *C. tabellaeformis* are probably part of the morphological cycle but proof of this is not available. The questions as to whether or not the microspheric stage is discorbian and if so what species of *Discorbis* is involved act as stopgaps to an effective solution of this taxonomic problem.

Tretomphalus bulloides and *Discorbis orbicularis* seem also to be closely related and possibly are different stages of one species, but again, absolute proof is not available.

Although none of the above species or genera have been put into synonymy, their close morphological relationship is emphasized by their proximity in the fauna list.

FAUNAL REFERENCE LIST

The faunal reference list contains both the current and original (appearing in that order) names for the species listed in Table 1. The information was extracted from Ellis and Messina's *Catalogue of Foraminifera* (1940–1962).

Acervulina inhaerens Schultze, 1854, Organismus Polythal., p. 68, pl. 6, fig. 12.

Alveolina melo (Fichtel and Moll) = *Nautilus melo* Fichtel and Moll, 1798, Test. Micr., p. 118, pl. 24, figs. a–h.

Ammonia beccarii (Linnaeus) = *Nautilus beccarii* Linnaeus, 1758, Syst. Nat., ed. 10, v. 1, p. 710.

Amphistegina lessonii d'Orbigny, 1826, Ann. Sci. Nat., ser. 1, v. 7, p. 304, Modèles no. 98; Parker, Jones, and Brady, 1865, Ann. Mag. Nat. Hist., v. 16, ser. 3, p. 14, pl. 3, fig. 92 (after d'Orbigny's model).

Angulogerina carinata Cushman, 1927, California Univ., Scripps Inst. Oceanography Bull., Tech. Ser., v. 1, p. 159, pl. 4, fig. 3.

Anomalina maculosa Todd, 1957, U.S. Geol. Survey Prof. Paper 280-H, p. 296, pl. 92, figs. 12a–c.

Archaias angulatus (Fichtel and Moll), 1798, Test. Micr., p. 113, pl. 22, figs. a–e.

Articulina sagra d'Orbigny, 1839, in: de la Sagra, Hist. Phys. Pol. Nat. Cuba, Foraminifères, v. 8, p. 183, pl. 9, figs. 23–26.

Baculogypsina sphaerulata (Parker and Jones), 1860, Ann. Mag. Nat. Hist., v. 6, ser. 3, p. 33, 38.

Baggina indica (Cushman), 1921, U.S. Natl. Mus. Bull., v. 4, no. 100, p. 332.

Bigenerina robusta Brady, 1881, Part III, Quart. Jour. Micros. Sci., v. 21, p. 53.

Bolivina compacta Sidebottom = *Bolivina robusta* Brady var. *compacta* Sidebottom, 1905, Part II, Manchester Let. Philos. Soc., Mem. Proc., v. 49, no. 5, p. 15, pl. 3, figs. 7a–b.

Bolivina rhomboidalis (Millett) = *Textulia rhomboidalis* Millett, 1899, Part VI, Royal Micros. Soc. London Jour., p. 559, pl. 7, figs. 4a–b.

Bolivina striatula Cushman, 1922, Carnegie Inst. Washington Pub. 311 (Dept. Marine Biol., Papers, v. 17), p. 27, pl. 3, fig. 10.

Bolivina tortuosa Brady, 1881, Part III, Quart. Jour. Micros. Sci., v. 21, p. 57.

Buliminella milletti Cushman, 1933, Cushman Lab. Foram. Research, Contr., v. 9, pt. 4, no. 137, p. 78, pl. 8, figs. 5–6.

Cassidulina minuta Cushman, 1933, Cushman Lab. Foram. Research, Contr., v. 9, pt. 4, no. 132, p. 92, pl. 10, fig. 3.

Cibicides lobatulus (Walker and Jacob) = *Nautilus lobatulus* Walker and Jacob, 1798, in: Kanmacher, F., Adam's Essays on the Microscope, p. 642, pl. 14, fig. 36 (3 figs. after Walker and Boys).

Cibicides mayori (Cushman) = *Truncatulina mayori* Cushman, 1924, Carnegie Inst. Washington Pub. 342 (Dept. Marine Biol., Papers, v. 21), p. 39, pl. 12, figs. 3–4.

Clavulina multicamerata Chapman = *Clavulina parisiensis* d'Orbigny var. *multicamerata* Chapman, 1907, Quekett Micr. Club Jour., ser. 2, v. 10, no. 61, p. 127, pl. 9, fig. 5.

Clavulina pacifica Cushman, 1924, Carnegie Inst. Washington Pub. 342 (Dept. Marine Biol., Papers, v. 21), p. 22, pl. 6, figs. 7–11.

Cornuspira involvens (Reuss) = *Operculina involvens* Reuss, 1850, Denkschr. Akad. Wiss., Wien, v. 1, p. 370, pl. 46, fig. 20.

Cymbaloporetta bradyi Cushman = *Cymbaloporetta poeyi* d'Orbigny var. *bradyi* Cushman, 1915, U.S. Natl. Mus. Bull. 71, p. 25, pl. 10, fig. 2; pl. 14, fig. 2.

Cymbaloporetta squammosa (d'Orbigny) = *Rosalina squammosa* d'Orbigny, 1839, in: de la Sagra, Hist. Physiq. Pol. Nat. Cuba, Foraminifères, v. 8, p. 91, pl. 3, figs. 12–14.

Cymbaloporetta tabellaeformis (Brady) = *Cymbalopora tabellaeformis* Brady, 1884, Rept. Voyage Challenger, Zool., v. 9, pt. 22, p. 637, pl. 102, figs. 15–18.

Discorbis mirus (Cushman) = *Discorbis mira* Cushman, 1922, Carnegie Inst. Washington Pub. 311 (Dept. Marine Biol., Papers, v. 17), p. 39, pl. 6, figs. 10–11.

Discorbis nipponica (Ishizaki) = *Valvulineria nipponica* Ishizaki, 1944, Nat. Hist. Soc. Taiwan, v. 34, no. 244, p. 103, pl. 3, figs. 7a–c.

Discorbis opima Cushman, 1933, Cushman Lab. Foram. Research, Contr., v. 9, pt. 4, no. 137, pl. 9, fig. 3.

Discorbis orbicularis (d'Orbigny) = *Rosalina orbicularis* d'Orbigny, 1850, Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés, v. 2, p. 408.

Discorbis orientalis Cushman, 1925, Bernice P. Bishop Mus., Honolulu, Bull. 27, p. 130.

Elphidium advenum (Cushman) = *Polystomella advena* Cushman, 1922, Carnegie Inst. Washington Pub. 311 (Dept. Marine Biol., Papers, v. 17), p. 56, pl. 9, figs. 11–12.

Elphidium craticulatum (Fichtel and Moll) = *Nautilus craticulatus* Fichtel and Moll, 1798, Test. Micr., p. 51, pl. 5, figs. h–k.

Elphidium sagrum (d'Orbigny) = *Polystomella sagra* d'Orbigny, 1839, Foraminifères, in: de la Sagra, Hist. Phys. Pol. Nat. Cuba, v. 8, p. 55, pl. 6, figs. 19–20.

Elphidium mexicanum Kornfeld = *Elphidium incertum* Williamson var. *mexicanum* Kornfeld, 1931, Stanford Univ. Dept. Geol. Contr., v. 1, p. 89, pl. 16, figs. 1–2.

Epistomaroides rimosa (Parker and Jones) = *Discorbina rimosa* Parker and Jones, 1862, in: Carpenter, Intro. Study Foram., Royal Soc. London, p. 205.

Epistominella tubulifera (Heron-Allen and Earland) = *Truncatulina tubulifera* Heron-Allen and Earland, 1915, Zool. Soc. London Trans., v. 20, p. 710, pl. 52, figs. 37–40.

Eponides orientalis Asano, 1937, Sendai, Saito Ho-on Kai Mus., Res. Bull. 13, p. 117, pl. 16, figs. 8a–c.

Fissurina lagenoides Williamson = *Entosolenia marginata* Walker var. *lagenoides* Williamson, 1858, Royal Soc. London, p. 11, pl. 1, figs. 25–26.

Fissurina marginata (Montagu) = *Vermiculum marginatum* Montagu, 1803, Test. Brittanica, p. 524.

Gaudryina quadrangularis Bagg, 1908, U.S. Natl. Mus. Proc., v. 34, no. 1603, p. 133, pl. 5, fig. 1.

Gaudryina rugulosa Cushman, 1932, U.S. Natl. Mus. Bull. 161, p. 15, pl. 4, fig. 1.

Gaudryina (Siphogaudryina) siphonifera (Brady) = *Textularia siphonifera* Brady, 1881, Part III, Quart. Jour. Micros. Sci., London, v. 21, p. 53.

Globigerinoides conglobata (Brady) = *Globigerina conglobata* Brady, 1879, Quart. Jour. Micros. Sci., v. 19, p. 286.

Globigerinoides sacculifera (Brady) = *Globigerina sacculifera* Brady, 1877, Geol. Mag., decade 2, v. 4, p. 535.

Globigerinoides triloba (Reuss) = *Globigerina triloba* Reuss, 1850, Denkschr. Akad. Wiss. Wien, v. 1, p. 314, pl. 47, fig. 11.

Globorotalia menardii (d'Orbigny) = *Rotalia (Rotalie) menardii* d'Orbigny, 1826, Ann. Sci. Nat., ser. 1, v. 7, p. 304, Modèles no. 98.

Globorotalia murrayi (Heron-Allen and Earland) = *Rotalia murrayi* Heron-Allen and Earland, 1915, Part II, Zool. Soc. London Trans., v. 20, pt. 17, p. 721, pl. 53, figs. 27–34.

Gypsina vesicularis Parker and Jones = *Orbitolina concava* Lamarck var. *vesicularis* Parker and Jones, 1860, Ann. Mag. Nat. Hist., ser. 3, v. 6, p. 31–38.

Hastigerina aequilateralis (Brady) = *Globigerina aequilateralis* Brady, 1879, Quart. Jour. Micros. Sci., v. 19, p. 285.

Hauerina ornatissima (Karrer) = *Quinqueloculina ornatissima* Karrer, 1868, Sitzber. Akad. Wiss. Wien, v. 58, pt. 1, p. 151, pl. 3, fig. 2.

Heterostegina depressa d'Orbigny, 1826, Ann. Sci. Nat., ser. 1, v. 7, p. 305, pl. 17, figs. 5–7.

Loxostomum limbatum (Brady) = *Bolivina limbata* Brady, 1881, Part III, Quart. Jour. Micros. Sci., v. 21, p. 57.

Marginopora vertebralis Blainville, 1834, Manuel d'Actinologie ou de Zoophytologie, p. 412, pl. 69, fig. 6.

Miliolinella australis (Parr) = *Quinqueloculina australis* Parr, 1933, Part I, Royal Soc. Victoria Proc., v. 44, p. 7, pl. 1, fig. 8.

Miliolinella circularis (Bornemann) = *Triloculina circularis* Bornemann, 1855, Geol. Gesell. Zeitschr., v. 7, pt. 2, p. 349, pl. 19, fig. 4.

Nonion grateloupi (d'Orbigny) = *Nonionina grateloupe* d'Orbigny, 1839, in: de la Sagra, Hist. Physiq. Pol. Nat. Cuba, Foraminifères, v. 8, pl. 6, figs. 6–7.

Peneroplis arietina (Batsch) = *Nautilus (Lituus) arietinus* Batsch, 1791, Conch. Seesandes, p. 3, 6, pl. 6, figs. 15a–b.

Peneroplis carinatus d'Orbigny, 1839, Voyage dans l'Amérique mèridionale, v. 5, pt. 5 Foraminifères, p. 33, pl. 3, figs. 7–8.

Peneroplis pertusus (Forskål) = *Nautilus pertusus* Forskål, 1775, Descr. Anim., no. 65, p. 125.

Pileolina (?) patelliformis (Brady) = *Discorbina patelliformis* Brady, 1884, Rept. Voyage Challenger, Zool., v. 9, pt. 22, p. 647, pl. 88, fig. 3; pl. 89, fig. 1.

Planispirinella exigua (Brady) = *Haverina exigua* Brady, 1879, Quart. Jour. Micros. Sci., v. 19, p. 267.

Planorbulina acervalis Brady, 1884, Rept. Voyage Challenger, Zool., v. 9, pt. 22, p. 657, pl. 92, fig. 4.

Pyrgo denticulata Brady = *Biloculina ringens* Lamarck var. *denticulata* Brady, 1884, Rept. Voyage Challenger, Zool., v. 9, p. 143, pl. 3, figs. 4–5.

Quinqueloculina agglutinans d'Orbigny, 1839, in: de la Sagra, Hist. Physiq. Pol. Nat. Cuba, Foraminifères, v. 8, pl. 12, figs. 11–13.

Quinqueloculina bosciana, 1839, in: de la Sagra, Hist. Physiq. Pol. Nat. Cuba, Foraminifères, v. 8, pl. 11, figs. 22–24.

Quinqueloculina crassa d'Orbigny, 1921, U.S. Natl. Mus. Bull., v. 4, no. 100, p. 432, pl. 89, fig. 4.

Quinqueloculina granulocostata Germeraad, 1946, in: Rutten and Hotz, Geol. Pet. and Paleo. Results, ser. 3 (Geol.), no. 2, p. 63.

Quinqueloculina lamarckiana d'Orbigny, 1939, in: de la Sagra, Hist. Physiq. Pol. Nat. Cuba, Foraminifères, v. 8, pl. 11, figs. 14–15.

Quinqueloculina parkeri (Brady) = *Miliolina parkeri* Brady, 1881, Part III, Quart. Jour. Micros. Sci., v. 21, p. 46.

Quinqueloculina plana d'Orbigny, 1850, Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés, v. 2, p. 409.

Quinqueloculina plana d'Orbigny, 1839, in: de la Sagra, Hist. Physiq. Pol. Nat. Cuba, Foraminifères, v. 8, pl. 11, figs. 25–27.

Quinqueloculina protea (Parker) = *Massilina protea* Parker, 1953, Cushman Found. Foram. Research Spec. Pub. 2, p. 10, pl. 2, figs. 1–4.

Quinqueloculina samoaensis Cushman, 1924, Carnegie Inst. Washington Pub. 342 (Dept. Marine Biol. Papers, v. 21), p. 59, pl. 21, figs. 4–7.

Rectobolivina tombigbeensis (Hadley) = *Bifarina timbigbeensis* Hadley, 1935, Bull. Am. Paleontology, v. 22, no. 74, p. 8, pl. 1, fig. 7.

Reussella simplex (Cushman) = *Trimosina simplex* Cushman, 1929, Washington Acad. Sci. Jour., v. 19, no. 8, p. 158, fig. 2.

Rotaliammina mayori Cushman, 1924, Carnegie Inst. Washington Pub. 342 (Dept. Marine Biol. Papers, v. 21), p. 11, pl. 1, figs. 4–5.

Siphogenerina raphanus (Parker and Jones) = *Uvigerina* (*Sagrina*) *raphanus* Parker and Jones, 1865, Royal Soc. London Philos. Trans., v. 155, p. 364, pl. 18, figs. 16a–b.

Siphonina tubulosa Cushman, 1924, Carnegie Inst. Washington Pub. 342 (Dept. Marine Biol. Papers, v. 21), p. 40, pl. 13, figs. 1–2.

Siphoninoides echinata (Brady) = *Planorbulina echinata* Brady, 1879, Quart. Jour. Micros. Sci., v. 19, p. 283, pl. 8, figs. 31a–c.

Spirillina denticulata Brady = *Spirillina limbata* Brady var. *denticulata* Brady, 1884, Rept. Voyage Challenger, Zool., v. 9, pt. 22, p. 632, pl. 85, fig. 17.

Spirolina acicularis (Batsch) = *Nautilus* (*Lituus*) *acicularis* Batsch, 1791, Conch. Seesandes, p. 3, 6, pl. 6, figs. 16a–b.

Spiroloculina acescata Cushman = *Spiroloculina grateloupi* d'Orbigny var. *acescata*, 1932, U.S. Natl. Mus. Bull. 161, pt. 1, p. 35, pl. 9, fig. 2.

Spiroloculina angulata Cushman, 1944, Cushman Found. Foram. Research, Spec. Pub. 11, p. 50, pl. 7, figs. 18–22.

Spiroloculina grateloupi d'Orbigny, 1852, Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés, v. 3, p. 161.

Textularia candeiana d'Orbigny, 1839, in: de la Sagra, Hist. Physiq. Pol. Nat. Cuba, Foraminifères, v. 8, p. 143, pl. 1, figs. 25–27.

Textularia conica d'Orbigny, 1839, in: de la Sagra, Hist. Physiq. Pol. Nat. Cuba, Foraminifères, v. 8, p. 143, pl. 1, figs. 19–20.

Tinoporus calcar (d'Orbigny) = *Calcarina calcar* d'Orbigny, 1826, Ann. Sci. Nat., ser. 1, v. 7, p. 276.

Tinoporus delicata (Todd and Post) = *Calcarina delicata* Todd and Post, 1954, U.S. Geol. Survey Prof. Papers 260-N, p. 563, pl. 201, figs. 5–6.

Tinoporus hispida (Brady) = *Calcarina hispida* Brady, 1876, Royal Irish Acad. Proc., ser. 2, pt. 6, p. 589.

Tinoporus spengleri (Gmelin) = *Nautilus spengleri* Gmelin, 1791, Linné Syst. Nat., ed. 13, v. 1, pt. 6, p. 3371.

Tretomphalus bulloides (d'Orbigny) = *Rosalina bulloides* d'Orbigny, in: de la Sagra, Hist. Physiq. Pol. Nat. Cuba, Foraminifères, v. 8, p. 98, pl. 3, figs. 2–5.

Tretomphalus grandis Cushman, 1934, Cushman Lab. Foram. Research Contr., v. 10, pt. 4, p. 95, pl. 11, fig. 10; pl. 12, figs. 23–24.

Triloculina affinis d'Orbigny, 1852, Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés, v. 3, p. 161.

Triloculina bertheliniana (Brady) = *Miliolina bertheliniana* Brady, 1884, Rept. Voyage Challenger, Zool., v. 9, p. 166, pl. 114, fig. 2.

Triloculina bikiniensis Todd, 1954, U.S. Geol. Survey Prof. Papers 260-H, p. 338, pl. 85, fig. 19.

Triloculina kerimbatica (Heron-Allen and Earland) = *Miliolina kerimbatica* Heron-Allen and Earland, 1915, Part II, Zool. Soc. London Trans., v. 20, pt. 17, p. 574, pl. 43, figs. 13–23.

Triloculina oblonga (Montagu) = *Vermiculum oblongum* Montagu, 1803, Test. Brittanica, p. 522, pl. 14, fig. 9.

Triloculina oceanica Cushman, 1932, U.S. Natl. Mus. Bull. 161, p. 54, pl. 12, fig. 3.

Triloculina striolata Cushman, 1918, Carnegie Inst. Washington Pub. 213 (Dept. Marine Biol. Papers, v. 9), p. 290, pl. 96, figs. 3a–c.

Triloculina subgranulata Cushman, 1918, Carnegie Inst. Washington Pub. 213 (Dept. Marine Biol. Papers, v. 9), p. 290, pl. 96, figs. 4a–c.

Triloculina terquemiana (Brady) = *Miliolina terquemiana* Brady, 1884, Rept. Voyage Challenger, Zool., v. 9, pt. 22, p. 166, pl. 114, fig. 1.

Triloculina tricarinata d'Orbigny, 1826, Ann. Sci. Nat., ser. 1, v. 7, p. 299.

Trochammina pacifica Cushman, 1925, Cushman Lab. Foram. Research Contr., v. 1, no. 11, p. 39.

Valvulina davidiana Chapman, 1900, Linnean Soc. London Jour., Zoology, v. 28, no. 179, p. 9, pl. 1, fig. 4.

REFERENCES

Allee, W. C., and Schmidt, K. P., 1951, Ecological Animal Geography: New York, John Wiley and Sons, Inc., 715 p.

Bandy, O. L., 1960, Rafting of benthonic foraminifera: Internat. Geol. Cong., 21st., Copenhagen, vol. of abstracts, 241 p.

Brönniman, P., 1949, Pflanzenbewohnende tropische Foraminiferen nebst Beschreibung von *Cymbalopora tobagoensis* n. sp.: Natur. Gesell. Basel Verh., v. 60, p. 179–185.

Chapman, F., 1900, Foraminifera from the lagoon at Funafuti: Linnean Soc. London Jour., Zoology, v. 28, p. 111–210.

Coe, W. R., 1957, Fluctuations in littoral populations: Geol. Soc. America Mem. 67, v. 1, p. 935–940.

Cromwell, T., and Austin, T. S., 1954, Mid-Pacific oceanography, Parts II and III, transequatorial waters, 1950–51. Special Scientific Report—Fisheries, no. 131.

Cushman, J. A., Todd, R., and Post, R. J., 1954, Bikini and nearby atolls, Part 2, Oceanography (Biologic): U.S. Geol. Survey Prof. Paper 260-H, p. 799–861.

Ellis, B. F., and Messina, Angelina R., 1940–62, Catalogue of foraminifera: Am. Mus. Nat. History.

Emery, K. O., 1956, Marine geology of Johnston Island and its surrounding shallows, central Pacific Ocean: Geol. Soc. America Bull., v. 67, p. 1505–1520.

Fuller, H. J., and Oswald, T., 1958, College botany: New York, Henry Holt and Co., 993 p.

Glaessner, M. F., 1947, Principles of micropaleontology (2nd ed.): New York, John Wiley and Sons, 296 p.

Graham, J. J., and Militante, P. J., 1959, Recent foraminifera from the Puerto Galera area, Northern Mindoro, Philippines: Stanford Univ. Pub. Geol. Sci., v. 6, 171 p.

Headlee, L., 1961, Transportation of foraminifera by ducks: Southern California Univ., unpub. term paper.

Johnson, M. W., 1949, Zooplankton as an index of water exchange between Bikini Lagoon and the open sea: Am. Geophys. Union Trans., v. 30, p. 238–244.

Lessard, R. H., 1960, Rafting of marine animals by marine algae: Southern California Univ., unpub. term paper.

Meyers, G. S., 1939, The fish fauna of the Pacific Ocean with special reference to zoogeographical regions and distribution as they affect the international aspects of the fisheries: Pacific Sci. Cong., 6th Proc., v. 3, p. 201–210.

MONFORT, D. DE, 1808, Conchyliologie systematique et clasification methodique des coquilles: tome 1, p. 147.

MORSKOI ATLAS, 1953, Voenno-morskoe ministerstvo: Russia, 83 p., pls. 1–76.

MYERS, E. H., 1943, Biology, ecology, and morphogenesis of a pelagic foraminifera: Stanford Univ. Pub. Biol. Sci., v. 9, 30 p.

MYERS, E. H., and COLE, W. S., 1957, Foraminifera: Geol. Soc. America Mem. 67, v. 1, p. 1075–1082.

OKAMURA, K., 1932, The distribution of marine algae in Pacific waters: Records of Oceanographic works in Japan, v. 4, p. 30–150.

PARKER, W. K., and JONES, T. R., 1859, I. On the species enumerated by Linnaeus and Gmelin: Ann. Mag. Nat. History, ser. 3, v. 3, p. 474–482.

RESIG, J. M., 1969, Paleontological investigations of deep borings on the Ewa Plain, Oahu, Hawaii: Hawaii Inst. Geophysics-69-2, p. 1–99.

REVELLE, R., and FAIRBRIDGE, R., 1957, Carbonates and carbon dioxide: Geol. Soc. America Mem. 67, v. 1, p. 239–296.

SVERDRUP, H. U., JOHNSON, M. W., and FLEMING, R. H., 1942, The oceans: New York, Prentice-Hall, 1087 p.

THORSON, G., 1957, Bottom communities (sublittoral or shallow shelf): Geol. Soc. America Mem. 67, v. 1, p. 461–534.

TODD, R., 1960, Some observations on the distribution of Calcarina and Baculogypsina in the Pacific: Tohoku Univ. Sci. Rep., 2nd Ser. (Geol.), Spec. Vol., no. 4, p. 100–107, pl. 10.

———, 1961, Foraminifera from Onotoa Atoll, Gilbert Islands: U.S. Geol. Survey Prof. Paper 354-H, p. 171–191, pls. 22–25.

TODD, R., and LOW, E., 1960, Smaller foraminifera from Eniwetok drill holes: U.S. Geol. Survey Prof. Paper 260-X, p. 798–861, pls. 255–264.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 59–67, 1980

PLEISTOCENE OCCURRENCE OF *MELONIS POMPILIOIDES* IN THE CALIFORNIA BORDERLAND AND ITS IMPLICATION FOR FORAMINIFERAL PALEOECOLOGY

GREGG H. BLAKE[1] AND ROBERT G. DOUGLAS
Department of Geological Sciences, University of Southern California, Los Angeles, California 90007

ABSTRACT

Prevalent concepts of foraminiferal paleobathymetric interpretations are based on the modern distribution of living benthic faunas and assume that species depth habitat have not changed with time. Recent studies by Streeter (1973), Schnitker (1974), and Lohmann (1978), suggest that the distribution of benthic foraminifera is not as static in space and time as had been previously believed. Present-day deep sea benthic foraminiferal assemblages appear to be controlled more by the distribution of bottom water masses than by bathymetry.

Melonis pompilioides (Fichtel and Moll) is a benthic foraminifer presently inhabiting lower bathyal to abyssal environments. The species is described by Bandy and Chierici (1966) as a typical example of an isobathyal species. The use of *M. pompilioides* as a bathymetric indicator in modern and ancient environments rests upon two assumptions: First, that it is an isobathyal species and its upper depth limit is approximately the same in different oceans. Second, that the depth habitat of the species, at least its upper depth limit, has not changed with time.

Data from the southern California Borderland support a different model, one which explains the Pleistocene distribution of *M. pompilioides* as the result of faunal migration. Late Pleistocene and Holocene occurrences of the species in basins with sill depths shallower than 2,300 m, the present-day upper depth limit of the species, is evidence of water-mass changes in the last 16,000 years. The apparent bathymetric change of the species is a faunal response to changing environmental conditions rather than evidence of tectonic uplift of the seafloor.

INTRODUCTION

Benthic foraminifera are commonly characterized in terms of their depth habitats and used as a basis for bathymetric zonation in modern and ancient environments. Bandy and Echols (1964) and Bandy and Chierici (1966) introduced the concept of isobathyal and heterobathyal species. Isobathyal species are benthic foraminifers with the same upper depth limit (UDL) in different oceanic areas whereas heterobathyal species are those with different upper depth limits in contrasting oceanic areas. These authors proposed that the distribution of isobathyal species is controlled by water depth rather than other physical variables and therefore of particular importance in establishing depth zonation in modern marine environments. Subsequently, the concept of isobathyal species has been repeatedly applied as a paleoecologic tool in estimating paleobathymetry.

Information has accumulated in the past several years (Streeter, 1973; Schnitker, 1974; Douglas, 1974, 1975: Douglas and Heitman (in press)) suggesting that the vertical and horizontal distribution of benthic fo-

---

[1] Current address: Paleontology and Stratigraphy Section, Union Oil Company of California, P.O. Box 6176, Ventura, California 93006.

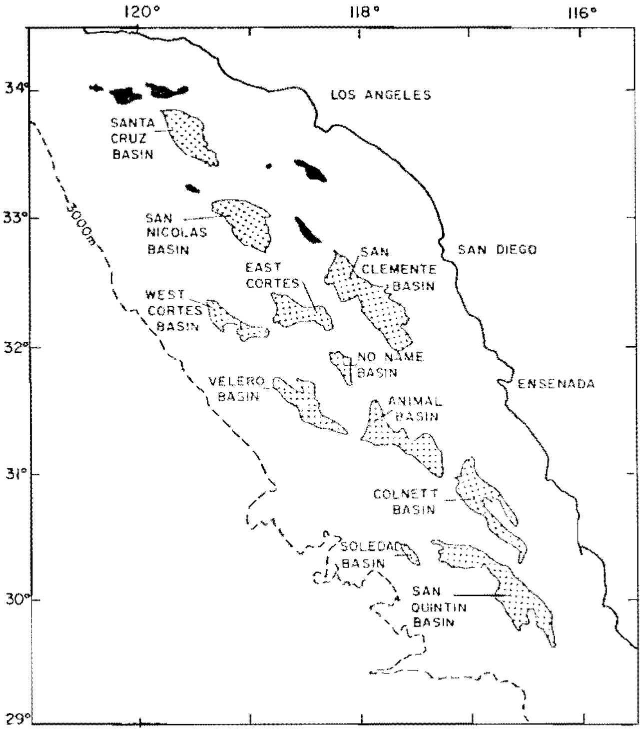


FIGURE 1
Location of basins in the southern California Borderland investigated in this study. The basins to the south, west of Baja California, are generally deeper with deeper sill depths than the basins to the north (See Table 1 for water depths).

raminifera change in space and time. We believe that the data challenges the validity of some paleoecologic concepts based on empiric observations which are used for quantitative assessment of paleodepth. Here we focus on the concept of isobathyal species and its use as a means for evaluating paleodepths.

In the following discussion we briefly review the evidence for the UDL of *Melonis pompilioides* in the present-day ocean and how it has been used as a paleodepth indicator. We then examine the late Pleistocene occurrence of the species in the California Borderland and propose a new interpretation of its depth habitat in time. Finally, we consider the results of our findings on the concept of isobathyal species and its implication for paleoecology.

ACKNOWLEDGMENTS

This paper is part of a long term research project on the ecology and paleoecology of the California Borderland supported by research funds from the National Geographic Society and the National Science Foundation, Oceanography Section, grants OCE 76-01435 and OCE 76-00156. Ship time was provided by block funding from the National Science Foundation to the University of Southern California. We appreciate comments and criticisms of the manuscript by a number of colleagues, especially Charles Pflum, J. C. Ingle, Fay Woodruff and James Kennett.

STRATIGRAPHIC-AGE CONTROL

Seventeen cores from basins in the southern California Borderland were examined to determine the Pleistocene and Holocene occurrences of *Melonis pompilioides* (Fig. 1) (Table 1). In addition, both the benthic and planktic foraminiferal populations were identified and counted. The coiling ratio of *Neogloboquadrina pachyderma* (Ehrenberg) was determined to establish stratigraphic and climatic intervals.

Primary importance in this study has been placed on the use of *N. pachyderma* as a biostratigraphic datum. Radiometric dating (C^{14}) of basin cores off southern California has shown that the last shift in coiling direction of *N. pachyderma* from sinistral-coiling populations to dextral-coiling populations occurred 11,000 to 12,000 ys. B.P. (Bandy, 1960). The change from dextral-coiling (currently found living offshore southern California) to sinistral-coiling populations represents a southward migration of the subarctic water masses and a reorganization of the water mass distribution of the borderland region. This occurred during the last glacial episode, 18,000 to 11,000 ys. B.P. (Bandy, 1967). It is interesting to note that the occurrence of *Melonis pompilioides* in cores from basins with water depths shallower than 2,300 m is restricted to sediments that also contain sinistral-coiling specimens of *Neogloboquadrina pachyderma*.

Stratigraphic ages were also determined by studying regular patterns in the maximum carbonate content with depth in the core. Gorsline and others (1968) obtained radiocarbon dates of 7,500 ys. B.P. for the first prominent carbonate peak downcore. In addition, an absolute chronology was obtained from Bandy (1960) which includes C^{14} dates taken on cores from several different basins in the southern California Borderland.

The resultant stratigraphic control for this paper is based on three different datums: a carbonate maxima at 7,500 ys. B.P., change in coiling-populations of *Neogloboquadrina pachyderma* at 12,000 ys. B.P., a lesser carbonate peak at 17,000 ys., and absolute C^{14} dates.

Sedimentation rates were determined from plotting these datums against their depth in the cores and then compared to rates previously calculated by Gorsline and others (1968) and Gorsline and Prensky (1975). The position of the last occurrence of *Melonis pom-*

TABLE 1

		Water depth (m)		Depth in core (cm) to stratigraphic levels used for age control			Last occurrence of *Melonis pompilioides*	
Core	Basin	Sill	Core	7,500 ys.	12,000 ys.	17,000 ys.	Depth in core	Age (ys.)
AHF 14690	Colnett	2,100	2,057	20	30 (35)	140	30	11,200
AHF 14696	N. San Quintin	2,290	2,304	60	80 (75)	180	0	P
AHF 16827	Animal	1,920	2,012	20	50 (65)	170	50	10,500
AHF 16832	No name	1,550	1,829	80	120 (135)	330	160	12,600
AHF 18017	West Cortes	1,340	1,732	60	110	—	NP	
AHF 16830	Velero	1,870	2,451	70	100 (105)	250	110	12,200
AHF 16635	S. San Quintin	2,290	2,780	60	80 (85)	180	70	9,200
AHF 14486	San Clemente	1,780	1,971	15	100	220	95	11,800
AHF 14682	Soledad	2,290	3,109	20	45	130	40	11,100
AHF 14684	Outer	(2,000)	2,012	10	35	150	30	11,400
AHF 14685	Outer	(2,000)	2,048	20	85	130	40	9,400
AHF 14689	Colnett	2,100	2,286	60	110	330	100	11,000
AHF 14687	Colnett	2,100	2,140	20	65	130	40	10,000
AHF 16831	Velero	1,870	2,304	30	85	180	70	10,800
AHF 1983	East Cortes	1,420	1,975	—	—	—	88	16,300
AHF 1981	Long	1,690	1,925	—	—	—	110	13,200
AHF 10709	Santa Cruz	1,070	1,865	120	—	—	NP	

pilioides was plotted against its depth in the core and the timing of the last occurrence was established.

BASINS OF THE SOUTHERN CALIFORNIA BORDERLAND

There is a unique relationship between the basins in the southern California Borderland where the sill depth determines the water mass parameters of the basin (Emery, 1960). That is, the physical properties (temperature, salinity, oxygen, etc.) characteristic of the water mass located at the sill depth of the basin will remain relatively uniform throughout the basinal environment. This allows the physical parameters of the basinal waters to depart from values associated with similar depths in the open ocean. Basinal waters in the borderland range from 0.8° to 2.0°C warmer and have salinity values 0.2‰ lower than the open ocean. The oxygen values for the different basins are dependent on the sill depth and its relationship to the depth of the oxygen minimum layer.

Further studies have shown that as a result of the interaction between the movement of the different water units across the borderland region, most basins have different "effective sill depth" from the topographic sill depth. In basins with topographic sills shallower than 1,000 m, the hydrographic sill is approximately 50 m shallower, whereas basins with sills deeper than 1,000 m have an effective sill approximately 200 m deeper (Emery, 1960).

A general pattern in the southern California Borderland is that the sill depths of the basins deepen toward the south (Table 1). Since the dominant flow of water across the borderland is towards the north, the sills systematically impede the flow of the deeper water units. Each sill of the basin in the path of water movement towards the north is shallower than the preceding basin; the sill acts as a submerged dam preventing the northward flow of successively shallower layers of bottom water (Emery, 1960).

The hydrographic conditions of the silled basins in the Borderland make these habitats ideal locations to examine the concept of isobathyal species and their relationship to water-mass distribution by studying the response of benthic species to the redistribution of water masses that accompany the glacial to interglacial climatic transitions. If a benthic species is related to depth and not to the water-mass parameters, then there should not be any change in the distribution of the species as a result of the reorganization of the water column during cycles of climatic variations. Because of the relationship between the sill depth and deep water movement, the reorganization of basinal water after the last glacial stage was traced across the borderland and the variation in the benthic populations were recorded.

MELONIS POMPILIOIDES AS AN ISOBATHYAL INDICATOR

Melonis pompilioides is widely regarded as indicative of lower bathyal or abyssal depths in the modern

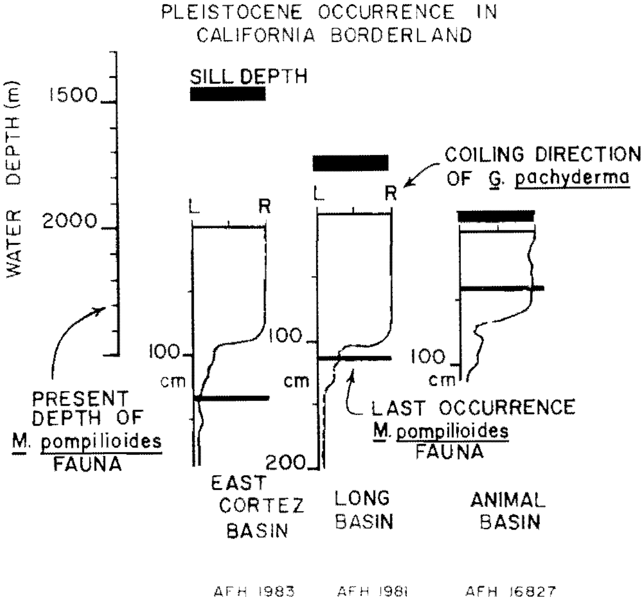


FIGURE 2

Diagram illustrating typical Pleistocene occurrences of *Melonis pompilioides* in cores from basins in the southern California Borderland. The examples are arranged by water depth and show the pattern of coiling direction of *Neogloboquadrina pachyderma* with depth in each core, and the level of disappearance (i.e., first occurrence down core). For example, core AHF 1983 from East Cortes Basin is located in 1,975 m of water, the change from predominately right to left coiling in *N. pachyderma* occurs at 88 cm and specimens of *M. pompilioides* are found below 110 cm in the core. The sill depth of the basin is 1,490 m. Modern occurrences of *M. pompilioides* are found in water depths of about 2,300 m in the borderland.

Note that for basins in which *M. pompilioides* disappears before the major change in coiling direction of *N. pachyderma* (dated as about 12,000 ys. B.P.: Bandy, 1960), basin sill depths approach the present-day bathymetric distribution of the species and the last occurrence becomes progressively younger, i.e., Holocene in age.

ocean. Bandy and Chierici (1966) reported the species UDL at about 2,300 m in the Gulf of Mexico, the Gulf of California and off the coast of California. A similar UDL has been reported for occurrence in modern sediments off Oregon (Kulm and Fowler, 1974). In Antarctic waters, Bandy and Echols (1964) state that the species is particularly prominent below 3,000 m and Echols (1971) does not record it at depths of less than 2,924 m in the Scotia Sea area. The species has its shallowest depth limit at about 2,830 m in the western North Pacific (unpub. data). Records of the species are less common in the Atlantic than in the Pacific and Antarctic. Phleger and others (1953) found *Melonis pompilioides* from depths of 1,995 m or greater in the North Atlantic while the species occurs at depths of 2,020 m in the Gulf of Mexico (Pflum and Frerichs, 1976).

Melonis pompilioides has been reported in modern sediments from depths of less than 2,000 m but such reports involve either fossil occurrences (Crouch, 1952; Natland, 1957) or are different species. Todd (1958) and Murray (1971), for example, list the occurrence of *M. pompilioides* from depths as shallow as 128 m in the British Isles. However, the figures given by these authors show a compressed form with small pores and imperforate sutures that should be referred to as *Nonion formosum* (Williamson) or *N. barleeanus* (Williamson) (Parker, 1958; Phleger and others, 1953). It should be noted that there is some dispute as to whether the robust form with deep umbilicus or the compressed form with straight sides best matches the generalized drawings of Fichtel and Moll (1798). Some European workers consider the type to be the compressed form generally referred to as *N. barleeanus* by many American specialists (P. Ascoli, pers. comm. 1975). We have followed the common practice and herein regard the robust form, such as figured by Bandy (1953, pl. 21, fig. 12), Bandy and Chierici (1966, Fig. 8), Pflum and Frerichs, 1976, pl. 7, Figs. 7, 8) and Lohmann (1978, pl. 1, Figs. 12, 13), as *Melonis pompilioides*.

Taxonomic arguments aside, *Melonis pompilioides* typifies the concept of the isobathyal species and has been widely applied as a means for identifying sediments deposited at lower bathyal or abyssal depths (Bandy and Chierici, 1966; Doyle and Bandy, 1972; Kulm and Fowler, 1974; and Pflum and Frerichs, 1976).

LATE PLEISTOCENE DISTRIBUTION IN THE CALIFORNIA BORDERLAND

Melonis pompilioides is reported from surface sediments in the California Borderland at depths of 2,300 m or greater (Bandy and Chierici, 1966; unpub. data). However, few of these reports discriminate living and dead populations by staining or other methods and some of the occurrences are undoubtedly not modern.

Crouch (1952) and Natland (1957) found specimens of the species in cores from East and West Cortes and Long basins (Fig. 1), basins in which the species is not presently living (Doyle and Bandy, 1972; unpublished data). Later studies discovered occurrences in cores from nearly all of the southern basins in the Borderland in which it is not presently found in surface sediments (Prensky, 1973; Doyle and Bandy, 1972; Morin, 1971) (Fig. 2). The sill depths in these basins range from 1,220 to 2,300 m which would give a much shallower upper depth limit for *M. pompilioides* in the borderland.

Doyle and Bandy (1972) assumed that the upper depth limit of the species has remained unchanged since the Pleistocene and postulated that the basins or sills or both have been uplifted to explain the fossil occurrences (Fig. 3a). Thus, it would appear that an uplift of 500 to more than 900 m has taken place in the Borderland between late Pleistocene and the present. This represents rates of uplift that are more than an order of magnitude higher than the accelerated rates of tectonism documented in southern California by Yeats (1978).

However, there are several problems with this model. First, most of the last appearances of *Melonis pompilioides* in the cores occur close to the change in coiling direction of *Neogloboquadrina pachyderma*, a datum which has been determined to be about 12,000 ys. B.P. (Bandy, 1960; 1967). Thus, most of the uplift has occurred in the latest Pleistocene or Holocene time, in turn requiring average rates of 12 to 16 cm per year to account for the apparent amount of bathymetric change (Doyle and Bandy, 1972). Second, the pattern of uplift suggested by Doyle and Bandy's model fails to explain the pattern of occurrences of *M. pompilioides*, that is, why the species is absent from adjacent basins within the same structural block. Finally, Emery (1960) noted wave-cut terraces on the Patton Escarpment and Santa Rosa-Cortes Ridge which indicate a down-warping of the outer Borderland during the Holocene rather than a major uplift. Furthermore, Yeats (1978) has shown that adjacent portions of the Borderland in southern California are undergoing accelerated rates of uplift.

A NEW MODEL: THE FAUNAL MIGRATION MODEL

A new model, the faunal migration model, is proposed which accounts for the data and requires little or no tectonic movement. The faunal migration model assumes that the distribution of benthic species is related to water-mass distribution, in much the same way as planktic foraminifera are related to surface water-mass character (Bé, 1977) and that the depth habitat of species changes in response to vertical and horizontal changes in water-mass distribution. In this model the depth habitat of *Melonis pompilioides* is assumed to have changed in response to changes in the water-mass distribution that accompanied the transition from glacial to interglacial (Holocene) climates (Fig. 3b).

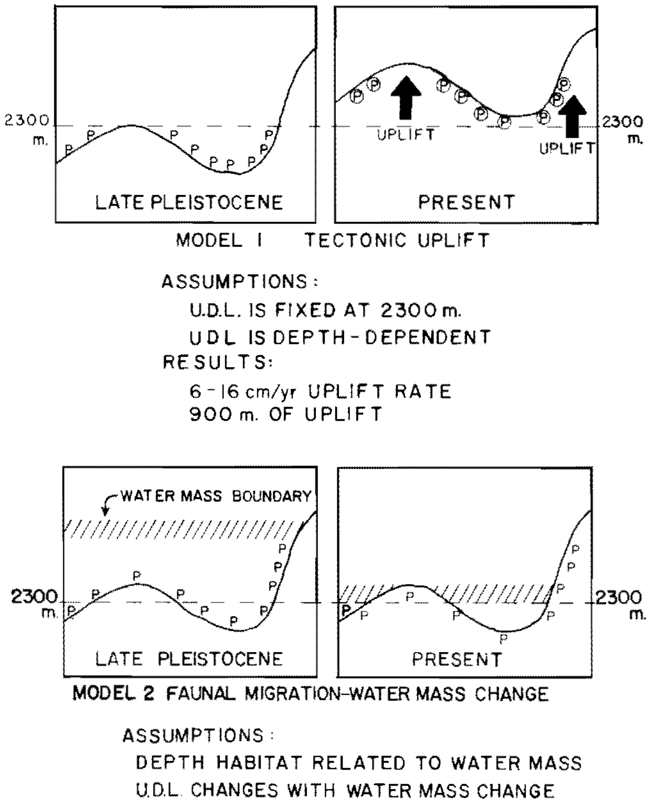


FIGURE 3

Diagrammatic representation of the two models proposed to explain the Pleistocene distribution of *Melonis pompilioides* in cores from the southern California Borderland.

Figure 3a. Tectonic Uplift Model. This model was proposed by Doyle and Bandy (1972) who suggested that the occurrence of the species in cores from basins which are currently shallower than the UDL of the species, about 2,300 m, is evidence of approximately 900 m of uplift since the late Pleistocene. This explanation assumes that *M. pompilioides* is an isobathyal species and that the UDL of the taxon is depth dependent and unchanging with time.

Figure 3b. Faunal Migration Model. This model assumes that the depth range of the species, including its upper depth limit, is directly related to water-mass distribution and that changes in water masses, as caused by climatic fluctuations (e.g., glacial to interglacial conditions) will produce a corresponding shift in the species depth distribution. According to this model, the late Pleistocene and early Holocene occurrences of *M. pompilioides* in basins with sill depths shallower than 2,300 m is evidence of a deepening of the upper boundary of Pacific Deep Water, to which the species is presently restricted, in the past 16,000 ys. thus, the apparent bathymetric change of the species is a faunal response to changing environmental conditions and is not evidence of tectonic uplift.

The basis for this model is drawn from Streeter (1973), Schnitker (1973) and Lohmann (1978) who have shown that deep sea benthic foraminifera in the Pleistocene of the Atlantic responded to climatically induced changes by bathymetric migration. North Atlantic assemblages today are closely correlated to the

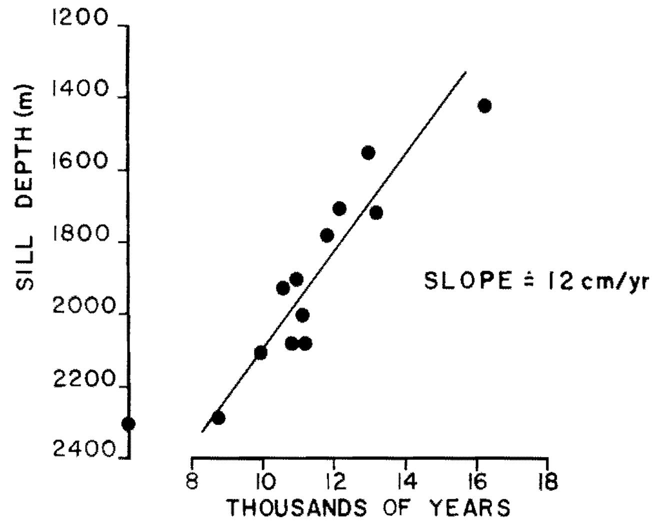


FIGURE 4

The relationship of the age of the last occurrence of *Melonis pompilioides* and basin sill depth. The line was calculated from a least squares fit and has a slope of approximately 12 cm per year for the interval between 8,000 and 16,000 ys. B.P. Since sill depth controls the water quality in silled basins, the correlation suggests that the disappearance of *M. pompilioides* from these basins (Table 1) is related to changes in water-mass distribution in the late Pleistocene and early Holocene.

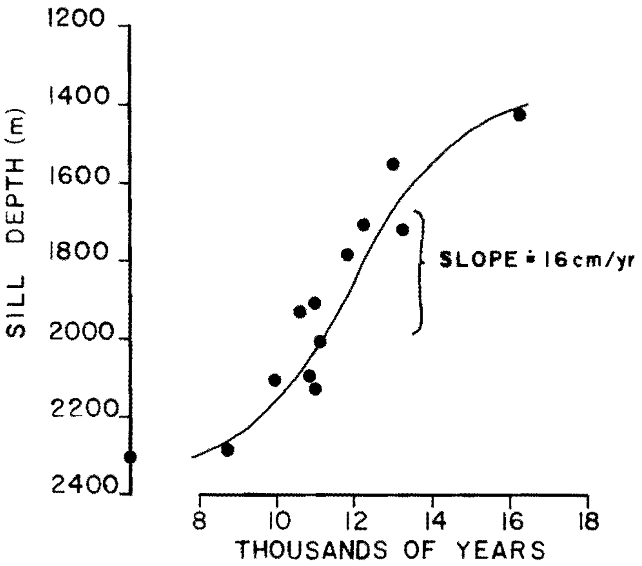


FIGURE 5

The relationship of the age of the last occurrence of *Melonis pompilioides* and basin sill depth. The curvilinear line is fitted and has a slope of approximately 16 cm per year for the interval between 10,000 and 14,000 ys. B.P. (Same data points as shown in Fig. 4.)

distribution of water masses and a marked faunal change occurs at the boundary between North Atlantic Deep Water and Antarctic Bottom Water (Streeter, 1973). Faunal boundaries cross depth contours in a pattern that follows the distribution of water masses. The shift in geographic and bathymetric distribution of late Pleistocene assemblages can be attributed to the changes in deep water masses associated with glacial and interglacial conditions. Recently, Lohmann (1978) demonstrated a similar response for benthic assemblages in the South Atlantic.

From the two models we can predict that a plot of the age of the last occurrence of *Melonis pompilioides* as a function of water depth (either basin depth or sill depth) will show no particular relationship if the effect is due primarily to tectonic uplift. However, since the water in the basins is determined by the depth of the basin sill, a plot of age of last occurrence versus sill depth should show a correlation if distribution of the species is related to water mass. Conversely, the age of last occurrence and basin water depth should not be correlated. Figures 4 and 5 show that there is indeed a strong correlation between the timing of the disappearance of the species from the basins in the Borderland (i.e., its last occurrence) and the water depth at the basin sill. The last occurrence of the species is not related to basin water depth (Fig. 6). *Melonis pompilioides* disappeared from the shallowest-silled basins first, approximately 16,000 ys. B.P. and from the deepest-silled basins last, approximately 8,000 ys. B.P. the species is still present in basins with sill depths at or below 2,300 m.

The strong correlation between the last occurrence of *Melonis pompilioides* and sill depth but not basin depth is difficult to explain by a tectonic uplift model. It requires a constant rate of uplift of the basins and hingement of the entire Borderland along a north-south line with the greatest motion to the south. It requires uniform movement across major faults such as the Santa Tomas Fault.

The faunal migration model suggests that the change in the UDL of *Melonis pompilioides* is related to a change in deep water circulation in the borderland. Climatic curves for the late Pleistocene and Holocene show that the last glacial maximum occurred about 17,000 ys. B.P. and was followed by rapid deglaciation between about 16,000 and 10,000 ys. B.P. (Cline and Hays, 1976). An oxygen isotope curve based on benthic foraminifera (Oba, Kahn and Ku, 1975) is in close agreement with the oceanic signal and indicates a major change in bottom waters in the bor-

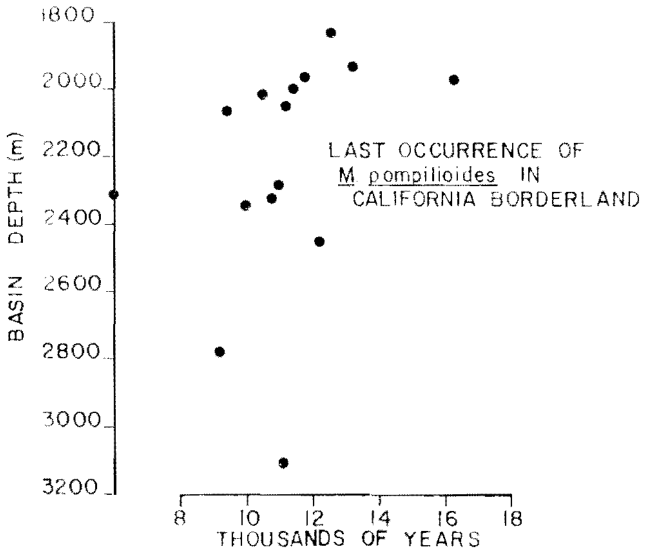


FIGURE 6

The relationship of the age of the last occurrence of *Melonis pompilioides* and basin water depth. The lack of correlation with water depth suggests that change in the elevation of the seafloor with time is not an important factor in the pattern of disappearance of the species from basins in the Borderland.

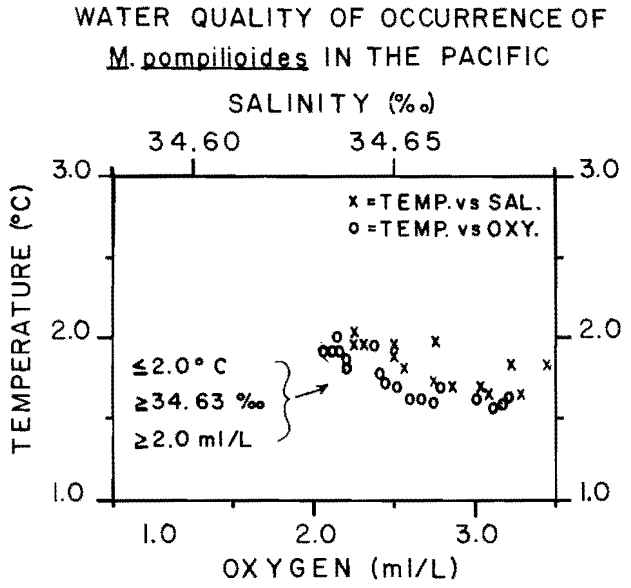


FIGURE 7

Water quality (temperature, salinity and oxygen) values for known occurrences of *Melonis pompilioides* in the Pacific. Data derived from references mentioned in the text and unpublished information.

derland occurred at this time. Deglaciation resulted in a warming of water temperature, rise in eustatic sea-level and a shift in bottom water circulation in the borderland. The warming trend is reflected in the change in planktic faunas from assemblages dominated by subarctic species to assemblages dominated by transitional-temperate species and the change in bottom water circulation by a shift in the depth habitat of benthic faunas, including *M. pompilioides*. In the core samples examined, the greatest change in planktic foraminiferal assemblages took place between 12,000 to 10,000 ys. B.P. and in benthic assemblages between 14,000 and 10,000 ys. B.P. The difference in the duration of these faunal changes suggests that surface water masses were replaced more rapidly than bottom water masses.

If the distribution of *M. pompilioides* is controlled by water quality, then it should be restricted to water with distinct properties. A plot of the modern occurrence of the species shows that its distribution is limited to an envelope of water that is defined by temperature, salinity and oxygen equal to 20°C, 34.63‰ and 2 ml O_2/l (Fig. 7). These parameters characterize the Pacific Bottom Water. At the present time, the upper depth boundary of this water mass is at approximately 2,200 m in the eastern Pacific Ocean.

SUMMARY AND IMPLICATIONS

The use of *M. pompilioides* as a bathymetric indicator in modern and ancient environments rests upon two assumptions: First, that it is an isobathyal species and that its UDL is approximately the same in different oceans. Second, that the depth habitat of the species, at least its upper depth limit, has not changed in time. This requires that its depth distribution has been static, regardless of changes in the oceans. However, distribution studies of modern foraminifera reveal that the species does not in fact have the same upper depth limit in different oceanic areas. In continental margins, its shallowest limit appears to be around 2,300 m and in the deep ocean and southern high latitude closer to 3,000 m.

The data from the southern California Borderland supports a model which explains the Pleistocene distribution of *Melonis pompilioides* as the result of faunal migration rather than tectonic uplift of the seafloor. During the climatic transition of the late Pleistocene to Holocene, there was a reorganization of both surface and bottom water mass circulation in the borderland. The changes in bottom water circulation caused the UDL of lower bathyal species to migrate updepth approximately 900 m. We associate this shift with the boundary between Pacific Intermediate Water and Pa-

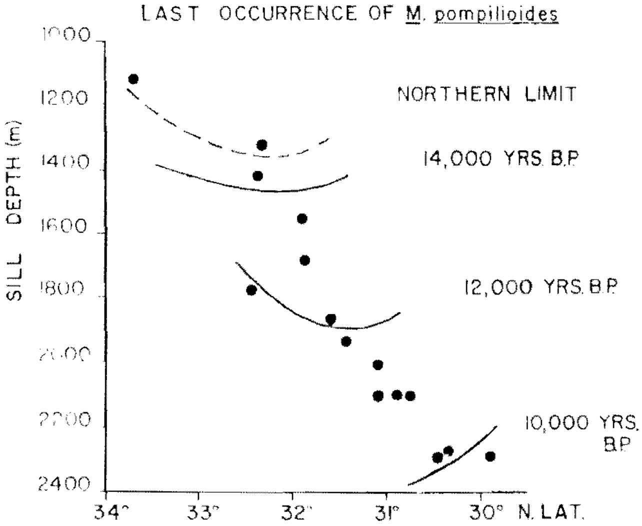


FIGURE 8

The latitudinal pattern of disappearance of *Melonis pompilioides* from basins in the southern California Borderland. The species disappeared first from northern basins with the shallowest sill depth, about 16,000 ys. B.P., and progressively from deeper silled basins to the south for the next 6,000 ys. This pattern of geographic distribution in time closely compares with the routes of deep circulation between basins which are controlled by topography in the southern portion of the Borderland (Emery, 1960).

cific Bottom Water. If this last occurrence of *Melonis pompilioides* is plotted by sill depth as a function of latitude, it is apparent that the boundary between these two water masses migrated southward as well as becoming deeper (Fig. 8).

At the present time, *M. pompilioides* appears to be restricted to water with distinct temperature, salinity and oxygen properties. This may explain why the species has different UDL in different oceanic areas that are at or below 2,300 m in contrast to the concept of isobathyal species.

If *Melonis pompilioides* can be taken as a general case, it suggests that paleodepths based on present-day distribution and especially on supposed isobathyal species should be used with caution. It appears from recent investigations of Pleistocene deep sea foraminifera in the Atlantic (Streeter, 1973; Schnitker, 1974; Lohmann, 1978) that benthic species adjusted their vertical and horizontal distributions in response to climatically induced changes in oceanic circulation.

The application of the species as a paleoecologic indicator also typifies the approach of using ecologic concepts, based on modern distribution patterns, as a means for evaluating changes in paleobathymetry. Modern distributional patterns may not be infallible keys to interpreting paleobathymetric relationships of the past. However, better understanding of water-mass control of benthic distribution should allow more precise paleobathymetric interpretation to be made.

REFERENCES

Bandy, O. L., 1953, Ecology and paleoecology of some California foraminifera, Part I: The frequency distribution of Recent foraminifera off California: Jour. Paleontology, v. 27, p. 161–182.

———, 1960, Geological significance of coiling ratios in the foraminifer *Globigerina pachyderma* (Ehrenberg): Jour. Paleontology, v. 34, p. 671–681.

———, 1967, Foraminiferal definition of the boundaries of the Pleistocene in southern California, U.S.A., *in* Sears, M., ed., Progress in Oceanography: London, Pergamon Press, v. 41, p. 27–49.

Bandy, O. L., and M. Chierici, 1966, Depth-temperature evaluation of selected California-Mediterranean bathyal foraminifera: Marine Geology, v. 4, p. 254–271.

Bandy, O. L., and R. Echols, 1964, Antarctic foraminiferal zonation: Antarctic Research Ser., Am. Geophys. Union, v. 1, p. 73–91.

Bé, A. W. H., 1977, Part I: An ecological, zoogeographic and taxonomic review of Recent planktonic foraminifera, *in* Ramsay, A.T.S., ed., Oceanic Micropaleontology, v. 1, Academic Press, London, p. 1–100.

Cline, R. M., and Hays, J. D., eds., 1976, Investigation of Late Quaternary paleoceanography and paleoclimatology: Geol. Soc. America Mem. 145, p. 1–464.

Crouch, R. W., 1952, Significance of temperature on foraminifera from deep basins off southern California coast: Am. Assoc. Petroleum Geologists, v. 36, p. 807–843.

Douglas, R. G., 1974, Biogeography and bathymetry of Late Cretaceous-Cenozoic abyssal benthic foraminifera. Woods Hole Oceanographic Institute Symposium: Organisms and Continents through Time, 2: p.1–6.

———, 1975, Concepts of foraminiferal paleoecology: A review (abs.): First Benthonic Conference, Halifax, Nova Scotia.

Douglas, R. G., and H. Heitman, in press, Slope and basin benthic foraminifera from the California Borderland: Soc. Econ. Mineralogists and Paleontologists Spec. Pub.

Doyle, L. J., and O. L. Bandy, 1972, Southern Continental Borderland, Baja California: its tectonic and environmental development: Geol. Soc. America Bull., v. 83, p. 3785–3794.

Echols, R. J., 1971, Distribution of foraminifera in sediments of the Scotia Sea area, Antarctic waters, *in* Antarctic Oceanology, I: Antarctic Research Ser., v. 15, p. 93–168.

Emery, K. O., 1960, The sea off southern California: New York, John Wiley and Sons, Inc., p. 366.

Fichtel, L., and Moll, J.P.C., 1798, Testacea microscopica, aliaque minuta ex generibus Argonauta et Nautilus, ad naturam picta et descripta (Microscopische und andere Klein Schalthiere aus den Geschlechern Argonaute und Schiffer): p. 123.

Gorsline, D. S., 1968, Holocene sedimentation in Tanner Basin, California continental borderland: Geol. Soc. America Bull., v. 79, p. 659–674.

Gorsline, D. S., and Prensky, S., 1975, Paleoclimatic inferences for late Pleistocene and Holocene from California Continental Borderland basin sediments: Royal Soc. New Zealand, Bull. 13, p. 147–154.

KULM, L. D., and G. A. FOWLER, 1974, Oregon continental margin structure and stratigraphy: a test of the imbricate thrust model, *in* Burk, C. A., and Drake, C. L., eds., The Geology of Continental Margins: New York, Springer-Verlag, p. 261–283.

LOHMANN, G. P., 1978, Abyssal benthonic foraminifera as hydrographic indicators in the western South Atlantic Ocean, Jour. Foram. Research, v. 8, p. 6–34.

MORIN, R. W., 1971, Late Quaternary biostratigraphy of cores from beneath the California Current: Micropaleontology, v. 17, p. 475–491.

MURRAY, J. W., 1971, An atlas of British Recent foraminiferids: London, Heinemann, p. 244.

NATLAND, M. L., 1957, Paleoecology of west coast Tertiary sediments: Geol. Soc. America, Treatise on Marine Ecology and Paleoecology, v. 2, p. 543–572.

OBA, T., KAHN, M. I., and T. L. KU, 1975, Late Pleistocene and Holocene climatic history of Tanner Basin, California (abs.): Am. Geophys. Union Trans., v. 56, p. 1006.

PARKER, F. L., 1958, Eastern Mediterranean foraminifera: Swedish Deep-sea Exped. Repts., v. 8, p. 219–283.

PFLUM, C. E., and W. FRERICHS, 1976, Gulf of Mexico deep water foraminifers: Cushman Found. Foram. Research Contr., Spec. Pub. 14, p. 1–125.

PHLEGER, F. B., PARKER, F. L., and PEIRSON, J. F., 1953, North Atlantic core foraminifera: Swedish Deep-sea Exped. Repts., v. 7, p. 1–122.

PRENSKY, S. E., 1973, Carbonate stratigraphy and related events, California Continental Borderland: University of Southern California, Los Angeles, unpub. MS Thesis, p. 208.

SCHNITKER, D., 1974, West Atlantic abyssal circulation during the past 120,000 years: Nature, v. 248, p. 385–387.

STREETER, S., 1973, Bottom water and benthonic foraminifera in the North Atlantic, Glacial-Interglacial contrasts: Quaternary Research, v. 3, p. 131–141.

TODD, R., 1958, Foraminifera from western Mediterranean deep-sea cores: Swedish Deep-sea Exped. Repts., v. 8, p. 169–215.

YEATS, R., 1978, Neogene acceleration of subsidence rates in southern California: Geology, v. 6, p. 456–460.

Cushman Foundation Special Publication No. 18
Memorial to Orville L. Bandy
p. 68–85, 1980

PALEOECOLOGY OF LATE EOCENE BENTHONIC FORAMINIFERA FROM POSSAGNO (TREVISO—NORTHERN ITALY)

ANGELA GRÜNIG AND RENÉ HERB
Geological Institute, University of Bern, Sahlistrasse 6, 3012 Bern, Switzerland

ABSTRACT

The stratigraphic distribution of benthonic Foraminifera in a regressive sedimentary sequence ranging from the latest middle Eocene throughout most of the late Eocene was investigated and interpreted paleoecologically. The greater part of the species show distinct ranges within this sequence. The most important can be divided into groups of species which are diagnostic for certain intervals of the section. Ten such groups are distinguished: *Gyroidinoides soldanii, Hoeglundina eocaenica, Nuttallides truempyi, Clavulina parisiensis, Vulvulina lacera, Cyclammina acutidorsata, Bulimina midwayensis, Quinqueloculina juleana* and *Pararotalia audouini* groups as well as a group of larger Foraminifera. Based on the combined ranges of these groups five assemblage zones are established. They are interpreted to be mainly paleobathymetric zones. Estimated values for the water depth of the assemblage zones are at around 1,000 m for zone 1, between approximately 1,000 and 600 m for zone 2, between approximately 600 and 150 m for zone 3, between 150 and 30 to 40 m for zone 4, and between 30 to 40 and almost 0 m for zone 5.

The distribution and development of some representatives of the genus *Bolivina* were studied in particular. *Bolivina nobilis,* which is present mainly in the lower part of the section, grades into *B. gracilis* in the upper part. This transition is thought to be ecologically controlled. A similar development is noted in the group of *Bolivina antegressa,* where three subspecies are recognized. In this case, however, we may be dealing with an evolutionary sequence at least in the earlier part of the sequence, whereas the occurrence of one or the other of the intergrading later forms is probably ecologically controlled.

INTRODUCTION

Our knowledge on the ecology of Recent benthonic Foraminifera, has made great progress during the last two decades especially in terms of their geographic distribution and their depth zonation. A great amount of data are now available in a long series of papers dealing with Recent Foraminifera, which includes many important contributions by Orville L. Bandy.

Less numerous are the attempts to apply these data to the paleoecologic interpretation of Cenozoic sediments. One of the first was O. L. Bandy's work on the "Ecology and Paleoecology of Some California Foraminifera" (Bandy, 1953). In 1963 Bandy published, together with Kolpack, a report on early Cenozoic assemblages of smaller benthonic Foraminifera from California. These authors interpreted the sequence of faunas paleoecologically by analyzing quantitatively their composition and by estimating the water depth at the time of deposition.

Since 1970 more attention has been paid to the paleoecology of early Cenozoic Foraminifera. The work of Le Calvez (1970), although mainly taxonomically oriented, contains many paleoecologic discussions on the Paris basin Foraminifera. Berggren (1974) interprets the paleobathymetry of a Paleocene section from the North Atlantic, and in papers of Berggren and

Aubert (1975) and Aubert and Berggren (1976) paleogeographic and paleoecologic aspects of Paleocene assemblages from Atlantic and Tethys areas are discussed. The most detailed paleoecologic papers on paleogene smaller Foraminifera are those by Wright and Murray (1972) and Murray and Wright (1974) on the Anglo-Paris basin.

A basic method of paleoecologic interpretation consists of comparing fossil assemblages with modern ones. The application on early Cenozoic or older sequences, however, is limited by the fact that virtually none of the species, except for the primitive arenaceous ones, are living today. Although we can find modern relatives for many of the Eocene taxa of smaller benthonic Foraminifera, a direct application of modern ecologic data on similar older forms has to be undertaken with caution and therefore must often result in rather vague statements about water depth, temperature or other factors of ecologic importance.

The late Eocene Possagno clay (Marna di Possagno) offers an opportunity to study well-preserved and, in most samples, abundant assemblages of benthonic Foraminifera in a stratigraphic sequence. As will be discussed below, its paleoenvironmental situation is within a regressive sequence, which is indicated by sedimentologic and faunistic evidence. The paleoecologic significance of the succession of different foraminiferal associations can therefore be evaluated to a certain degree by comparing them with modern assemblages as well as by crosschecking the obtained results with other data which are available in the section itself. In the present paper, the succession of assemblages of smaller benthonic Foraminifera can be related to the distribution of other groups of fossil organisms, such as planktonic Foraminifera, larger Foraminifera, mollusks and corals.

The stratigraphy and micropaleontology of the early Cenozoic sequence of Possagno have been treated in a number of previous papers (Cita and others, 1968; Toumarkine and Bolli, 1970; Herb and Hekel, 1973). The present knowledge is summarized in volume 97 of the "Schweizerische Paläontologische Abhandlungen" (1975), in which contributions covering the major groups of microorganisms are compiled by various authors. The reader is particularly referred to the introduction and stratigraphic description by Cita (1975), to the description of middle and late Eocene planktonic Foraminifera (Toumarkine and Bolli, 1975), of late Eocene Nummulites (Herb and Hekel, 1975) and of ostracods (Ascoli, 1975). Some of these data are summarized and used in the present paper.

Included in this monograph is a first account on smaller benthonic Foraminifera (Braga, de Biase, Grünig and Proto Decima, 1975). The paleoecologic significance and a first attempt of a paleoecologic zonation was the subject of a first draft for the present paper in 1974. Subsequently, one of the authors (A. Grünig) extended her work to other sections in the vicinity of Possagno and to middle to late Eocene sections of the Pamplona-Jaca basin in Northern Spain, in order to check the general validity of the ecologic zonation obtained in the Possagno section. The results of these investigations, including some taxonomic work, are described in detail in her dissertation (Grünig, 1977). They corroborate and complete the earlier results which were obtained from the Possagno section alone. In the present paper, however, only the results from the Possagno section are presented and reference to other sections is made only occasionally.

METHODS

Samples were washed through a sieve of 0.06-mm mesh, which permits the recognition of very small forms, such as some of the small bolivinids. The number of benthonic individuals per gram sediment was calculated on a small portion of each sample. Qualitative and quantitative determinations of benthonic species were then carried out using 300 or more individuals, and their percentages among the total benthonic foraminiferal assemblages were calculated.

To interpret the assemblages of smaller Foraminifera the following data were determined:

1. Planktonic/benthonic ratio.
2. Number of benthonic species.
3. Similarity index (Sanders, 1960).
4. Position in the Rotaliina-Textulariina-Miliolina (RTM) diagram (Murray, 1973).

The species were listed and grouped in tables according to the Braun-Blanquet method. This method, originally established by Braun-Blanquet (1928, 1951, 1964) for defining plant communities, was used by Hiltermann (1973) and Hiltermann and Tüxen (1973) for characterizing recent foraminiferal assemblages. The principal aim of this method is to describe groups of assemblages which are defined by the joint occurrence of diagnostic species. These are recognized by regrouping the original listing of species (rough table, "Rohtabelle") in two intermediate tables (presence table, "Stetigkeitstabelle," and subtable, "Teiltabelle"). The method is described in detail by Ellenberg (1956) and, for our investigations, by Grünig (1977). In the present paper, only the final table ("Endtabelle") is presented (Table 1). Diagnostic species ("Trennarten") are grouped in blocks of species with similar ranges. Ten such groups of diagnostic species are recognized. Below these blocks species are listed which occur within the stratigraphic range of the respective blocks or species groups, but which also occur less consistently or, usually with low abundance, outside of these blocks. Species which occur in samples throughout the section or only sporadically to rare are discarded from the main part of the table and are listed at the end of the table ("other species").

The combined ranges of species can be used as a base for defining five assemblage zones. As will be shown below the result is essentially a paleobathymetric zonation.

STRATIGRAPHY

The following formations are recognized in the Paleocene and Eocene of Possagno:

1. *Scaglia rossa*
   Reddish micritic limestones and argillaceous limestones with marly intercalations. 40 m exposed. Late Cretaceous to basal early Eocene.
2. *Scaglia variegata*
   Alternation of reddish-brown, green, and gray marls and argillaceous micritic limestones, 50 m. Early Eocene to basal middle Eocene.
3. *Scaglia cinerea*
   Predominance of gray to olive-gray marls with intercalations of argillaceous limestones, except for the uppermost part which consists exclusively of marls. Approximately 170 m. Basal middle Eocene to basal late Eocene.
4. *Marna di Possagno*
   550 m of blue-gray clay which is increasingly silty in the upper part of the formation. See details below. Late Eocene.
5. *Calcare di S. Guistina*
   Thin-bedded algal limestones in the lower part and thick-bedded limestones with corals, coralline algae, and abundant larger Foraminifera in the upper part. Approximately 60 m. Late Eocene.
6. *Marne siltose*
   Gray to olive-gray silty marls. Approximately 30 m. Late Eocene.

The present paper deals with the paleoecology of the uppermost part of the Scaglia cinerea and the Marna di Possagno. Therefore, some further stratigraphic details of this part of the section are given in the following paragraphs. The section is also shown on Figure 3.

SCAGLIA CINEREA (UPPER PART)

In its general lithologic appearance the uppermost part of the Scaglia cinerea is very similar to the lower part of the Marna di Possagno. The main difference between the two is in the $CaCO_3$ content of the sediment, which is approximately 40 percent in the Scaglia cinerea and less than 20 percent in the Mar di Possagno. The foraminiferal assemblages are dominated by planktonic Foraminifera (over 90%). The formation represents essentially a pelagic environment, but, compared with the older Scaglia formations, contains an increased amount of detrital argillaceous components and has been deposited in slightly shallower water.

MARNA DI POSSAGNO

This formation is extensively, but unfortunately not continuously, exposed in a series of quarries southwest and south of Possagno. The lower part (up to sample 33, Figs. 1 and 2), occurs north of the main road which leads from Possagno to Bassano. It is a sequence of uniform, poorly bedded, blue-gray clays, sometimes slightly silty, interrupted by four levels of sands rich in biotite, each only a few centimeters thick. No megafossils were observed. In the foraminiferal assemblages an increasing percentage of benthonic forms can be observed with 8 to 25 percent at the base to 65 to almost 90 percent in the higher levels.

The upper part of the formation (from sample 36 upwards, Figs. 2 and 3) is characterized by an increasing content of silt and by rich assemblages of megafossils. A first occurrence of gastropods and few pelecypods could be noted in a small quarry just south of the above-mentioned road (samples 71/34 to 35), and in a small outcrop between the main road and Cunial (samples 71/36 to 38). Thereafter, about 90 m of section are not exposed. This sequence can partly be covered by a section near Curogna, 5 km east-northeast of Possagno. The uppermost part of the for-

→

TABLE 1

Relative abundances of benthonic Foraminifera in the sections of Possagno-Cunial, Val Organa and Curogna. For sample locations see Figures 1 to 4. x = abundances less than 0.5 percent.

SECTIONS	POSSAGNO					CUROGNA	VAL ORGANA
SAMPLE NUMBERS	47 55 49 50 51	54 48 57 58 61 1 2 3 4 5	6 9 11 16 17 18 19 22 23 24 25 26 28 30 33 38	34 40 41 42 45 72	75 80 83 86 88 89 95 96 121 135 139	16 18 19 20 21 22 23 24 25 26 27 28 30 32 33 34	66 67 68 69 70 71
ASSEMBLAGE ZONES	1	2	3	4	5	4	5
NUTTALLIDES TRUEMPYI-GROUP							
Nuttallides truempyi (Nuttall)	7 12 15 4 7						
Fissurina orbignyana Seguenza	x 1 x 1 1						
Bulimina trinitatensis Cushman & Jarvis	2 x x x x	3					
Cibicidoides parki (Finlay)	2 12 16 24						
Pleurostomella acuta Hantken	1 1						
Buliminella grata Parker & Bermudez	x x						
CLAVULINA PARISIENSIS-GROUP							
Clavulina parisiensis d'Orbigny	x x	2 7 4 1 1					
Heterolepa ungeriana (d'Orbigny)	2 1	2 3 6 x					
Globocassidulina inexculpta (Franzenau)	2 1 1 1	x 2 x					
Planulina? ammophila (Gumbel)	11 6 x 2	x 3 x					
Stilostomella hispida (d'Orbigny)	7 2 2 5 x	4 3 3 x x	x x				
Bolivina antegressa angulata Sahakjan-Gezaljan	2 6 5 1	1 10 1 2 3 1	3 x				
Osangularia pteromphalia (Gumbel)	4 x x	5 3 6 x 3 x x 2	x				
Vaginulinopsis cumulicostata (Gumbel)	1 2 2	1 3 x x	x				
Karreriella cubensis Cushman & Bermudez	1 x 1 x	x x x					
Lenticulina indet.	15 18 10 5	26 4					
Anomalina capitata (Gumbel)	x x	6 x 2					
Rhabdammina eocaenica Cushman & Hanna	3 x 16	20 x					
VULVULINA LACERA-GROUP							
Vulvulina lacera (Reuss)	1	3 6 5 9 4 x 5 x					
Cylindroclavulina colomi Hagn	10 8	x 4 2 x					
Aragonia janoscheki Gohrbandt		30 8 x 7	x 1				
GYROIDINOIDES SOLDANII-GROUP							
Gyroidinoides soldanii (d'Orbigny)	2 2 2 2	2 1 x x 2 2 1 x 3	2 7 3 1 4 4 3 5 4 3 5 6 4 4 1 4	x			
Uvigerina chirana Cushman & Stone	1 15 1	8 1 2 17 9 9 8 50	16 11 3 x 1 1 2 2 1 1 2 x	7			
Uvigerina spinicostata Cushman & Jarvis	5 1 4 9 11	11 x 2 x	3 25 26 37 24 2 16 25 20 26 3 1 1 2				
Uvigerina eocaena Gumbel	x x x	1 9 14 21 12 28 14 10	2 4 21 9 9 8 2 3 x 5 1 5 7 1 2			15 8 22 x x x	
Trochammina sp.	6 3 1 1	2 8 x 4 x 2 3	4 6 4 3 10 9 12 4 4 3 3 1 11 7 x	x x	x	5 4 9 7 7 4 2 2 2 1 3 5 5 1 2	
Bathysiphon eocaenicus Cushman & Hanna	6 2 x 2 8	x 4 4 4 3 x 2 x 4 x	8 2 2 6 x 1 x 4				
Oridorsalis umbonatus (Reuss)	3 2 4 1 x	2 1 1 x	4 x x x x x 2 x x				
Stilostomella adolphina (d'Orbigny)	4 5 9	3 x 2 x x	3 2 x 1 2 x	1 1 1			
Dorothia trauni (Hagn)	2 x x x	x 2 x 8 4 x x	1 2 x x 3				
Marginulina pediformis Bornemann	2 x	x x x x	x 2 2 x	x x			
Ammodiscus glabratus Cushman & Jarvis	x 1	x x x x	x x x x				
Lagena acuticosta Reuss	x x x	x x x x	x x x				
Lagena hexagona (Williamson)	x x	x x x x	7 x	x			
Heterolepa eocaena (Gumbel)	1 x	1 x 8 x	x				
Nodosaria longiscata d'Orbigny	x	x	x 1 x 1				
Plectina dalmatina (Schubert)	7	4	x 2			25 3 6 6 3 3 1 2 2 2 3 4 x x	
HOEGLUNDINA EOCENICA-GROUP							
Hoeglundina eocenica (Cushman & Hanna)		6 x 4 5 2 5	2 4 x 3 1 3 2 x 1 1 2 3 2 1				
Bolivina nobilis Hantken	x	2 x 1 x x x	2 5 1 1 13 x 2 6 1 2 x 4 3 2 2 3			1 x x x x	
Tritaxia szaboi (Hantken)	2	5 2 9 3 1 2 1 1	x 3 3 7 5 15 10 5 31 15 7 4 4 2				
Heterolepa reussi (Silvestri)		19 6 9 15 24 21 25 6	18 12 15 7 9 14 2 7 15 14 5 18 4				
Bulimina ovata d'Orbigny		x 2 2 1 x x	3 3 x 2 x x 1 x				
Planulina wuellerstorfi gigas Hagn		2 x 2 1 1	x x x x x x x				
Bulimina truncana Gumbel		3 2 x	7 3 9 8 4 3 5 4				
CYCLAMMINA ACUTIDORSATA-GROUP							
Cyclammina acutidorsata (Hantken)			x x 1 3 5 1 3 5 5 x 3 3 x			x	
Triferina labrum Subbotina			1 x x 3 20 1			x	
Bolivina antegressa dentata Sahakjan-Gezaljan		x x	2 2 2 4 6 4 16 4 2 x	1			
Triferina cooperensis (Cushman)			2 x 1 2 x	1		x	
Bolivina antegressa interposita Sahakjan-Gezaljan		x 11	x 2 1 3 1 1 1 5 5 3 7	5 x			
Glandulina ovata d'Orbigny			1 x x 2 x			x 3	
BULIMINA MIDWAYENSIS-GROUP							
Bulimina midwayensis Cushman & Parker			4 x 2 x x 3 2 x 3 1 1	5 2 1 1	1	4 4 2 x 3 2 1 1 1 x 1	
Globocassidulina globosa (Hantken)		x 1	1 2 x x x 1 x 1 1 x x 10 3	x 8 6 5 x		x 1 4 11 4 1	
Bolivina nobilis-B. gracilis			1 x 1 x x x 2 2 x 3	2 1 2 x	3 2 2	x x	
Siphonina prima Plummer			x x 3 4 1	3 x x 2		x 1 1 x x x 1 x	
Bolivina striatocarinata Cushman			3 x 1 1 2 2 2 x 2 x	1 2 2 1 4 2	1 2 2 1 x	2 2 1 1 1 1 1 2 1 1 x 4 1 1 x 2	x
Bolivina denticulata Bandy			1 2 3 x 4 1 2	x			
Gyroidinoides octocamerata (Cushman & Hanna)			1 4 8 7	6 16 1			
Vulvulina aff. pectinata Hantken			x 1 1 x x x x 1 x 1 1 1 x	2 4 1 2 2 1	3 4 x x		
QUINQUELOCULINA JULEANA-GROUP							
Quinqueloculina juleana d'Orbigny			x 1 x	3 6 5 8 8 9	3 2 18 13 23 10 15 10 4 4	x 3 x x 1 x 1 7 6 17 5 8 8 3 2 3	5 2 3 x x
Heterolepa dutemplei (d'Orbigny)			2	3 7 20 10 7 12	21 5 12 4 2 18 4 2 9 18	16 11 12 9 18 40 30 12 16 10 18 15 11 33 16 7	18 13 25 35 21 10
Asterigerina bartoniana (Ten Dam)				x x x 1 1	x 10 5 14 21 28 25 6 7	x x 1 2 17 6 30 44	x
Asterigerina wilcoxensis Cushman & Garrett			x	2 8 1	8 2 8 6 1 1 2 x	1	
Melonis affinis (Reuss)			1 x	x 1 5 3 6 6	2 7 3 8 8		x 5 3
Bolivina gracilis Cushman & Applin			x 1	3 6 3 14	7 1 4 6 4 x 1	1 x 2 x	3 2 x 13 18 6
Fursenkoina dibollensis (Cushman & Applin)			x x x 1	x 1 x 1	1 x 2 2 1	x x 1 1 x 2 x	1
Nonion scaphum (Fichtel & Moll)			3 x	4 13	4 4 2 1 6		4 2 x 3 6 1
Sigmoilopsis sp.				x 1 1 1 3	2 1 x x	1 x 1 1 2 4 2 2 5 3 2 1	3 x 2
Pyrgo subsphaerica d'Orbigny				1 1	2 2 x x 2 x	x	
Alabamina acutimargo (Haikyard)				x 1 2	x x	4 x 1 1 x 1 1 1 1 x 1	
Reussella oberburgensis (Freyer)				6 x	x 1 x 1 7	x x x	x 1
Triloculina gibba d'Orbigny				2 1 1	x 3 x x	2 2 2 8 4 3	
Heterolepa pygmea (Hantken)			3 8 10 25	11 12 3 5 6 6	15 4 7 23 2 2 13 x 21 2 1		
LARGER FORAMINIFERA							
Nummulites spp.				x 7 12 x 5	4 16 5 6 17 21 16 44 2 44 x	x x 1 1 1 2 2 8 12 27 8	45 39 42 26 9 13
Operculina alpina Douvillé				2 5 12 12 x 8	4 27 3 3 6 8 x 7 2 13	1 3 5 3 1 3 15 22 22 19 17 15 16 16 11 13	x 1 8 1
Discocyclina spp.				2 4 1 x 1	2 x x 6 1 1 x 12	2 6 1 4 7 3	x 1 12
Asterocyclina, Actinocycline				x		2 3 4	
Spiroclypeus				x			
PARAROTALIA AUDOUINI-GROUP							
Pararotalia audouini (d'Orbigny)				x	1 x x 1 1 2 1 16	x x 1 x	12 4 5
Asterigerina aff. adarkeyensis Cole					1 1 1	x	2 11 5 10 14
Elphidium latidorsatum (Reuss)					28		x x
Bifarina aff. selseyensis (Heron-Allen&Earland)					8		x x
OTHER SPECIES							
Lenticulina arcuatostriata (Hantken)	11 6 11 9 6	6 11 4 20 11 5 7 9 8 9	3 12 8 4 1 6 8 2 5 4 6 2 11 6 x 7	2 3 3 5 x 2	1 3 1 x 3 2 2 2 3 2	3 3 6 2 2 3 4 4 6 3 1 2 1 1 4 3	7 x 1
Stilostomella verneuili (d'Orbigny)	9 7 2 5	1 1 3 1 11 12 8 1	4 5 3 4 3 3 6 10 4 4 6 2 6 3 1 1	2 1 3 5 1 1	x 1 1 1	1 1 3 2 1 2 7 1 2 3 3 2 2 x 1	1 1 1
Marginulinopsis fragaria (Gumbel)	2 x 3 4 3	3 x 8 x 1 1 x x 2	x x x 2 1 x x 1 1 x	x 2 1 1 1	x 1 1 1 2 x	5 4 5 6 9 5 7 4 7 8 3 3 2 x x 2	x
Saracenaria triangularis (d'Orbigny)	1 1 3 1 1	x 1 2 1 x 2 x	x 1 x x x 2 x x x 1	x x x x	x 2 1	1 x x	
Marginulina behmi (Reuss)		x 2 x 2 4 2 x 1	x x x 2 2 1 2 2 x x 2 x	x 1 1 2	x 1	3 2 3 1 1 x 1 1 x x x	x
Bulimina subtruncana Hagn		3 13 x 2	4 2 4 x 18 11 2 4 1 7 4 10	25 1 x 3 4	3 1 1 x	15 17 9 14 9 4 5 3 4 2	
Gavelinella micra (Bermudez)	x 2 x 4 2	8 x	4 2 x x x 4 21 4	4 4 6 15 8 4	3 x x x	2 1 11 4 3 7 6 6 4 4 2 7 7 3 2	6
Eponides toulmini Brotzen			3 1 4 3 10	6 10 x 4 22 3	21 1 16 12 5 9 17 2 43 5 11	1	3 x x x
Lagena striata (d'Orbigny)	x x x	x x x	x 1 1 x	1 x			
Quinqueloculina imperialis Hanna & Hanna		x x	x	x 1 8 7 x	1 x 4 1	3 19 14 12 20 10 12 17 9 3 4 5 2	x
Haplophragmoides indet.	1	1 x	3 2 2 2 5 1 3	5			
Dentalina consobrina d'Orbigny	1	x x	x x 1		x 1 x		
Globulina inaequalis Reuss		x	2	x 2	2 2 2 3		
Vulvulina haeringensis (Gumbel)	2 x 2	x 2	1 x 1				
Spiroloculina excavata d'Orbigny	x 2	2 x		x		2 x 1 x 2 x	
Haplophragmoides rotundidorsatum (Hantken)		x	x 3 x	x			
Lenticulina cassis (Fichtel & Moll)		x 1 1	x				
Quinqueloculina badenensis d'Orbigny			x x	2	x		
Pyrulina fusiformis (Roemer)				1	1 x x	1 x x 1 1 x x 1 1 2 x	
Globulina gibba (d'Orbigny)				1 x	1	x 1 2	x x
Textularia dibollensis Cushman & Applin				1	x 1	1 1 1 7 6 3 1 3 2 4	x 1
Glomospira charoides (Jones & Parker)	x		2 x				
Anomalinoides subalpinus Hagn		1 x	2				
Lagena scarenaensis Hantken	x x	x					
Dentalina alabamensis Cushman	1 x						
Dentalina soluta Reuss	2 x						
Marginulina propinqua Hantken	x	3					
Lagena castrensis Schwager	1	x					
Plectofrondicularia mexicana (Cushman)			x x				
Melonis holkyardi (Cushman)				x 2		x 1 x 1 x x 1 4 7 x x	
Glandulina laevigata (d'Orbigny)				x x		1 2 1 1 x 1 1 1 1 1 x x	
Sagrina vicksburgensis (Howe)					2 4		
Pyrgo simplex (d'Orbigny)				1	x	x x 1 2 x	1
Ceratocancris contraria (Reuss)				2 1		1 1 x	x x x
Spiroloculina jarvisi Cushman & Todd					x		
Gaudryina jacksonensis Cushman				1		3 2 1 x x 2 1 1	
Eponides jacksonensis (Cushman & Applin)				x		x x	
Pullenia bulloides (d'Orbigny)				x		x x x x x	x
Pseudonodosaria conica (Neugeboren)				x		x 2 1 x x x	
Frondicularia budensis (Hantken)			x			x 1 x x x x x	
Siphonina wilcoxensis Cushman		x					
Uvigerina nitidula Schwager		1					
Bolivina plicatella Cushman		3					
Heterolepa grimsdalei (Nuttall)	x						
Nodosarella tuberosa (Gumbel)	x						
Sphaerogypsina globulus (Reuss)						1 x	
Vaginulinopsis asperula (Gumbel)						1 x x	
Siphotextularia concava (Karrer)						x x	
Baggina dentata Hagn						x	
Uvigerina mexicana nuda Gohrbandt						1 x 10	
Karreriella siphonella (Reuss)						3 x	
Discorbis circularis (Sidebottom)							23

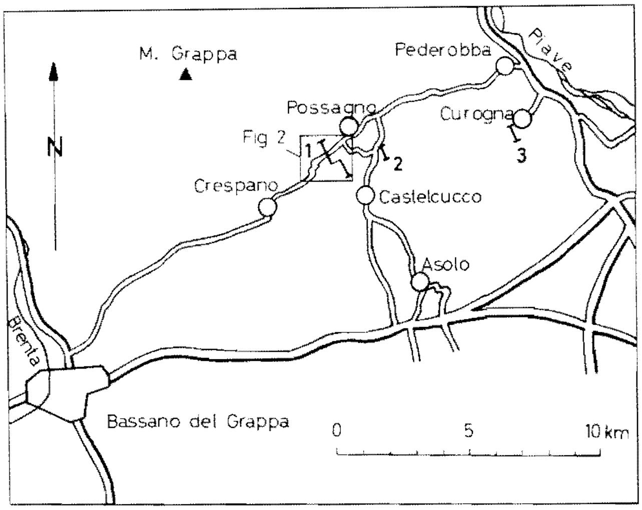


FIGURE 1
Index map showing the location of the sections of (1) Possagno (Figure 2), (2) Val Organa and (3) Curogna, approx. 55 km NNW of Venezia.

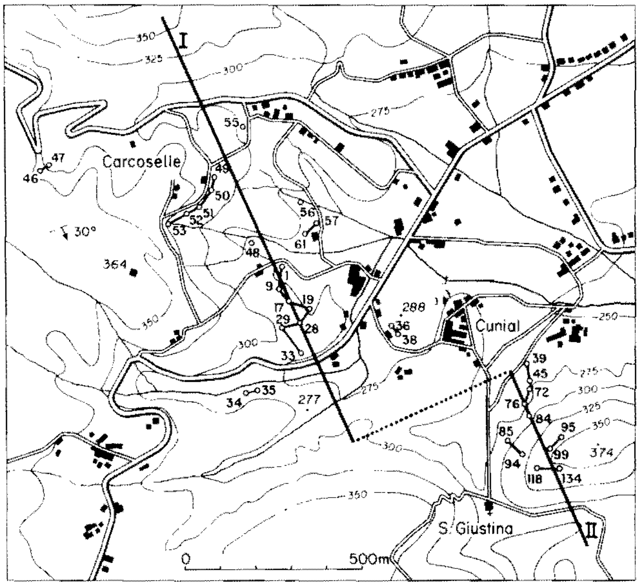


FIGURE 2
Map of the section and of sample locations for the Possagno-Cunial section.

mation was sampled in a quarry southeast of the small village of Cunial, and in a roadcut along the road leading from Castelcucco to Possagno through the Val Organa (Fig. 3). The clay sequence contains an increasing but varying amount of silt upwards. Pelecypods, gastropods and solitary corals are frequent throughout the section of the Cunial quarry and in the Val Organa. Solitary corals are especially abundant in the upper part, which also contain several intercalations of indurated siltstones, occasionally rich in larger Foraminifera, particularly *Nummulites fabianii retiatus* (Herb and Hekel, 1975). The topmost 20 m are characterized by an alternation of highly fossiliferous clay, sandy clay, and shell beds rich in mollusks and mollusk debris, with solitary corals. They are particularly well exposed in the section of the Val Organa (Fig. 4). A lignitic lens was observed in the uppermost 2 m. This indicates very shallow water conditions at the top of the Possagno clay.

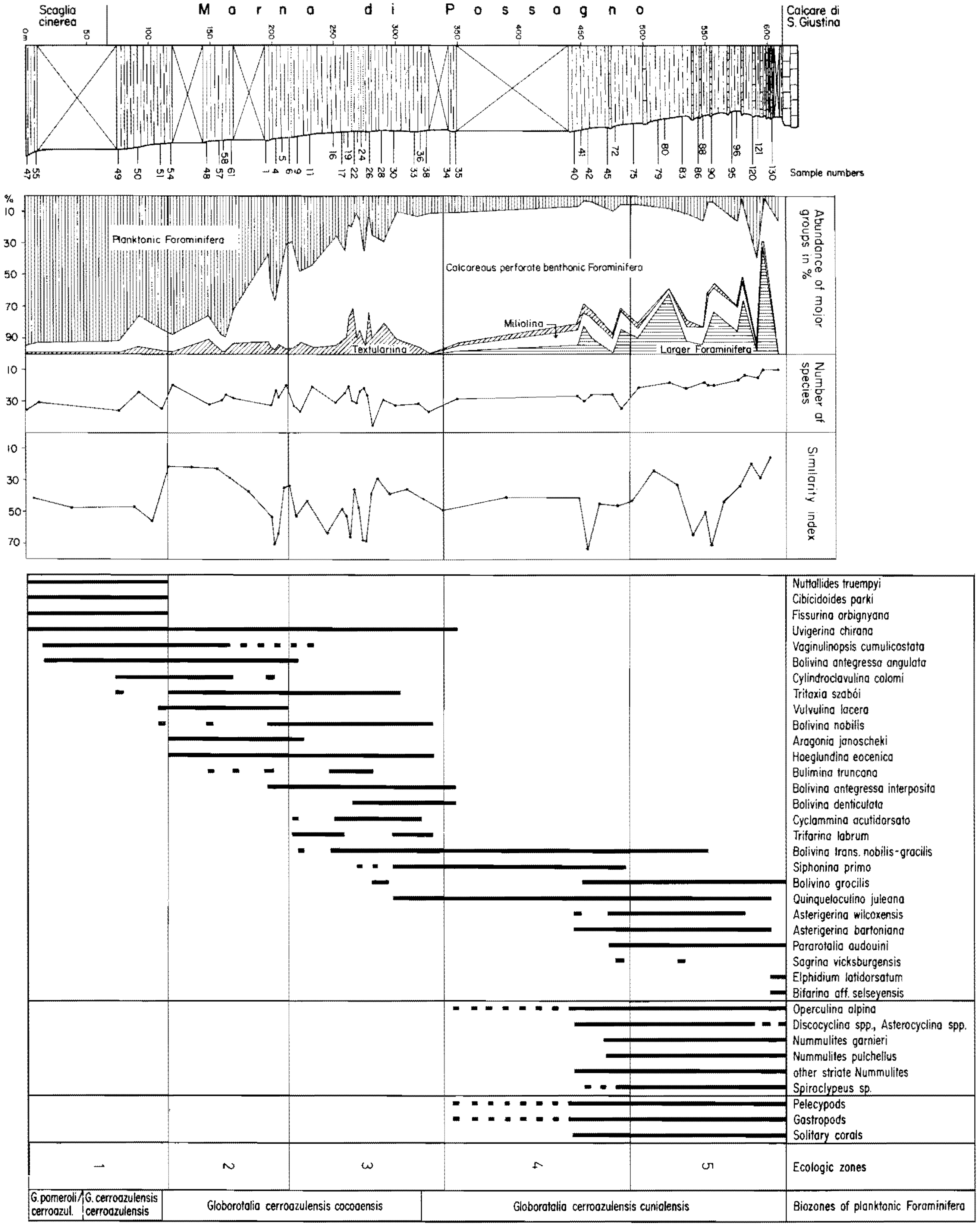
Benthonic Foraminifera in the upper part of the Possagno clay usually dominate the foraminiferal assemblages and comprise approximately 85 percent of the fauna, except for the uppermost part, where planktonic forms again form up to 40 percent of the assemblages (Fig. 3). Most of these, however, are reworked (see Toumarkine and Bolli, 1975); this again reflects the supply of coarser detrital material in the uppermost part of the formation. Among the benthonic Foraminifera the presence of larger Foraminifera (Nummulitidae and Discocyclinidae) is particularly significant.

At the top of the Cunial quarry and in the Val Organa the Marna di Possagno formation is overlain by algal limestones of the Calcare di S. Giustina.

As a whole, these sedimentary and faunistic patterns clearly show that the Marna di Possagno represents a rapidly filled sedimentary basin with a more or less steady decrease of the water depth from the base to the top of the formation. An opportunity is therefore given to study the succession of benthonic foraminiferal assemblages in a transition from deep-to shallow-water environments. Due to the short time span represented in the section, first occurrences and extinctions of taxa are virtually all related to changes in the paleoenvironment. The presence of larger Foraminifera and macrofossil assemblages furnishes important clues for the interpretation of the smaller benthic communities.

→

FIGURE 3
Stratigraphic section of Possagno-Cunial with abundances of major foraminiferal groups and stratigraphic distribution of selected species or groups of smaller and larger Foraminifera and Metazoans. Number of species refers to smaller benthonic Foraminifera only. Similarity index after Sanders (1960).


Scaglia cinerea
M a r n a d i P o s s a g n o
Calcare di S. Giustina
0 m
50
100
150
200
250
300
350
400
450
500
550
600
47
55
49
50
51
54
48
57
58
61
1
4
5
6
9
11
16
17
19
22
24
26
28
30
33
36
38
34
35
40
41
42
45
72
75
79
80
83
86
88
90
95
96
120
121
130
Sample numbers
%
10
30
50
70
90
Planktonic Foraminifera
Calcareous perforate benthonic Foraminifera
Miliolina
Textulariina
Larger Foraminifera
Abundance of major groups in %
10
30
Number of species
10
30
50
70
Similarity index
Nuttallides truempyi
Cibicidoides parki
Fissurina orbignyana
Uvigerina chirana
Vaginulinopsis cumulicostata
Bolivina antegressa angulata
Cylindroclavulina colomi
Tritaxia szabói
Vulvulina lacera
Bolivina nobilis
Aragonia janoscheki
Hoeglundina eocenica
Bulimina truncana
Bolivina antegressa interposita
Bolivina denticulata
Cyclammina acutidorsata
Trifarina labrum
Bolivina trans. nobilis-gracilis
Siphonina primo
Bolivina gracilis
Quinqueloculina juleana
Asterigerina wilcoxensis
Asterigerina bartoniana
Pararotalia audouini
Sagrina vicksburgensis
Elphidium latidorsatum
Bifarina aff. selseyensis
Operculina alpina
Discocyclina spp., Asterocyclina spp.
Nummulites garnieri
Nummulites pulchellus
other striate Nummulites
Spiroclypeus sp.
Pelecypods
Gastropods
Solitary corals
1
2
3
4
5
Ecologic zones
G. pomeroli / cerroazul.
G. cerroazulensis cerroazulensis
Globorotalia cerroazulensis cocoaensis
Globorotalia cerroazulensis cunialensis
Biozones of planktonic Foraminifera

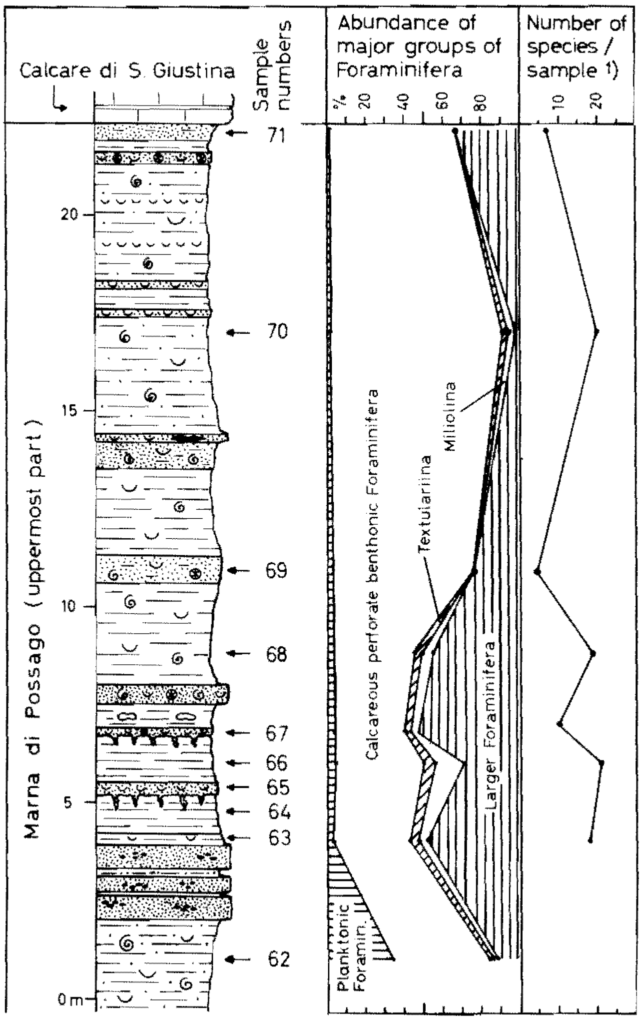


FIGURE 4

Stratigraphic section of the uppermost Marna di Possagno in the road cut of Val Organa, southeast of Possagno, with abundances of major foraminiferal groups. (1) Smaller benthonic Foraminifera only.

DISTRIBUTION AND PALEOBATHYMETRIC ZONATION OF BENTHONIC FORAMINIFERA

The stratigraphic distribution and the relative abundance of benthonic species in the Marna di Possagno is shown in Table 1. Many species have a distinct stratigraphic range which is mainly the result of the changing environment, as indicated above. Based on this distribution five assemblage zones can be recognized. They are mainly defined by the combined ranges of the following 10 groups of diagnostic species:

1. *Gyroidinoides soldanii* group with *Gyroidinoides soldanii* and three uvigerinid species (*Uvigerina chirana*, *U. spinicostata* and *U. eocaena*). It occurs in assemblage zones 1 to 3.
2. *Hoeglundina eocaenica* group with four well-known diagnostic species, *Hoeglundina eocaenica*, *Bolivina nobilis*, *Tritaxia szaboi*, and *Heterolepa reussi*, virtually restricted to assemblage zones 2 and 3.
3. *Nuttallides truempyi* group with *Nuttallides truempyi* and *Cibicidoides parki* as main diagnostic taxa, restricted to assemblage zone 1 and of major importance for paleobathymetric interpretations.
4. *Clavulina parisiensis* group with four species restricted to assemblage zones 1 and 2, but less consistent in occurrence than the species of the previous groups.
5. *Vulvulina lacera* group with three species mostly restricted to assemblage zone 2, but very variable in occurrence and abundance.
6. *Cyclammina acutidorsata* group, diagnostic for assemblage zone 3, with *Trifarina* as a very characteristic genus, although not always present.
7. *Bulimina midwayensis* group with four species mostly restricted to assemblage zones 3 and 4.
8. *Quinqueloculina juleana* group with four important and often very common species diagnostic for assemblage zones 4 and 5: *Quinqueloculina juleana*, *Heterolepa dutemplei*, *Asterigerina bartoniana*, and *A. wilcoxensis*.
9. *Pararotalia audouini* group, restricted to assemblage zone 5, with two important, but often missing species: *Pararotalia audouini* and *Asterigerina adarkayensis*. These, however, consistently occur in high percentages in the Val Organa section which covers the uppermost 16 m of the Marna di Possagno.
10. Group of larger Foraminifera with *Operculina alpina*, *Discocylina* sp. and a number of small nummulite species being the most important forms, restricted to zones 4 and 5.

The paleoecologic interpretation of the assemblage zones is mainly based on a comparison with the depth distribution of similar recent assemblages. Although none of the significant Eocene species is still living today, many show close affinities to Recent forms, and it seems not unreasonable to use the Recent data for a first estimate of the water depth in which the Eocene assemblages lived.

For the present paper the Eocene of Possagno was mainly compared with data on Recent Foraminifera from the Mediterranean (Blanc-Vernet, 1969), the Gulf of Gascogne (Caralp, Lamy, and Pujos, 1970), the Gulf of Mexico (Ludwick and Walton, 1957; Walton, 1964), the Lagoon of Ojo De Liebre, California (Phleger and Ewing, 1962), the Andaman Sea (Frerichs, 1970), the Carribean (Brasier, 1974), and the Solomon Islands (Hughes, 1977).

Based on the general stratigraphic situation and the faunal record, it is reasonable to assume a steady decrease in water depth from the base to the top of the section. The zonation established in this paper therefore is essentially a bathymetric zonation, however, with relative rather than absolute depth values. The latter are subject to interpretation. In the following paragraphs the five assemblage zones are characterized and estimations of the paleobathymetry and other paleoecologic factors are discussed.

ASSEMBLAGE ZONE 1

Assemblage zone 1 is delimited by the occurrence of the *Nuttallides truempyi* group. Also typical for this zone, but not restricted to it are the *Gyroidinoides soldanii* and the *Clavulina parisiensis* groups. The assemblages are usually dominated by nodosariid forms, most of which belong to the genus *Lenticulina*. These, however, occur often in great percentages also in higher zones. The similarity index shows rather constant values between 40 and 60. Assemblage zone 1 corresponds to the uppermost Scaglia cinerea and the basal Marna di Possagno.

An estimation of the water depth is particularly difficult for the lowermost zones. An important feature of zone 1 is the high percentage of planktonic to benthonic Foraminifera, with values of over 90 percent in the lower two-thirds of the zone. Although the planktonic/benthonic ratio must be used with caution for paleobathymetric interpretations, one would, based on modern data, generally assume a water depth of more than 1,000 m, possibly slightly less in the uppermost part of the zone, where 75 and 85 percent planktonics are noted.

Genera such as *Bathysiphon*, *Ammodiscus*, *Osangularia*, *Dorothia*, and *Stilostomella* are considered to be typical for depths corresponding to the lower and middle continental slope. The absence of *Hoeglundina eocaenica*, a species which will be discussed in the paragraph on zone 2, is significant.

In the RTM diagram (Fig. 6) all the samples are concentrated in the Rotaliina corner. This indicates open-marine conditions. The low percentage of arenaceous Foraminifera at the same time prohibits the assumption of very great water depths. Summarizing these considerations it seems reasonable to assume a water depth of 1,000 m or somewhat more for the greater part of zone 1, possibly a little less for the uppermost part of the zone.

ASSEMBLAGE ZONE 2

Assemblage zone 2 is characterized by the occurrence of the *Vulvulina lacera* group. Associated with it are the *Gyroidinoides soldanii* and the *Clavulina parisiensis* groups, whereas the *Gyroidinoides soldanii* group has its lower limit at the base of this zone. The similarity index varies between 20 and 70.

Planktonic Foraminifera decrease from 70–90 percent in the lower half to 30–65 percent in the upper half of this zone. Typical is the common occurrence of the hispid *Uvigerina chirana*. Hispid *uvigerinids* are usually found in water depths greater than 600 m (Frerichs, 1970). Open-marine conditions with water depths between approximately 1,000 and 600 m are most probable for zone 2.

ASSEMBLAGE ZONE 3

Assemblage zone 3 is delimited by the occurrence of the *Cyclammina acutidorsata* group. Associated with this group are the *Gyroidinoides soldanii*, the *Hoeglundina eocaenica*, and the *Bulimina midwayensis* groups. The greatest species diversity is reached within this zone; however, the number of species may vary considerably from sample to sample, between 21 in sample 18 and 46 in sample 26. The similarity index is also highly variable.

High species diversity is significant for the upper bathyal and the outer shelf (Frerichs, 1970). The strong reduction in the percentages of planktonic Foraminifera also indicates a significant decrease in water depth within this zone. The upper limit of zone 3 coincides with the disappearance of the *Hoeglundina eocaenica* group. The modern *H. elegans* has upper depth limits between 50 and 200 m in various oceans (Bandy and Chierici, 1966: 100 ± 50 m; McGlasson, 1959: >90 m; Parker, 1957: 50–82 m; and Frerichs, 1970: 200 m).

Zones 2 and 3 correspond to the maximum development of uvigerinid forms with *Uvigerina chirana*, *U. spinicostata* and *U. eocaena*. All these species are, however, also found in zone 1 and extend slightly into zone 4. *Trifarina labrum* is typical for the upper part of zone 3. In the Pamplona basin of Northern Spain, however, this species is restricted to equivalents of zone 4. The modern ribbed *Uvigerina peregrina* shows an upper depth limit of 100 ± 50 m (Bandy and

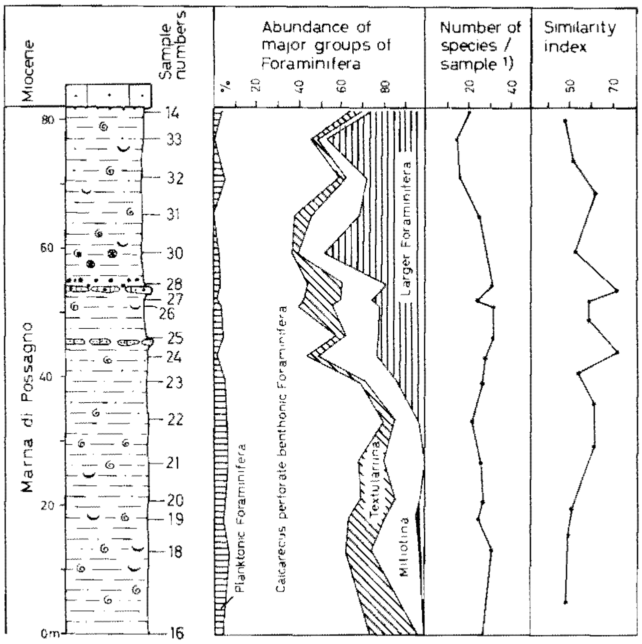


FIGURE 5

Stratigraphic section of the Marna di Possagno in the quarry near Curogna, east of Possagno, with abundances of major foraminiferal groups. (1) Smaller benthonic Foraminifera only. Similarity index after Sanders (1960).

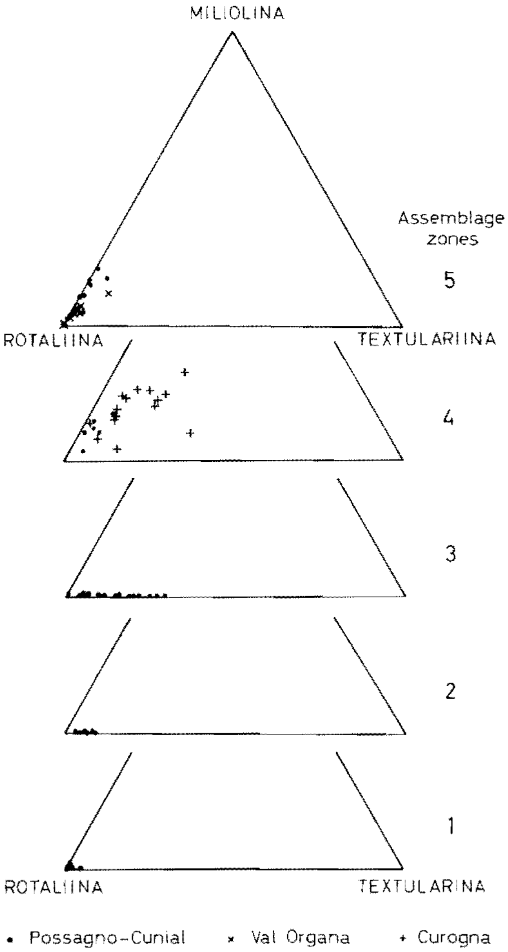


FIGURE 6

RTM-diagrams for assemblage zones 1 to 5 of the Marna di Possagno. Samples of the sections of Possagno-Cunial, Val Organa and Curogna are indicated with different symbols.

Chierici, 1966). In the Possagno section, the strongly ribbed *Uvigerina* (*U. spinicostata* and *U. eocaena*) also disappear at the limit between zones 3 and 4. These forms replace to a great extent the spinose uvigerinids of zones 1 and 2 and may form up to 40 percent of the total assemblage.

Zones 2, 3 and in part zone 4 are also noted for the diversity of bolivinid species (see discussion below).

Upper depth limits of *Cyclammina* are today 100 m or more (Murray, 1973).

Taking in account all these data, including the absence of larger Foraminifera, we can assume a bathymetric extension for zone 3 between around 600 m at the base and 150 m at the top.

ASSEMBLAGE ZONE 4

Many of the species which are typical for zone 3 or lower parts of the section, including the *Gyroidinoides soldanii*, the *Hoeglundina eocaenica*, and the *Cyclammina acutidorsata* groups, cannot be found any longer. The boundary between zones 3 and 4 therefore corresponds to a major faunal change.

Zone 4 is characterized by the joint occurrence of the *Bulimina midwayensis* and the *Quinqueloculina juleana* groups. Larger Foraminifera and mollusks are also typical.

A major gap of outcrops, corresponding to 90 m of sediment thickness, occurs in the Possagno section within zone 4. This interval is to a great extent covered by the section of Curogna 5 km east of Possagno (Figs. 1 and 5). Here, species of the *Bulimina midwayensis* and the *Quinqueloculina juleana* groups dominate all samples except for a few in the lowermost part, where *Uvigerina eocaena*, otherwise typical for zone 3, is still important. It is somewhat uncertain whether this part of the section should be placed in zone 3 or 4. With the presence of *Quinqueloculina juleana* and of larger Foraminifera we prefer to place it in zone 4. *Heterolepa dutemplei* and, in the uppermost samples, *Asterigerina bartoniana* are the most abundant species. With values between 60 and 85 percent the similarity indices are unusually high in the Curogna section. It is probable also that in Possagno zone 4 would form a quite homogenous unit.

The continuous presence of planktonic Foraminifera in abundances of less than 10 percent indicates open marine, shallow and nearshore conditions. Porcellaneous benthonic Foraminifera, which are very minor elements of the assemblages in zone 1 to 3, occur now in abundances of 5 to 30 percent. In the RTM-diagram (Fig. 6) the samples of zone 4 are therefore much more scattered than the samples of the other zones.

Phleger (1960) described an assemblage from the Gulf of Mexico at depths less than 100 m, which is very similar to that from zone 4 at Possagno, with several species of *Asterigerina*, *Quinqueloculina* with agglutinated grains and *Virgulina punctata*. The latter species is morphologically similar to our *Fursenkoina dibollensis*. A close relationship also exists between the assemblages from zone 4 and those from the Andaman Sea at depths between 46 and 100 m (Frerichs, 1970): *Sigmoilopsis asperula*, *Nonion scaphum*, and species of the genus *Cassidulina* in the Andaman Sea; *Sigmoilopsis* sp., *Nonion scaphum*, and *Globocassidulina globosa* at Possagno. Modern *Nonion scaphum* is also reported in depths of 30–70 m from the Solomon Islands area (Hughes, 1977).

Typical for zone 4 is the occurrence of larger Foraminifera. *Operculina alpina* alone occurs in low abundance (2 percent) at the base of the zone. In the higher parts of the zone it is associated with several species of small nummulites (Herb and Hekel, 1975), and total abundances of larger Foraminifera may be as high as 30 percent of the benthonic assemblages. Hottinger (1972, 1977) has found recent *Operculina ammonoides* at depths between 30 and 120 m, with a maximum frequency between 45 and 80 m, and *Heterocyclina tuberculata* down to the limit of the euphotic zone at 150 m. A water depth of not greater than 120–150 m can therefore be assumed for the lower part of assemblage zone 4. The upper limit of the zone is less distinct in the faunal record and a depth estimation is therefore made more difficult. It may be situated approximately between 30 to 40 m.

Assemblage Zone 5

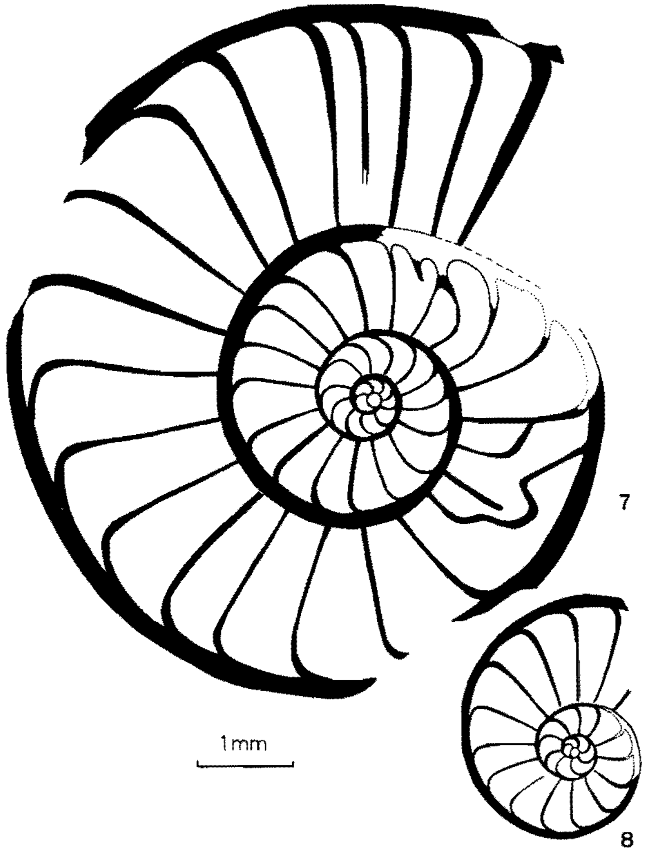
A rather gradual change in the composition of the smaller benthonic assemblages occurs in the upper part of the Possagno clay, within the Cunial section. The *Bulimina midwayensis* group is replaced by the *Pararotalia audouini* group and the latter, although discontinuously present in the Cunial section, is the most characteristic faunal element from sample 75 upward and defines zone 5. In the section of the Val Organa *Pararotalia audouini* and *Asterigerina adarkeyensis* occur more consistently and in higher percentages. Zone 5 can be particularly well defined in the Pamplona basin, where in four successive samples *Pararotalia audouini* was found in abundances of 74 to 100 percent. This reflects the fact that in these very shallow waters local environmental conditions vary to a great extent from one area to another, often within a short distance. Benthonic communities may therefore be subjected to important local or regional variations. Deviations from normal salinity must be taken into account in these environments. A typical example of this faunal variation is found in the uppermost sample in the Possagno-Cunial section (sample 130) where *Elphidium latidorsatum* is the dominant species. In the nearby Val Organa section (Fig. 4), in approximately the same stratigraphic level, this species occurs only rarely.

Abundances of planktonic Foraminifera vary between 0 and 10 percent, but may be as high as 40 percent due to reworking of middle Eocene species (Toumarkine and Bolli, 1975).

The number of smaller benthonic species, not counting the larger Foraminifera, decreases from between 20 to 30 in zone 4 to 21 at the base and 10 at the top of zone 5. Porcelaneous Foraminifera average 5 percent of the assemblages, but may occasionally reach 15 percent. In the RTM-diagram (Fig. 6) the samples are close to the RM line, in the field of a lagoon of normal to elevated salinity. In modern seas similar assemblages occur associated with seagrass or seaweed at depths of 0 to 35 m.

Larger Foraminifera, mainly *Discocyclina*, *Nummulites*, *Operculina*, and rarely *Spiroclypeus* and *Asterocyclina*, occur in abundances of up to 70 percent and prohibit the assumption of an important deviation from normal marine salinity. A steady decrease in the percentages of larger Foraminifera occurs in the uppermost part of the section, however. The sedimentological record also shows rapidly changing conditions in this interval; levels of loose sand with abundant mollusk debris, solitary corals and a lignitic layer are intercalated in the silty clay. The abundant occurrence of *Discorbis circularis* in a single sample at the top of the Val Organa section reflects such changes.

The specific spectrum of larger Foraminifera, especially of *Nummulites*, is quite particular. *Nummulites incrassatus ramondiformis*, *N. bouillei*, *N. pul-*



FIGURES 7, 8
Equatorial sections of *Operculina alpina* (megalospheric forms) from the Marna di Possagno and the Calcare di S. Giustina. Note the difference in size of the test and of the megalosphere. Figure 7. Calcare di S. Giustina, sample 728c, Val Organa section. Figure 8. Marna di Possagno, sample 674, section of Cunial. Location of samples see Herb & Hekel 1975, Figure 4. 12,5×.

chellus, *N. stellatus*, *N. cunialensis*, and *N. garnieri* occur in communities of small individuals where the size of the microspheric forms only slightly exceeds the megalospheric forms (Herb and Hekel, 1975). The absence or scarcity of some typical late Eocene forms, such as *Nummulites fabianii* and *Heterostegina*, is typical for the Marna di Possagno. The muddy and soft substratum does not seem to be an appropriate environment for them. These forms become abundant or common in the overlying limestone sequence of the Calcare di Possagno. *Nummulites fabianii* selectively occurs in great abundances in the hard siltstones intercalated in the upper part of the Marna di Possagno. It is possible that its scarcity in the lower part of zone 5 and the upper part of zone 4 is also related to increased water depth, which is unfavorable for this species.

As explained below, the transition from more striate to less striate and smooth bolivinids of the *B. nobilis–B. gracilis* sequence within zones 4 and 5 may indicate a reduced oxygen content of the water. This also could account for the particular nature of the assemblages of larger Foraminifera particularly with respect to their small size (Hallam, 1965).

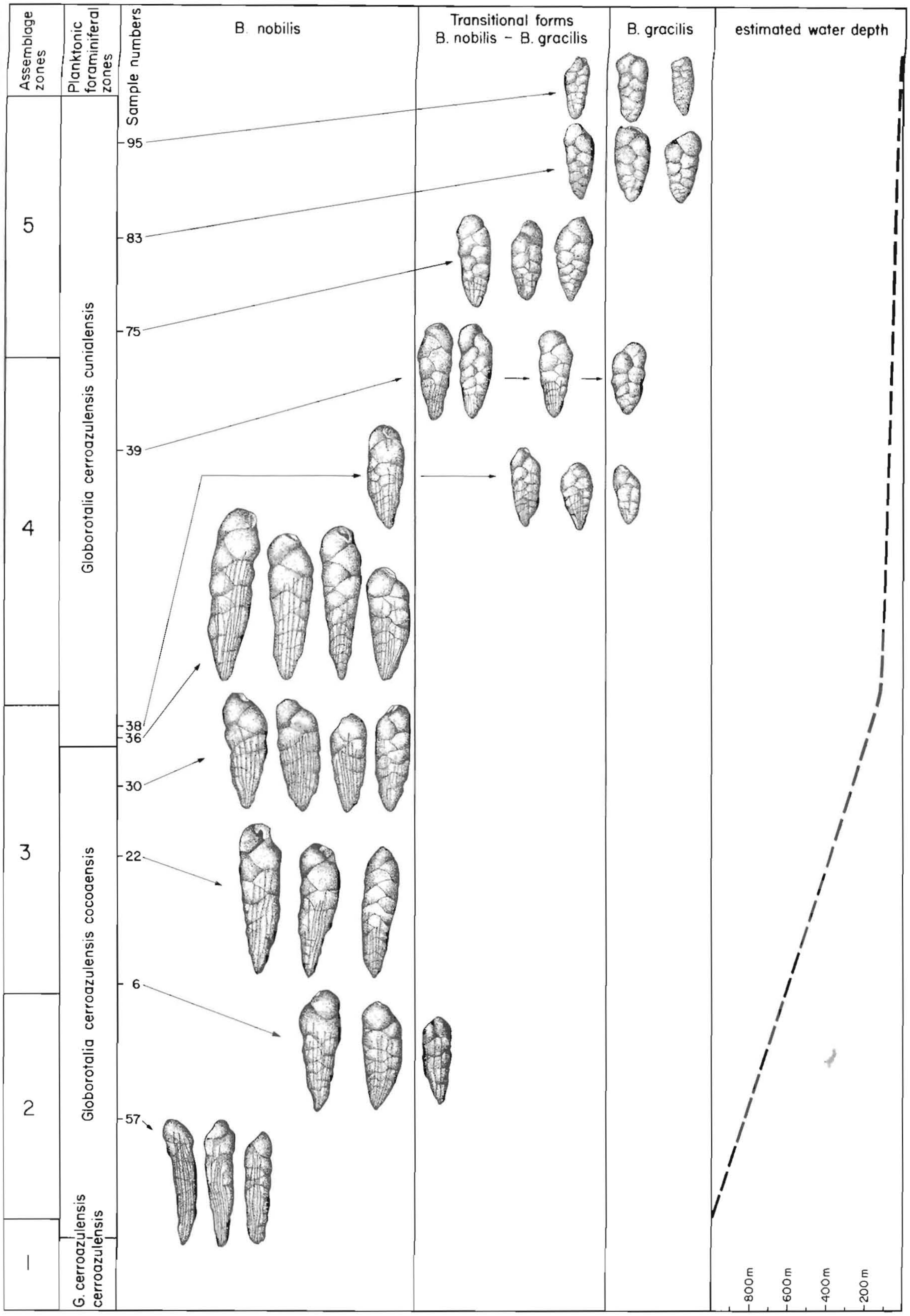
Arni (1965) has proposed an environmental scheme for nummulitid biofacies. The nummulites of the Marna di Possagno correlate closely with his "forebanc-facies" (faciès d'avant banc), which is characterized by the presence of mostly small nummulitid taxa.

Summarizing these data it seems appropriate to assume a further decrease of the water depth from approximately 30 to 40 m at the base of zone 5 to almost sea level at the top. Environmental conditions become variable in the upper part, with the possibility of slightly elevated salinities. The proliferation of the non-keeled *Elphidium latidorsatum* in sample 130 follows this interpretation.

The sudden change in the type of sedimentation at the boundary between the Possagno clay and the overlying S. Giustina limestone is mainly an effect of the reduced supply of terrigenous sediment, which enabled the coralline algae to develop in large quantities, whereas the water depth probably remained essentially unchanged. Thus we find in these limestones, particularly in their upper part, a more complete spectrum of larger Foraminifera, including *Heterostegina* and *Nummulites fabianii*, in which microspheric specimens reach normal diameters. In contrast, some of the small Nummulite species which are typical for the Possagno clay, such as *N. garnieri*, *N. pulchellus*, *N. bouillei*, *N. stellatus*, and *N. cunialensis*, do not occur in the limestones. The late Eocene strata of Possagno provide a good example of the distinct specialization of nummulitid species to certain environments, but the factors which are responsible for this are still not known (Herb and Hekel, 1973, 1975).

→

FIGURE 9
Stratigraphic distribution and phenotypic variation of the *Bolivina nobilis–Bolivina gracilis* lineage in the late Eocene Marna di Possagno. For sample locations see Figures 1 and 2. Estimated water depth values are in reference to the stratigraphic position of the samples at the left.


Assemblage zones
Planktonic foraminiferal zones
Sample numbers
B. nobilis
Transitional forms B. nobilis – B. gracilis
B. gracilis
estimated water depth
5
4
3
2
1
Globorotalia cerroazulensis cunialensis
Globorotalia cerroazulensis cocoaensis
G. cerroazulensis cerroazulensis
95
83
75
39
38
36
30
22
6
57
800m
600m
400m
200m

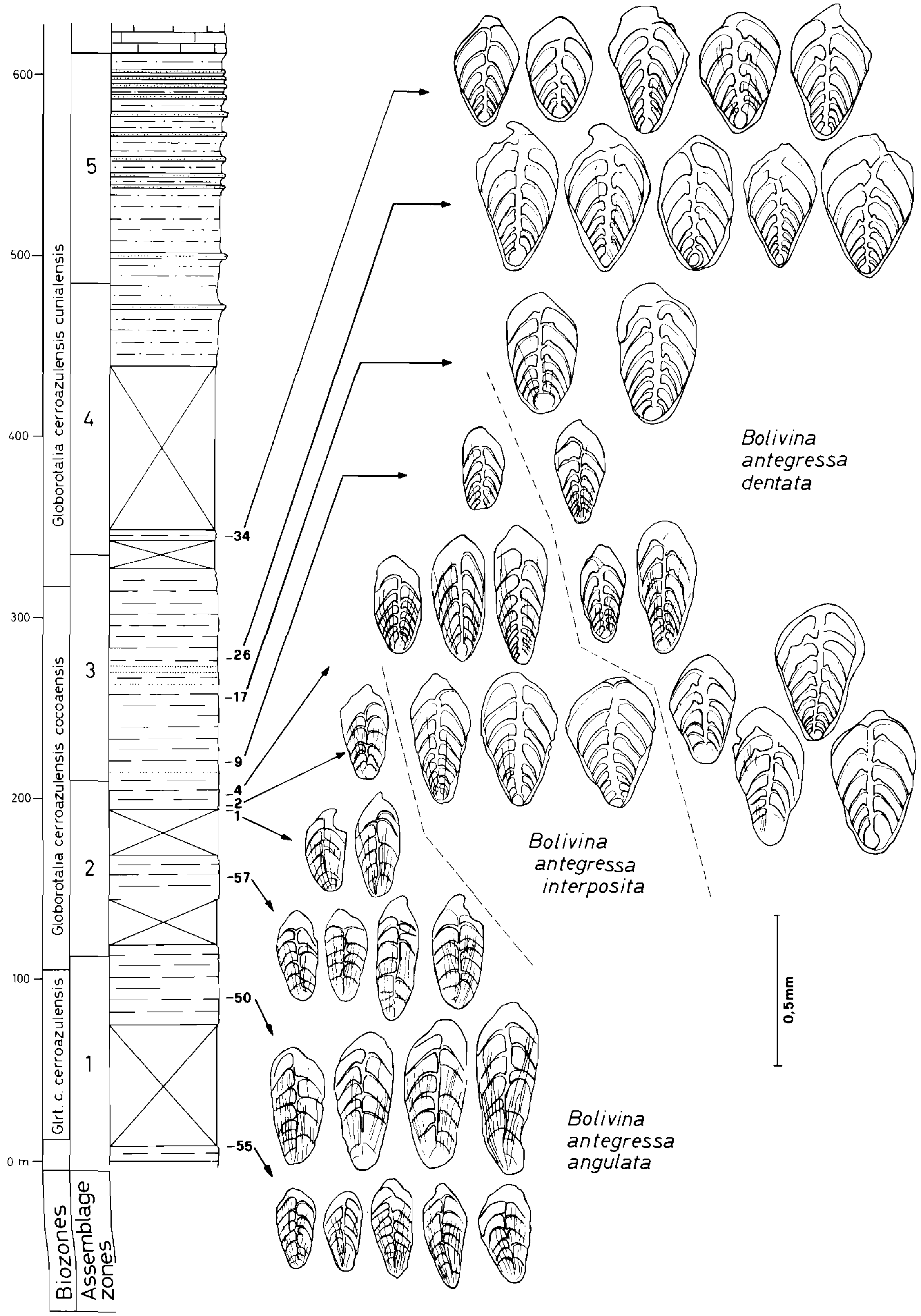


FIGURE 10
Stratigraphic distribution and phenotypic variation of the *Bolivina antegressa* lineage in the late Eocene of Possagno.

The section also exhibits the influence of particular environmental conditions on certain features of the test morphology in larger Foraminifera, such as the size of the test and, in some cases, the size of the megalosphere. Species like *Nummulites incrassatus ramondiformis* and *N. chavannesi*, which occur in the clay as well as in the carbonate facies, are smaller and show smaller diameters of the megalosphere in the Marna di Possagno than in the Calcare di S. Giustina. This trend is particularly significant in *Operculina alpina*. Megalospheric forms of this species are three times as large in the Calcare di S. Giustina and show megalospheres which are twice as large than the specimens from the Marna di Possagno (Figs. 7 and 8).

DISTRIBUTION OF SOME BOLIVINIDS

Bolivina nobilis and *Bolivina gracilis*

A number of bolivinid forms are important diagnostic species for certain assemblage zones of the Possagno section. Particularly interesting is the distribution and development of *Bolivina nobilis* Hantken and *Bolivina gracilis* Cushman and Applin. As shown in Figure 9 the two species are connected by intermediate forms. Typical *B. nobilis* has its distribution in the lower part of the section, in zones 2 and 3. It is followed by intermediate forms from the top of zone 3 to the middle of zone 5. Typical *B. gracilis* occasionally occur in the upper part of zone 3 and in the lower part of zone 4, but its main distribution ranges from the uppermost part of zone 4 throughout zone 5. In Figure 9 the phenotypic variation is shown for a selection of samples.

Specimens in sample 57 (zone 2) are slender forms with a length of approximately 0.6 mm. They are striate over nearly the entire length of the test.

In zone 3 (samples 6–38) the specimens reach their maximum length of 0.9 mm; the apex of the test is tapering and the ribs are restricted to the lower half or two-thirds of the test, leaving the last 3 (and sometimes more) chambers without ornamentation.

Between samples 38 and 95 (top of zone 3, zone 4, and zone 5) the tests become gradually smaller and broader, the smallest specimens having a length of only 0.3 mm. Ribs can only be noted on the early portion of the test and finally disappear on the specimens from sample 95.

The definition of several species within a lineage, such as shown in Figure 9, is certainly artificial. We call *B. nobilis* those forms which are longer than 0.5 mm and whose tests show fine ribs over at least half of their length. Specimens smaller than 0.45 mm, which show no ribs but instead have parallel rows of small pores, are, according to the original description by Cushman and Applin, called *B. gracilis*. Between the two we find transitional forms with tests smaller than 0.5 mm, which still show fine ribs on the early portion of the test.

It is interesting to compare this "ecologic lineage" with the phenotypic variation of *Bolivina argentea* in two recent basins off southern California (Lutze, 1964). This author distinguished a long, slender, unornamented basin form living in a low-oxygen environment, from a wider, keeled form with ribs, living in an oxygen-rich environment. The two are linked together by transitional forms. It is suggested here that the two "species" *B. nobilis* and *B. gracilis* from Possagno with their transitional forms may in fact represent such phenotypic variants of one and the same species. The question of whether in this case the variation is also caused by changes in the O_2 content of the water or by other ecologic factors cannot be definitely answered.

Bolivina antegressa with Subspecies

Sahakjan-Gezaljan (1960; *in* Akopiana and others, 1974) described three subspecies of *Bolivina antegressa* Subbotina from the Paleogene of the Erewan and Armenian basin (USSR) and proposed an evolutionary lineage from *B. antegressa angulata* in the middle Eocene to *B. antegressa dentata* in the Oligocene, with *B. antegressa interposita* (late Eocene and early Oligocene) as an intermediate form. It seemed, therefore, that these subspecies could be used as biostratigraphic markers.

Bolivina antegressa angulata is a small, slender form with a central keel and fine, subparalled ribs which may be limited to the first few chambers or are extended over the entire test. In *B. antegressa interposita* the fine ribs are more scarce; they are missing in *B. antegressa dentata*. The test is broader in *B. antegressa interposita* and trapezoidal in *B. antegressa dentata*. The elevated sutures show a tendency of forming dentitions in the "more evolved" forms, particularly in the last chambers.

Sahakjan-Gezaljan noted a general increase in the size of the test from older to younger forms. This seems to be mostly ecologically controlled, since the specimens from Northern Italy are definitely bigger in size than the ones from Spain and those described from the USSR.

The forms described by the Russian authors may eventually be junior synonyms of previously described species. *Bolivina tectiformis* Cushman seems to have an intermediate position between *B. antegressa angulata* and *B. antegressa interposita*. *Bolivina scalprata* Schwager is similar to *B. antegressa interposita*, but apparently is much more tapering in the initial portion. *Bolivina fastigia* Cushman is close to *B. antegressa dentata* except for its smaller size.

According to Lindenberg (1965) *Bolivina antegressa* Subbotina is a junior synonym of *Bolivina vaceki* Schubert. Within the Eocene/Oligocene group of *Bolivina vaceki* Lindenberg has distinguished a number of species or subspecies using biometrical data, such as the relations of length to width or width to thickness of the test. Although Lindenberg's approach may be more correct with respect to the rules of priority, we prefer, for the time being, to adopt the nomenclature of Sahakjan-Gezaljan, since it seems to be more suitable for the definition of morphotypes in the Possagno section. We are aware, however, that both ways of handling the taxonomy are in some respect artificial. The usage of subspecies in gradational sequences, as described here for the *Bolivina antegressa* group is not in accordance with a biological concept of subspecies. Lindenberg (1965) has discussed these problems in detail.

In the Possagno section *Bolivina antegressa* ssp. is found between the lower part of zone 1 and the base of zone 4, with occasional occurrences near the top of zone 4. In zone 1 and in the major part of zone 2 only *Bolivina antegressa angulata* is present. This subspecies discontinuously persists up to the lowermost part of zone 3. *Bolivina antegressa interposita* and *Bolivina antegressa dentata* show similar stratigraphic ranges between the uppermost part of zone 2 to the top of zone 4. *Bolivina antegressa interposita* dominates in zone 2 and the lower part of zone 3, *Bolivina antegressa dentata* in the middle part of zone 3. No definite trends, however, exist in the upper part of zone 3 and zone 4. The distribution and phenotypic variation is shown in Figure 10.

As indicated above, *Bolivina antegressa dentata* is restricted to the Oligocene in its type area. *Bolivina scalprata*, probably synonymous with *antegressa dentata*, has been reported from the Oligocene of Belgium (Batjes, 1958). The occurrence of this form in the late Eocene of Possagno (*Globorotalia cerroazulensis cocoaensis* and *G. cerroazulensis cunialensis* zones) may be interpreted as being to a great extent ecologically controlled, *Bolivina antegressa angulata* preferring deeper water than the other two subspecies. A possible correlation with the oxygen content of the water is not indicated, however.

In the Pamplona basin of Northern Spain only *Bolivina antegressa angulata* was found and occurs in equivalents of zones 2 and 3 (lower half). It has therefore a similar paleobathymetric extension as in Possagno. The fact that the other two subspecies are missing in the respective assemblage zones may be due to the slightly greater age of the section (uppermost middle to lowermost late Eocene). This in turn is an indication that we are in fact dealing with an evolutionary sequence in which the more evolved two subspecies are both developed during the late Eocene and their occurrence is also ecologically controlled.

DISTRIBUTION OF METAZOA

Solitary corals, pelecypods, scaphopods and gastropods are abundant throughout the upper part of the Marna di Possagno. For the present study collections were made at 10 different levels of the Cunial quarry section. Based on these samples, the distribution of megafossils are briefly discussed, but no detailed analysis can be attemped at present. The megafauna of the Marna di Possagno was the subject of "classic" monographs by Vinassa de Regny (1896–1898) and Oppenheim (1901). It has been recently redescribed in an unpublished thesis by Simonetto (1969).

The lowermost occurrences of a few gastropods and pelecypods were noted in the small quarry just south of the main road (samples 34–35, Fig. 2) and west of Cunial (samples 36–38).

In the section of the Cunial quarry solitary corals, gastropods, scaphopods, and pelecypods are abundant from the base to the top. They are, however, in most cases very fragile and for many species it is very difficult or even impossible to obtain undamaged specimens. The most striking element of the assemblages are certainly the solitary corals. They belong to 8 species, the 4 most common being *Trochosmilia irregularis* (Deshayes), *Pattalophyllia subinflata* (Catullo), *Cycloseris orbicularis* (Catullo), and *Cycloseris patera* (d'Achiardi). All collected specimens of the discoid *Cycloseris orbicularis* and the patellate *C. patera* show a flat *Discocyclina* attached to them in the center of the lower face.[1] They obviously used the tests of these larger Foraminifera as a substrate for their growth in this muddy sediment. In the trochoid *Trochosmilia irregularis* and *Pattalophyllia subinflata* such an observation could not be made, possibly because the elongated and tapering basis of the individuals is usually broken. In one case of *Trochosmilia*

---

[1] Observation made by Therese Pfister, who also identified the species of solitary corals and collected most of the megafossils in the field.

irregularis an attachment on a Bryozoan fragment could be seen, but in some other specimens where the initial portion is almost completely preserved, it cannot be decided whether they were attached to a solid substratum or were directly growing on the muddy sediment.

Among the 50 species of gastropods *Turritella gradataeformis* v. Schauroth is the most abundant form. Its main distribution is in the lower and middle part of the Cunial section (top of zone 4 and lower half of zone 5). It is significantly less frequent in the upper part of zone 5 and seems to be missing in approximately the uppermost 30 m. Van Straaten (1960) found living *Turritella* in the delta of the Rhone River to be abundant only at depths of less than 50 m, with a maximum frequence between 10 and 30 m. These values are similar or slightly less than the water depth proposed for the interval of maximum occurrence in Possagno. Large naticids belonging to several species, as well as *Dentalium* (Scaphopoda), are further typical elements of the Possagno megafauna.

The pelecypods are represented by at least 28 species. Our preliminary survey has so far not shown significant trends in their vertical distribution. The occurrence of a narrow stratigraphic interval with abundant *Pinna helvetica* Mayer could be observed close to sample 84.

REGIONAL ASPECTS

In the Pamplona basin of Northern Spain, between the villages of Sansoain and Indurain, a regressive sequence of more than 3,000 m thickness beginning with a basin facies at the top of a flysch and ending with deltaic sediments was investigated in the same way as the Possagno section. A good number of diagnostic species, such as *Gyroidinoides soldanii, Clavulina parisiensis, Bolivina nobilis, Bolivina gracilis, Bolivina antegressa angulata, Uvigerina eocaena, Pararotalia audouini*, and others were found in the same succession and permit the same distinction of assemblage zones as for Possagno. An exception must be made for assemblage zone 1 which was not found in the Pamplona basin, the whole *Nuttallides truempyi* group being absent. It is interpreted that the deepest part of the basin was shallower than a depth corresponding to zone 1. Zone 5 is distinctly different in the two areas, *Pararotalia audouini* being very abundant in all samples from this zone in the Sansoain-Indurain section.

A detailed account and discussion of the assemblages from Northern Spain will be given elsewhere. It may be noted here, however, that the faunas from Northern Italy and Northern Spain differ considerably from each other in their species composition. Sixty-eight species occur in both areas, 53 only in Possagno, 32 only in Sansoain-Indurain.

Compared with the Possagno assemblages the faunas from the Pamplona basin show a much greater percentage of arenaceous Foraminifera throughout the section. This is probably due to the greater supply of detrital sediment and in the uppermost part to low salinity conditions in the deltaic environment.

The Possagno fauna, in contrast, compares well with other late Eocene occurrences of Northern Italy. Zones 1 to 3 show a close relationship to the faunas from Varignano (Monte Brione, Hagn, 1956) and from Nago and the Monte Baldo (Castellarin and Cita, 1969); zones 3 to 5, to late Eocene assemblages from the Colli Berici (Ungaro, 1969, Broglio-Loriga, 1969), except for the abundant occurrence of *Queraltina* and *Schlosserina* in this area, two genera which have not been found in Possagno.

CONCLUSIONS

According to the present data the stratigraphic distribution of fossil assemblages in the Possagno section is primarily related to water depth. This does not, however, necessarily imply that water depth was the only physical factor of importance. It may in many cases as well be the expression of other parameters; the penetration of light is a major factor for the existence of larger Foraminifera which carry zooxanthellae in their protoplasma. The important faunal change in the assemblages of smaller benthonic Foraminifera which occurs between zones 3 and 4, may thus be related to the limit of the euphotic zone. Other parameters are difficult to evaluate, and the interpretation of our data must in most instances be limited to an estimation of the water depth for the five assemblage zones recognized in this paper. This estimation, however, corresponds well to the interpretation of water depths obtained independently on the same section by the distribution of Ostracods (Ascoli, 1969).

The present results may serve as a guide for interpreting bathymetric relationships of Eocene benthonic Foraminifera in other areas. A first step in this direction has been made by the investigation of a section in the Pamplona Basin of Northern Spain. It shows that a bathymetric zonation, such as the one established in this paper, can be applied to other areas, since many of the diagnostic species used for establishing the zones are cosmopolitan forms. Faunal provincialism, as expressed by the selective occurrence of other species in one or the other area or, in some cases, different distributions with respect to the assemblage zones so far prohibit a more detailed zonation.

In the shallow-water environment of zone 5 the local ecologic conditions are of much greater influence on the specific composition of the assemblages than in deeper water, a well known fact in modern environments. Regional and local differences are therefore more pronounced in our zone 5 and their effects are superimposed on the bathymetric zonation. In some cases it is possible to give estimates about ecologic parameters of major importance, particularly concerning the salinity of the water. In other cases such estimations are difficult or so far impossible to give.

ACKNOWLEDGMENTS

The present work was supported by the Swiss National Science Foundation. Special thanks are expressed to Franca Proto Decima, Giampietro Braga, and Hanspeter Luterbacher for many helpful discussions and suggestions, to Thérèse Pfister for her cooperation in the field work and for identification of the megafossils, and to Jean-Pierre Beckmann for critically reading the first draft of the manuscript.

REFERENCES

Akopiana, B. T., and others, 1974, Atlas iskopajemoi fauni Armianskoi CCR. Jerewan.

Arni, P., 1965, L'évolution des Nummulitinae en tant que facteur de modification des dépôts littoraux: (France) Bur. Recherches Géol. et Minières Mém., v. 32, p. 7.

Ascoli, F., 1969, First data on the Ostracod biostratigraphy of the Possagno and Brendola sections (Paleogene, NE Italy): (France) Bur. Recherches Géol. et Minières Mém., v. 69, p. 51–71.

———, 1975, Gli Ostracodi della Sezione paleocenico-eocenica di Possagno, in Bolli, H. M., ed., Monografia micropaleontologica sul Paleocene e l'Eocene di Possagno, Provincia di Treviso, Italia: Schweizer. Paläont. Abh., v. 72, p. 137–139, 213–215.

Aubert, J., and Berggren, W. A., 1976, Paleocene benthic foraminiferal biostratigraphy and paleoecology of Tunisia: Centre Recherches Pau Bull., v. 10, p. 379–469.

Bandy, O. L., 1953, Ecology and paleoecology of some California foraminifera. Part I. The frequency distribution of recent Foraminifera off California: Jour. Paleontology, v. 27, p. 161–182.

Bandy, O. L., and Chierici, M. A., 1966, Depth-temperature evaluation of selected California and Mediterranean bathyal foraminifera: Marine Geology, v. 4, p. 259–271.

Bandy, O. L., and Kolpack, R. L., 1963, Foraminiferal and sedimentological trends in the Tertiary section of Tecolote Tunnel, California: Micropaleontology, v. 9, p. 117–170.

Batjes, A. J., 1958, Foraminifera of the Oligocene of Belgium: Belgique Inst. Royal Sci. Nat. Mém. 143, p. 186.

Berggren, W. A., 1974, Late Paleocene-early Eocene benthonic foraminiferal biostratigraphy and paleoecology of Rockall Bank: Micropaleontology, v. 20, p. 426–448.

Berggren, W. A., and Aubert, J., 1975, Paleocene benthonic foraminiferal biostratigraphy, paleobiogeography and paleoecology of Atlantic-Tethyan regions: Midway-type fauna: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 18, p. 73–192.

Blanc-Vernet, L., 1969, Contribution à l'étude des Foraminifères de Méditerranée: Receuil Trav. Stat. mar. Endoume, v. 48, p. 281.

Braga, G., 1970, L'assetto tettonico dei dintorni di Possagno (Trevigiano occidentale): Acad. Naz. Lincei Sci. Fis. Mat. Nat. (8), v. 48, p. 451–455.

Braga, G., de Biase, R., Grünig, A., and Proto Decima, F., 1975, Foraminiferi bentonici del Paleocene ed Eocene della Sezione di Possagno, in Bolli, H. M., ed., Monografia micropaleontologica sul Paleocene e l'Eocene di Possagno, Provincia di Treviso, Italia: Schweizer. Paläont. Abh., v. 97, p. 85–111, 187–199.

Brasier, M. D., 1974, Morphology and habitat of living benthonic foraminiferids from Carribean carbonate environments: Rev. Española Micropaleontologia, v. 7, p. 567–578.

Braun-Blanquet, J., 1928, 1951, 1964, Pflanzensoziologie. Grundzüge der Vegetationskunde: Biologische Studienbücher 7. 1st ed. Berlin, 2nd and 3rd ed. Wien.

Broglio-Loriga, C., 1969, I Foraminiferi bentonici delle Marne a Briozoi di Brendola (Vicenza, Colli Berici): (France) Bur. Recherches Géol. et Minières Mém., v. 69, p. 83–92.

Le Calvez, Y., 1970, Contribution à l'étude des Foraminifères paléogènes du Bassin de Paris. Cahiers Paléontol.

Caralp, A., Lamy, A., and Pujos, M., 1970, Contribution à la connaissance de la distribution bathymétrique des Foraminifères dans le Golf de Gascogne: Rev. Española Micropaleontologia, v. 2, p. 55–84.

Castellarin, A., and Cita, M. B., 1969, Etude de quelques coupes priaboniennes dans le Monte Baldo (Prov. Verona et Trento, Italie) et discussion des limites de l'étage.—La coupe priabonienne de Nago (Prov. Trento) et la limite Eocène-Oligocène: (France) Bur. Recherches Géol. et Minières Mém., v. 69, p. 93–103, 119–139.

Cita, M. B., 1975, Stratigrafia della Sezione di Possagno, in Bolli, H. M., ed., Monografia micropaleontologica sul Paleocene e l'Eocene di Possagno, Provincia di Treviso, Italia: Schweizer. Paläont. Abh., v. 97, p. 9–32.

Cita, M. B. and others, 1968, Guide de l'excursion en Italie. Colloque sur l'Eocène: Comité français de Stratigraphie, p. 82.

Ellenberg, H., 1956, Aufgaben und Methoden der Vegetationskunde, in Walter, H., Einführung in die Phytologie, v. 4, p. 1–136, Stuttgart.

Frerichs, W. E., 1970, Distribution and ecology of benthonic Foraminifera in the sediments of the Andaman Sea: Cushman Found. Foram. Research Contr., v. 21, p. 123–147.

Grünig, A., 1977, Paläoökologische Untersuchungen an eozänen benthonischen Kleinforaminiferen aus Norditalien und Nordspanien: Unpublished Dissertation Univ. Bern.

Hagn, H., 1956, Geologische und paläontologische Untersuchungen im Tertiär des Monte Brione und seiner Umgebung (Gardasee, Oberitalien): Palaeontographica, Bd. 107, Abt. A, p. 69–210.

Hallam, A., 1965, Environmental causes of stunting in living and fossil marine benthonic invertebrates. Paleontol., v. 8, pt. 1, p. 132–155.

Herb, R., and Hekel, H., 1973, Biostratigraphy, variability and facies relations of some upper Eocene Nummulites from northern Italy: Eclogae geol. Helvetiae, v. 66, p. 419–445.

———, 1975, Nummuliten aus dem Obereocaen von Possagno, in Bolli, H. M., ed., Monografia micropaleontologica sul Paleocene e l'Eocene di Possagno, Provincia di Treviso, Italia: Schweizer. Paläont. Abh., v. 97, p. 113–135, 201–211.

Hiltermann, H., 1973, Zur Soziologie von agglutinierenden Foraminiferen polarer, skandinavischer und äquatorialer Meere: Geol. Jahrb., ser. A., v. 6, p. 101–120.

Hiltermann, H., and Tüxen, J., 1973, Biosociology of recent benthonic Foraminifera after the Braun-Blanquet method: Rev. Española Micropaleontologia, v. 6, p. 75–84.

Hottinger, L., 1972, Larger Foraminifera in the Gulf of Elat (Red Sea), a provisional inventory: Hebrew Univ. Jerusalem, Dept. Geol., p. 5.

———, 1977, Foraminifères operculiniformes: Mus. Natl. Histoire Nat. Mém., n. sér., sér. C, v. 40, 159 p.

Hughes, G. W., 1977, Recent Foraminifera from the Honiara Bay area, Solomon Islands: Jour. Foram. Research, v. 7, p. 45–57.

Ludwick, J. C. and Walton, W. R., 1957, Shelf-edge, calcareous prominences in the northeastern Gulf of Mexico: Bull. Am. Assoc. Petroleum Geologists, v. 41, p. 2054.

Lutze, G. F., 1964, Statistical investigations on the variability of *Bolivina argentea* Cushman: Cushman Found. Foram. Research Contr., v. 15, p. 105–116.

McGlasson, R. H., 1959, Foraminiferal biofacies around Santa Catalina Island, California: Micropaleontology, v. 5, p. 217–240.

Murray, J. W., 1973, Distribution and Ecology of Living Benthic Foraminiferids: London, Heinemann Educational Books, 274 p.

Murray, J. W., and Wright, Ch. A., 1974, Paleogene Foraminiferida and Paleoecology, Hampshire and Paris Basin and English Channel: Spec. Papers Palaeontology, v. 14, p. 274.

Oppenheim, P., 1901, Die Priabonaschichten und ihre Fauna in Zusammenhang mit gleichaltrigen und analogen Ablagerungen: Palaeontographica 47, p. 348.

Parker, F. L., 1957, Eastern Mediterranean Foraminifera: Swedish Deep-sea Exped. Rept., v. 8, Sediment cores from the Mediterranean Sea and the Red Sea, no. 4.

Phleger, F. B., 1960, Ecology and distribution of recent Foraminifera: Baltimore, John Hopkins Press, 297 p.

Phleger, F. B., and Ewing, G. C., 1962, Sedimentology and oceanography of coastal lagoons in Baja California, Mexico: Geol. Soc. America Bull., v. 73, p. 145–181.

Sahakjan-Gezaljan, H. A., 1960, K woprosy isutschenja sony Bolivina w tretitschnich otloschenjach juga SSSR: Akad. Nauk Armyan, SSR Izv., v. 13.

Sanders, H. L., 1960, Benthic studies in Buzzards Bay III. The structure of the soft-bottom community: Limnology and Oceanography, v. 5, p. 138–153.

Simonetto, G., 1969, Studio paleontologico sulla fauna delle marne nummulitiche delle Cave di Cunial (Priaboniano)—Trevigiano Occidentale: Thesis Univ. Padova (unpublished).

Toumarkine, M., and Bolli, H. M., 1970, Evolution de Globorotalia cerroazulensis (Cole) dans l'Eocène moyen et supérieure de Possagno (Italie): Rev. Micropaléontologie v. 13, p. 131–145.

———, 1975, Foraminifères planctoniques de l'Eocène moyen et supérieur de la coupe de Possagno *in* Bolli, H. M., ed., Monografia micropaleontologica sul Paleocene e l'Eocene di Possagno, Provincia di Treviso, Italia: Schweizer. Paläont. Abh., v. 97, p. 69–83, 173–185.

Ungaro, S., 1969, Etude micropaléontologique et stratigraphique de l'éocène supérieur (Priabonien) de Mossano (Colli Berici): (France) Bur. Recherches Géol. et Minières Mém., v. 69, p. 267–281.

Van Straaten, L. M. J. U., 1960, Marine mollusc shell assemblages of the Rhône Delta: Geologie en Mijnbouw, v. 39, p. 105–129.

Vinassa de Regny, P. E., 1897, Synopsis dei Molluschi Terziarii delle Alpi Venete. Paleontographia Ital., v. 3, p. 145.

Walton, W. R., 1964, Recent foraminiferal ecology and paleoecology, *in* Imbri, J. and Newell, N. D., eds., Approaches to Paleoecology, New York, Wiley, p. 151–237.

Wright, Ch. A., and Murray, J. W., 1972, Comparisons of modern and paleogene foraminiferid distributions and their environmental implications: (France) Bur. Recherches Géol. et Minières Mém., v. 79, p. 87–96.

PLANKTONIC FORAMINIFERAL ECOLOGY and PALEOECOLOGY

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 89–95, 1980

AGULHAS CURRENT TEMPERATURE DISTRIBUTION DELINEATED BY OXYGEN ISOTOPE ANALYSIS OF FORAMINIFERA IN SURFACE SEDIMENTS

EDITH VINCENT[1] AND NICHOLAS J. SHACKLETON[2]

ABSTRACT

The oxygen isotopic composition of *Globigerinoides sacculifer* in 30 surface sediment samples from the southwestern Indian Ocean has been measured. The coverage is sufficient to enable isotherms to be constructed from isotopically estimated temperatures, which reflect the effect of the Agulhas Current. The isotopic measurements indicate near summer temperatures. Isotopic analysis of samples from the 18,000 B.P. level in cores should permit paleo-isotherms to be constructed for the Agulhas Current of the glacial period.

INTRODUCTION

Following the discovery of the oxygen isotope method of estimating paleotemperatures (Urey, 1947) and its development to the point of being a useful tool (Epstein and others, 1951, 1953), Emiliani (1955) applied the method to fossil foraminifera. Emiliani (1966) has emphasized the fact that the areas from which his data are derived, the Caribbean and the Equatorial Atlantic, are areas of very small seasonal temperature range. Thus the isotopic values obtained should correspond to mean annual temperature, whatever seasonal variations there may be in abundance. A second feature of the areas from which the best oxygen isotope data have so far been obtained is that all have rather similar temperature today. The Carribean studied by Emiliani, the central equatorial Indian Ocean studied by Oba (1969), and the western equatorial Pacific studied by Shackleton and Opdyke (1973) all have surface temperatures about 27°C. Little attempt to delineate temperature gradients during the Pleistocene has been made for this reason.

In this study we present isotopic analysis of a single planktonic foraminiferal species, *Globigerinoides sacculifer* (Brady) in 32 surface sediment samples from the southern Mozambique Channel and adjacent southwest Indian Ocean, covering a temperature range from a summer high around 27°C in the north, to a winter low about 17°C in the southeast.

THE REGIONAL SETTING

This investigation is based on samples collected by the late Dr. Orville L. Bandy in 1964 during the International Indian Ocean Expedition on Cruise 7 of R.V. ANTON BRUUN. Sediment distribution and planktonic foraminiferal trends in samples of this expedition were investigated in detail by Vincent (1972, 1976). Figure 1 shows the bathymetry of the area and the location of the samples selected for this study, which are core-tops (0–2 cm) of short gravity cores (Table 1). The area is of rugged submarine topography. It includes narrow shelves, steep slopes, the Mozambique and Madagascar Ridges at an average depth of 2,000 m, and the northern portion of the deep Mozambique Basin. A number of submarine canyons cross the slopes of the area.

This region is the source area of the Agulhas Cur-

---

[1] Scripps Institution of Oceanography, La Jolla, California.

[2] Sub-department of Quaternary Research, University of Cambridge, England, and Lamont-Doherty Geological Observatory of Columbia University, Palisades, New York.

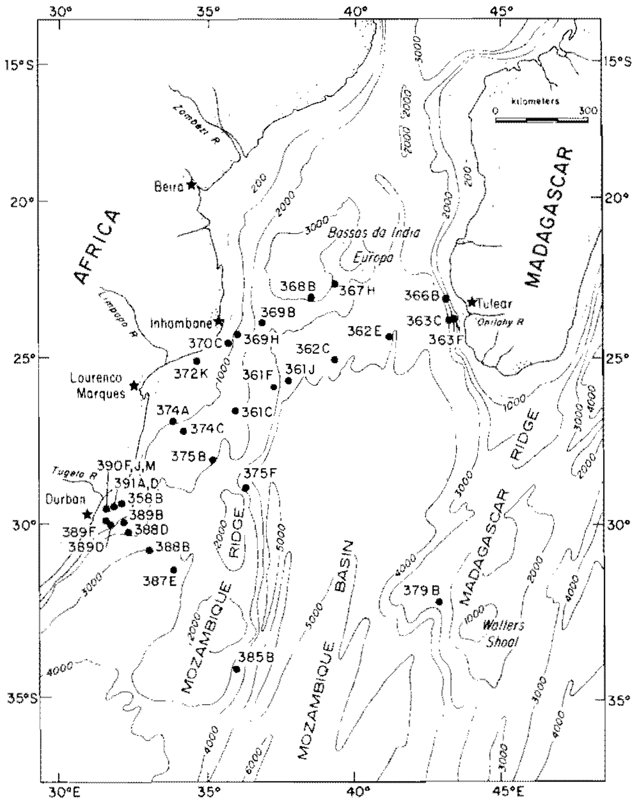


FIGURE 1

Bathymetry (adapted from Heezen and Tharp, 1966) and cores location.

rent, the western boundary current of the South Indian Ocean (Fig. 2). The Agulhas Current is a result of the merging of the Mozambique Current and the East Madagascar Current, both of which in turn derive from the South Equatorial Current (Michaelis, 1923; Dietrich, 1935; Schott, 1935; Orren, 1963, 1966; Darbyshire, 1964; Ménaché, 1963). Based on the large amount of data collected during the International Indian Ocean Expedition, recent comprehensive studies (Duncan, 1970; Wyrtki, 1971; Harris, 1972) have shown the complexity and pronounced seasonal variations of the supply of water to the Agulhas Current. The Mozambique-Madagascar-Agulhas current system is dependent on the South Equatorial Current, which varies seasonally in width and transport.

The relationship between sediment distribution and oceanographic factors was evaluated by Vincent (1976). Areas of nondeposition on parts of the African shelf and upper slope reflect the winnowing action of the Mozambique-Agulhas Current. The Mozambique Ridge, on which manganese nodules are abundant, is swept by an eddy of intermediate water. Displaced sedments occur in places, usually associated with submarine canyons, and are especially common in the Zambezi Canyon. Mozambique Basin sediments include pelagic clay associated with manganese nodules and turbidite layers derived from neritic and bathyal depths. Only undisturbed cores of calcareous ooze were selected for this study.

TABLE 1

Location of samples selected from cruise 7 of R.V. ANTON BRUUN (corers were used in tandem. Cores from each pair were differentiated by using the sign x or o following the station number).

Core	Interval (cm)	Latitude S	Longitude E	Water depth (m)
358 B x	0–2	29°20′	31°59′	421
361 C x	0–2	26°33′	36°00′	1,829
361 F x	0–2	25°50′	37°21′	2,750
361 J x	0–2	25°39′	37°45′	3,800
362 C o	0–2	24°54′	39°26′	3,570
362 E o	0–2	24°16′	41°25′	3,950
363 C x	0–2	23°45′	43°10′	2,980
363 F x	0–2	23°40′	43°21′	1,860
366 B o	0–2	23°09′	43°08′	2,300
367 H x	0–2	22°40′	39°21′	3,140
368 B x	0–2	23°01′	38°37′	2,995
369 B o	0–2	23°48′	37°46′	2,270
369 H x	0–2	24°12′	36°01′	1,185
370 C x	0–2	24°25′	35°37′	910
372 K x	0–2	25°07′	34°34′	106
374 A o	0–2	26°55′	33°50′	896
374 C o	0–2	27°09′	34°09′	1,335
375 B o	0–2	28°00′	35°16′	1,910
375 F o	0–2	29°03′	36°43′	3,840
379 B o	0–2	32°23′	42°56′	2,600
379 B x	0–2	id	id	id
385 B x	0–2	34°15′	35°59′	3,150
387 E o	0–2	31°23′	33°48′	3,260
388 B x	0–10	30°48′	32°58′	3,090
388 D x	2–8	30°19′	30°18′	1,820
389 B x	0–2	30°10′	32°04′	1,355
389 D o	0–2	30°10′	31°37′	930
389 F o	0–2	29°57′	31°31′	715
390 F x	0–2	29°38′	31°36′	200
390 J x	0–2	29°35′	31°38′	156
390 M x	0–2	29°34′	31°39′	115
391 A o	0–2	29°29′	31°45′	86
391 D o	0–2	29°26′	31°46′	77

Figure 3 shows the northeast-southwest-trending winter surface isotherms which reflect the current circulation pattern. Summer data are sparse; however, compilation of observations of various expeditions (Fig. 4) shows that the yearly surface temperature variation throughout the area is about 4°C, being greatest in the region of the Agulhas Current (up to 6°) and least in the area near Tulear (about 3°C).

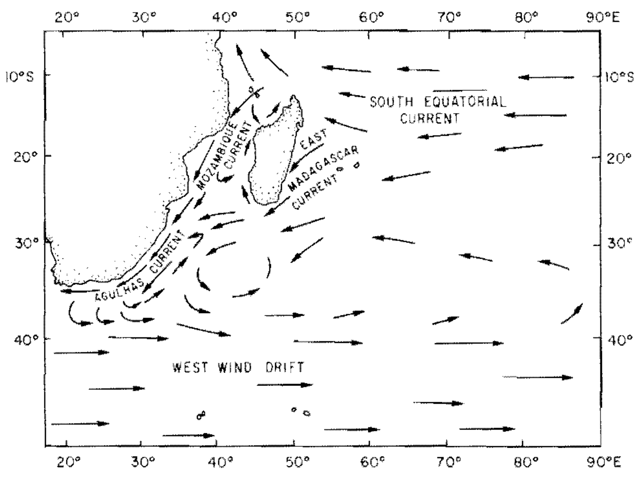


FIGURE 2
Surface currents in the southwest Indian Ocean (from Vincent, 1976).

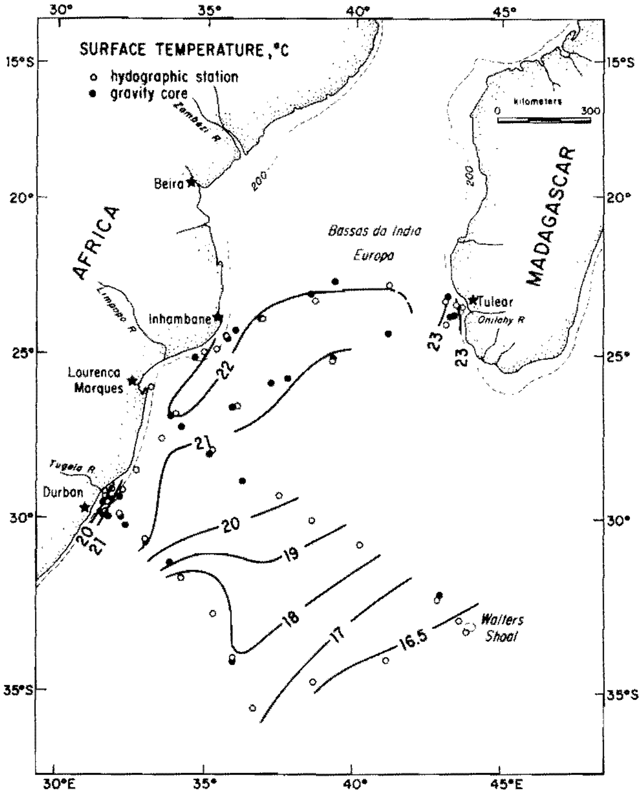


FIGURE 3
Surface water temperature in the southwest Indian Ocean for July 29 to September 9, 1964 (the austral winter). R.V. ANTON BRUUN data, Cruise 7. Temperatures greater than 23°C and lower than 16.5°C are not contoured. (Adapted from Vincent, 1976).

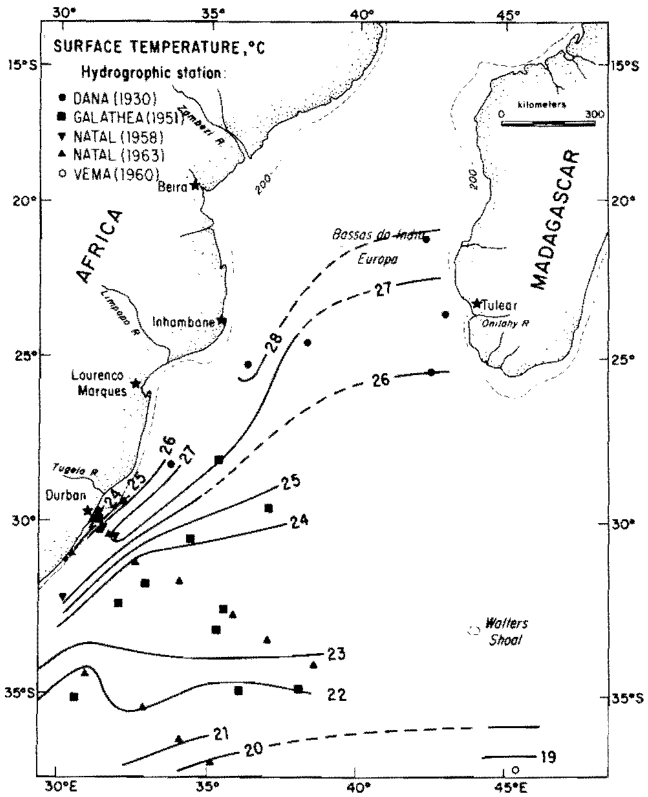


FIGURE 4
Surface water temperature in the southwest Indian Ocean for the months of January and February (the austral summer).

The planktonic foraminiferal fauna is diversified and typical of warm water. There is a general agreement between distributional patterns of planktonic foraminiferal species in surface waters (Bé and Tolderlund (1971) and in surface sediments of the area (Vincent, 1976). Both living and dead assemblages reflect the Agulhas Current pattern. Tropical species are predominant in the Mozambique Channel and along the African coast and decrease in relative abundance toward the southeast of the area, while temperate species show the reverse trend. For example, *Globigerinoides sacculifer* comprises 15 to 30 percent of the planktonic fauna in the surface sediments of the northern and western parts of the area and decreases southeastward to approximately 5 percent (Fig. 5).

OXYGEN ISOTOPE ANALYSIS

For each analysis about 20 specimens of *G. sacculifer* were extracted from selected core tops. These were lightly crushed to give access to inner chambers and cleaned ultrasonically to remove adhering mate-

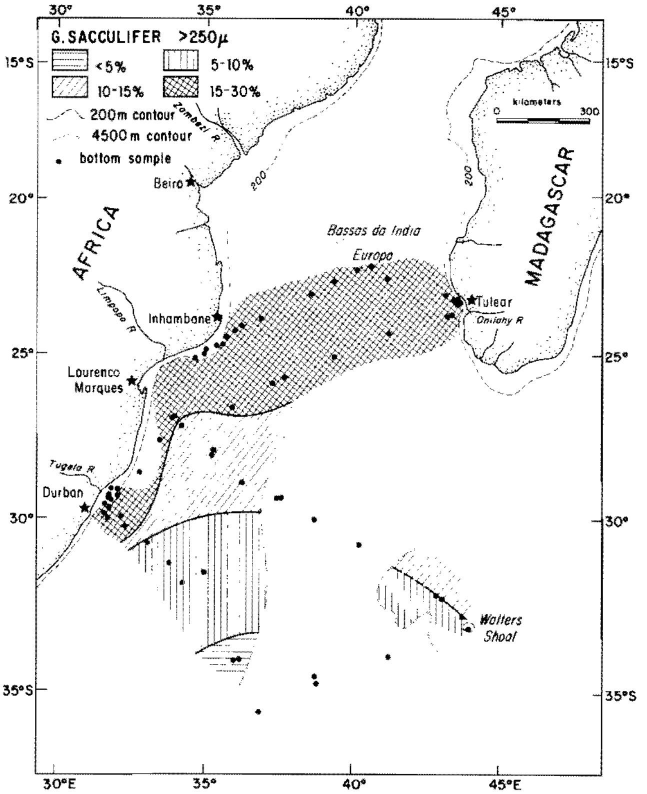


FIGURE 5

Relative frequency of *Globigerinoides sacculifer* in the planktonic foraminiferal fauna coarser than 250 microns in surface sediments. Bottom samples collected during cruise 7 of R.V. ANTON BRUUN (From Vincent, 1976.)

rials. Volatile organic impurities were removed by roasting at 450°C for 30 minutes in a vacuum. Carbon dioxide was released using 100 percent orthophosphoric acid at 50°C, and analyzed in a V. G. Micromass 602C mass spectrometer. Calibration to the P.D.B. standard of Epstein and others (1951) is effected by analyzing standard carbonates in the same manner, and in particular, Emiliani's belemnite standard B-1, which stands +0.29 per mil on the P.D.B. scale (Friedman, personal comm.; Shackleton, 1974).

We express our results using the usual delta notation:

$$\delta = 1{,}000\left(\frac{R_{\text{sample}}}{R_{\text{STANDARD}}} - 1\right)$$

where R is the ratio of the two isotopic species, $^{12}C^{16}O^{18}O$ (mass no. 46) and $^{12}C^{16}O_2$ (mass no. 44). For the carbon isotopic composition the same formula is used, but R is the ratio $^{13}C^{16}O_2$ (mass no. 45) to $^{12}C^{16}O_2$ (mass no. 44).

We estimate temperature from the oxygen isotope values using the equation:

$$T = 16.9 - 4.38(\delta_c - \delta_w) + 0.10(\delta_c - \delta_w)^2$$

Here we need δ_w, the isotopic composition of the water. This is because it is the relationship between the isotopic composition of the water and that of the carbonate depositing in that water that is affected by temperature. Providing that isotopic equilibrium is reached (see below), the form of this equation is determined by thermodynamic principles alone. The equation quoted differs slightly from that first obtained empirically for mollusks by Epstein and others (1953), because it is a rewritten version (Shackleton, 1974) of an equation obtained by O'Neil and others (1969) for inorganic calcite deposition. The new equation is almost negligibly different at the temperatures with which we are concerned here, but has the advantage of being valid at ocean bottom temperatures as well.

Over the surface of the ocean, δ_w varies slightly from place to place because in areas of excess evaporation, and high surface salinity, it is the isotopically lighter molecules that escape more readily in the form of vapor (Epstein and Mayeda, 1953). In the area we are considering, surface salinity varies between 35.3 and 35.6 parts per thousand. On the basis of Figure 8 in Craig and Gordon (1965) we estimate these figures to correspond to a range in δ_w from about +0.2 to 0.4 on the P.D.B. scale (0.4 to 0.6 on the SMOW scale used by Craig and Gordon). We have used a value of 0.3 per mil in calculation. Uncertainty of ±0.1 per mil δ_w corresponds to ±½ degree in our temperature estimates.

If the isotopic composition of organically deposited carbonate is not related to that of the water in the manner predicted by thermodynamic principles, then it is possibly variable in response to other variables as well as temperature. For this reason it is important to know whether isotopic equilibrium between ocean water and the foraminiferal carbonate is attained. Because Equation 2 is based on inorganic precipitation of carbonate, it is a good standard to judge by. Reported deviations from isotopic equilibrium (van Donk, 1970; Duplessy and others, 1970; Vergnaud-Grazzini, 1976; Shackleton and others, 1973) are in the isotopically negative direction. Since this means that the temperature calculated is too high, it is most easily detected by analyzing the foraminifera from the ocean surface. Shackleton and others (1973) analyzed a few species including *G. sacculifer* in the Indian Ocean and reported deviations including a figure of −0.35 per *G. sacculifer*. This figure is incorrect; we now know

TABLE 2

Oxygen and carbon isotopic composition of *Globigerinoides sacculifer* in R.V. ANTON BRUUN, Cruise 7, core tops.

Sample	$\delta^{18}O$	$\delta^{13}C$	T isotopic
358 B x	−1.05	+1.76	23.0
	−1.00	+1.97	
361 C x	−1.32	+1.73	24.3
361 F x	−1.53		25.4
361 F x	−1.61	+1.46	
361 J x	−1.37		24.1
361 J x	−1.19	+1.60	
361 J x	−1.12	+1.17	
362 C o	−1.41	+1.99	24.7
362 E o	−1.11	+1.76	23.3
363 C x	−1.58	+1.99	25.5
363 F x	−1.68		26.0
363 F x	−1.69	+1.50	
366 B o	−1.96		27.2
366 B o	−1.92	+1.41	
367 H x	−1.42	+1.96	24.3
367 H x	−1.19	+1.80	
368 B x	−0.68	+1.76	21.3*
369 B o	−1.52	+2.04	25.1
369 B o	−1.46	+1.84	
369 H x	−0.91	+1.51	22.6*
369 H x	−1.01	+1.89	
370 C x	−1.44	+2.15	24.8
372 K x	−1.22	+1.65	24.2
372 K x	−1.39	+1.63	
374 A o	−1.35	+2.00	24.5
374 C o	−0.80	+1.89	21.9*
374 C o	−0.79	+1.88	
375 B o	−1.16	+1.57	23.6
375 F o	−0.51	+1.53	20.5*
379 B o	−0.41	+1.16	20.1
379 B x	−0.38	+1.30	20.0
385 B x	−0.70		21.5
385 B x	−0.74	+0.63	
387 E o	−0.87	+1.43	22.2
388 D x	−1.18	+1.81	23.7
389 B x	−1.37	+2.01	24.5
389 D o	−1.20	+1.67	23.7
389 F o	−1.10	+1.92	23.4
389 F o	−1.21	+1.87	
390 F x	−1.03	+1.63	23.0
390 J x	−1.03	+1.46	23.0
390 M x	−1.16	+1.71	23.6
391 A o	−1.53	+1.79	25.3
391 D o	−1.15	+1.34	23.5

* Assumed contaminated, not plotted on fig. 6.

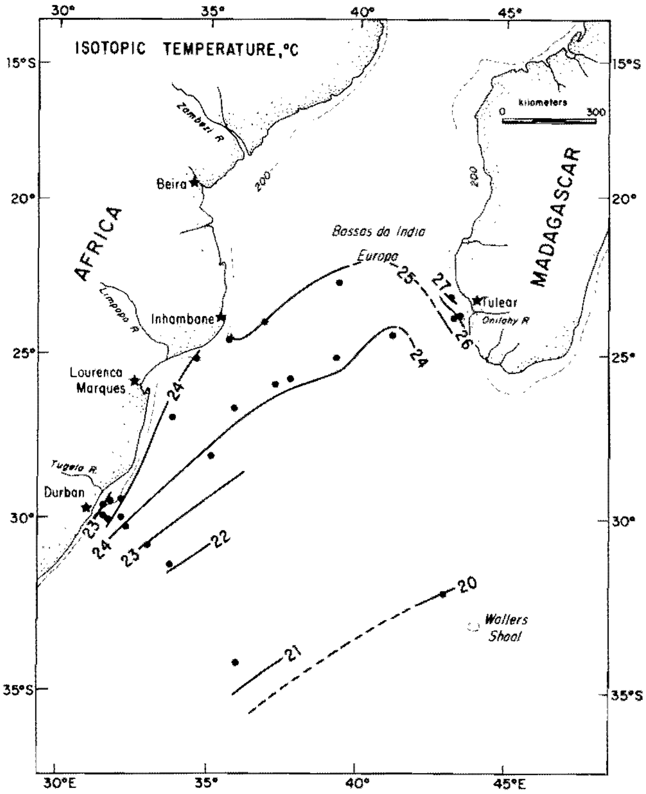


FIGURE 6

Isotopic temperature estimated from oxygen isotopic composition of *Globigerinoides sacculifer* in surface sediments.

that B-1 analyzes +0.29 to P.D.B. and not +0.1 as was then believed, so that the measured deviation from isotopic equilibrium is only −0.16 per mil. We have not taken this figure into account in our calculations because it is small in relation to the uncertainties involved in its measurement.

Analytical results are given in Table 2. The duplicate analyses given imply 68 percent confidence limits (1 − δ) of ±0.07 per mil for oxygen, and ±0.13 per mil for carbon, in estimating the isotopic composition of the population in a sample using a single analysis. For homogeneous clean calcite the figure is ±0.05 per mil for both isotopes, so that there is probably appreciable between-specimen variability at least in carbon isotopic composition.

We have not attempted to map variations in carbon isotopic composition. If there are variations in surface carbon isotopic composition within this small region, they are small and we would need to analyse many more foraminifera at each location in order to detect them with confidence.

In Table 2 we have estimated T using Equation 2, and taking a value of +0.3 per mil for δw. In Figure 6, these are plotted on the map and roughly contoured, ignoring samples 368B, 369H, 374C, and 375F, whose low values are clearly anomalous. The anomaly is due to the samples not being recent (Vincent, 1976), but containing fossil material. We draw attention to this, because oxygen isotope analysis is a useful tool in detecting glacial contamination in surface samples.

DISCUSSION

Figure 6 indicates that the analyses we have made demand isotherms trending northeast-southwest such as exist at present under the influence of the Agulhas Current. We do not wish to evince surprise at this observation; at the same time it is worth emphasizing in view of its paleoenvironmental significance. The emphasis of oxygen isotope analysis in the Pleistocene has always been on down-core sequences, with the objective of providing "generalized temperature curves." This direction has gained impetus from the realization that these are in reality "generalized Northern Hemisphere Ice Volume curves" and thus constitute a fundamental stratigraphic framework (Shackleton and Opdyke, 1973, 1976). On the other hand it may not be fully appreciated that even in the present state of uncertainty as to the exact isotopic composition of the world's ocean during the last glacial maximum (Emiliani and Shackleton, 1974) synoptic oxygen isotope "palaeotemperature" maps may be of considerable value. In the region under discussion, for example, it is clear from an examination of Figure 6 that only a very modest number of full-glacial analyses would be needed to gain a meaningful impression of isotherm trends associated with the glacial Agulhas Current. The second observation that may be made regarding Figure 6 concerns that absolute values plotted, which are near surface summer temperatures.

The population analyzed may be presumed to represent on the one hand, the distribution of *Globigerinoides sacculifer* through the year and on the other, the distribution of the species with depth in the water column. More precisely, what we are measuring is the mean temperature of calcite secretion of *G. sacculifer* weighted in reflection of its seasonal depth distribution. The fact that in spite of this, we obtain a value near surface summer temperature, gives us confidence that in this region surface temperature distribution can be mapped on the basis of oxygen isotope analysis in *G. sacculifer*.

ACKNOWLEDGMENTS

We wish to express our sincere gratitude to the late Orville L. Bandy who was chief scientist on Cruise 7 of the R.V. ANTON BRUUN and collected the samples for this study. Edith Vincent is especially indebted to him for guidance through fruitful years of study at the University of Southern California. N. J. Shackleton gratefully acknowledges the Lamont-Doherty Geological Observatory for the 1974–75 Senior Visiting Research Fellowship, and his CLIMAP colleagues with whom he had stimulating discussion of this work.

This study was supported under grants from the Oceanographic Section, National Science Foundation, GA-34145 and DES 75-04335 to E.V. and from the National Environment Research Council, GR3-1762, to N.J.S.

REFERENCES

Bé, A. W. H., and Tolderlund, D. S., 1971, Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and Indian Oceans, *in* Funnell, B. M., and Riedel, W. R., eds., Micropaleontology of the Oceans: Cambridge Univ. Press, p. 105–149.

Craig, H., and Gordon, L. I., 1965, Deuterium and oxygen 18 variations in the ocean and the marine atmosphere, *in* Tongiorgi, E., ed., Stable isotopes in oceanographic studies and paleotemperatures, Spoleto, 1965: Consiglio Nazionale delle Ricerche, Laboratorio di Geologia Nucleare, Pisa, p. 9–130.

Darbyshire, J., 1964, A hydrological investigation of the Agulhas Current area: Deep-Sea Research, v. 11, p. 781–815.

Dietrich, G., 1935, Aufbau und Dynamik des Südlichen Agulhas-Stromgebietes: Veröff Inst. Meeresk. Berlin, N.F., A, v. 27, p. 1–79.

Duncan, C. P., 1970, The Agulhas Current: Hawaii Univ., Unpub. Ph.D. dissert., 73 p.

Duplessy, J. C., Lalou, C., and Vinot, A. C., 1970, Differential isotopic fractionation in benthic foraminifera and paleotemperatures reassessed: Science, v. 168, p. 250–251.

Emiliani, C., 1955, Pleistocene temperatures: Jour. Geology, v. 63, p. 538–578.

———, 1966, Palaeotemperature analysis of Caribbean cores P 6304-8 and P 6304-9 and a generalised temperature curve for the last 425,000 years: Jour. Geology, v. 74, p. 109–126.

Emiliani, C., and Shackleton, N. J., 1974, The Brunhes Epoch: isotopic paleotemperatures and geochronology: Science, v. 183, p. 511–514.

Epstein, S., Buchsbaum, R., Lowenstam, H. A., and Urey, H. C., 1951, Carbonate-water isotopic temperature scale. Geol. Soc. America Bull. v. 62, p. 417–426.

———, 1953, Revised carbonate-water isotopic temperature scale. Geol. Soc. America Bull. v. 64, p. 1315–1326.

Epstein, S., and Mayeda, T., 1953, Variation of O^{18} content of waters from natural sources. Geochm. et Cosmochim. Acta, v. 4, p. 213–224.

Harris, T. F. W., 1972, Sources of the Agulhas Current in the Spring of 1964: Deep Sea Research, v. 19, p. 633–650.

Heezen, B. C., and Tharp, M., 1966, Physiography of the Indian Ocean: Royal Soc. London Philos. Trans., ser. A., v. 259, p. 137–149.

Ménaché, M., 1963, Première campagne océanographique du "Commandant Robert Giraud" en Canal de Mozambique: Cah. Oceanogr., v. 15, p. 224–235.

Michaelis, G., 1923, Die Wasserbewegung an der Oberfläche des Indischen Ozeans im Januar und Juli: Veroff. Inst. Meeresk., Berlin, N.F., A, v. 8, p. 1–32.

Oba, T., 1969, Biostratigraphy and isotopic paleotemperature of some deep-sea cores from the Indian Ocean: Tohoku Univ. Sci. Repts., 2, Geology, v. 41, p. 129–195.

O'Neil, J. R., Clayton, R. M., and Mayeda, T. K., 1969, Oxygen isotope fractionation in divalent metal carbonates: Jour. Chem. Physics, v. 51, p. 5547–5558.

Orren, M. J., 1963, Hydrological observations in the southwest Indian Ocean: South African Div. Sea Fisheries Inv. Rept. 45, p. 1–61.

———, 1966, Hydrology of the Southwest Indian Ocean: South African Div. Sea Fisheries Inv. Rept. 55, p. 1–35.

Schott, G., 1935, Geographie des Indischen und Stillen Ozeans Hamburg, Verlag von C. Boysen, 413 p.

Shackleton, N. J., 1974, Attainment of isotopic equilibrium between ocean water and the benthonic Foraminifera genus *Uvigerina*: isotopic changes in the ocean during the Pleistocene: Colloq. Int. C.N.R.S. No. 219-Les methodés quantitatives d'étude des variations du climat au cours du Pleistocène, p. 203–209.

Shackleton, N. J., and Opdyke, N. D., 1973, Oxygen isotope and paleomagnetic stratigraphy of Equatorial Pacific core V28-238: oxygen isotope temperatures and ice volumes of a 10^5 year and 10^6 year scale: Quaternary Research, v. 3, p. 39–55.

———, 1976, Oxygen isotope and paleomagnetic stratigraphy of Equatorial Pacific core V28-239, late Pliocene to latest Pleistocene, *in* Cline, R. M., and Hays, J. D., ed., Investigation of late Quaternary Paleo-oceanography and Paleoclimatology, Geol. Soc. America Mem. 145, p. 449–464.

Shackleton, N. J., Wiseman, J. D. H., and Buckley, H. A., 1973, Non-equilibrium isotopic fractionation between seawater and plankton foraminiferal tests: Nature, v. 242, no. 5394, p. 177–179.

Urey, H. C., 1947, The thermodynamic properties of isotopic substances: Jour. Chem. Soc., p. 562–581.

van Donk, J., 1970, The Oxygen isotope record in deep-sea sediments: Columbia Univ., Unpub. Ph.D. dissert., 228 p.

Vergnaud-Grazzini, C., 1976, Non-equilibrium isotopic compositions of shells of planktonic foraminifera in the Mediterranean Sea: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 20, p. 263–276.

Vincent, E., 1972, Oceanography and late Quaternary planktonic foraminifera, Southwestern Indian Ocean: Unpub. Ph.D. dissert., Southern California Univ., 353 p.

———, 1976, Planktonic foraminifera, sediments, and oceanography of the late Quaternary, Southwest Indian Ocean: Allan Hancock Monographs in Marine Biology, No. 9, 235 p.

Wyrtki, K., 1971, Oceanographic atlas of the international Indian Ocean Expedition. National Science Foundation, Washington, D.C., 531 p.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 96–126, pls. 1–12, 1980

PSEUDOPODIAL VARIABILITY AND BEHAVIOR OF GLOBIGERINIDS (FORAMINIFERIDA) AND OTHER PLANKTONIC SARCODINA DEVELOPING IN CULTURES

PATRICIA C. ADSHEAD
Department of Forest Science, Faculty of Agriculture and Forestry
University of Alberta, Edmonton, Alberta T6G 2E1

ABSTRACT

Globigerinids display a wide variety of pseudopodial types during their existence in cultures. Development of many long, flexible axopodia from reticulopodia extended into the water above the test allows newly collected specimens recovering on a substrate to float free. With time, the numerous axopodia present in young globigerinids are replaced by fewer brittle, calcifying spines, each coated with a motile cytoplasmic film which extends beyond the spine tip as a sticky, retractable "probe." Resorption of spines enables mature globigerinids to assume a benthic existence in cultures, moving and feeding with filopodia, reticulopodia, and pharopodia. Globigerinids are rivaled only by acantharians in the diversity of motile appendages which appear in cultured specimens. Radiolarians and heliozoans have much simpler pseudopodial arrays. Globigerinid axopodia are superficially similar to those of heliozoans, but apparently lack the ability to contract rapidly which is essential to food capture in some heliozoans. The greater firmness and length of globigerinid axopodia and young spines allows continuous utilization of detrital food while helping to support flotation of the relatively heavy test.

INTRODUCTION

The taxonomic position of the Foraminiferida within the Sarcodina has frequently been determined by the anastomosing network of granular pseudopodia which is commonly associated with benthic members of this order. Observations of living benthic foraminifera by numerous workers served to support this practice (for example, Leidy, 1879; Sandon, 1934; Jepps, 1942; and Arnold, 1953).

However, the spines of the planktonic globigerinid foraminifera have been a source of concern to micropaleontologists including Bé (1960a), Bé and Ericson (1963), and Parker (1962). Parker differentiated between the delicate spines of the Globigerinidae and the ornamental protuberances of the Globorotaliidae. Although globigerinids do develop spines (Bé and others, 1969; Hemleben, 1967, 1969; Bé and Hemleben, 1970), they first develop long, tenuous axopodia (Adshead, 1967b) some of which may contribute to the spinose condition of mature specimens. Parker (1962) noted that "several genera and species of the Globigerinidae have these spines in their young stages and do not have them in the adult stage." She described *Globigerina bulloides* d'Orbigny as having a hispid test and being spinose, that is, having long, thin spines when living. In living specimens of *Globigerina bulloides* and other globigerinids in culture, it is seen that the spines of young planktonic individuals are in fact preceded by flexible axopodia which develop (from preexisting reticulopodia) while the test is newly formed, smooth, and transparent (Adshead 1967a, b). Brittle spines appear as secondary calcification progresses, and may finally be resorbed.

More detailed observations on living planktonic foraminifera would clear up many problems about these organisms. Because benthic species have been more readily observed in cultures, the complete life cycles of many benthic species are well known (Leidy, 1879; Myers, 1936, 1937; Jepps, 1942; Arnold, 1954, 1964; Bradshaw, 1955; Sliter, 1965; Grell, 1973). Similar information is still not available for planktonic foraminiferans, although development of a simple culture method (Adshead, 1967a) enabled observation and photography of globigerinids, collected off of southern California, for periods up to three months during 1965–66. During these culture studies some globigerinid specimens developed into orbulinids, as described later. Observations on Caribbean globigerinids (especially *Globigerinoides ruber*) were made during a cruise aboard R/V *Alaminos* (Texas A & M University) in the summer of 1973. To gain a comparative view of pseudopodial structures, the following Sarcodina were watched in cultures: globigerinids, heliozoans, radiolarians, and acantharians from plankton tows, benthic calcareous and arenaceous foraminiferans, and the freshwater heliozoan *Echinosphaerium* (=*Actinosphaerium*) supplied by Carolina Biological Supply Co.

ACKNOWLEDGMENTS

I am especially grateful for Dr. Bandy's wholehearted support of these culture studies during 1964–1966. His interest and enthusiasm made the whole project thoroughly enjoyable. I also appreciate the willing assistance in collecting samples and setting up cultures provided by members of the Micropaleontology Laboratory at the University of Southern California (1964–1966) especially Ronald J. Echols, James C. Ingle, Mary Wade Echols, Edith Vincent, David Haner, Barbara Hackett Haner, and Fritz Theyer.

Southern California collections were made from R/V *Velero IV* (Allan Hancock Foundation) under Frederick B. Ziesenhenne, and those in the Caribbean from R/V *Alaminos* (Texas A & M University), captained by J. Leo Cox. The laboratory work at the University of Southern California was carried out in the Micropaleontology Laboratory of the Allan Hancock Foundation.

William D. Enns, William F. Sheridan, and David Daugherty at the University of Missouri obtained heliozoan cultures and made available their laboratory facilities. William Sheridan also obtained a University of Missouri Research Council grant to support travel expenses for the Caribbean cruise, and reproduction of plates for this paper. Cultures of globigerinids in the Caribbean were maintained on board the *Alaminos* during an eight-day cruise made possible by NSF and Chief Scientist Richard Casey of Rice University. I would like to thank all of these individuals for enabling me to continue the work which was started in Orville Bandy's laboratory.

COLLECTION AND MAINTENANCE

The routine used for collection and maintenance of globigerinids is highly flexible, depending on materials and methods readily available or easily obtained. The methods used are described by Adshead (1967a). Slight modifications were made on the Caribbean cruise, when foraminifera were isolated into individual plastic containers (5-milliliter clear DISPO beakers, Scientific Products), which were placed nine on each half of a square plastic petri dish (Integrid Petri Dish, 100 × 15 mm, Falcon Plastics #1012) and covered with plastic wrap. The smaller containers (as opposed to Pyrex custard dishes used in 1967) conserved space and simplified location of foraminiferans in culture. Because the ship's laboratory was air-conditioned, the covered dishes of foraminifera were kept in secured trays on the laboratory bench with no ill effects.

TERMINOLOGY

PSEUDOPODIAL STRUCTURES IN SARCODINA

Pseudopodia may be differentiated on the basis of form, structure, function, and movement of protoplasm and inclusions into the following arbitrary categories: (1) lobopodia, (2) filopodia, (3) pharopodia, (4) reticulopodia, and (5) axopodia. All of these categories except lobopodia are found in globigerinids at some stage and environmental condition. All will be described briefly to allow comparison.

(1) Lobopodia (characteristic of the common genera of large amoebas, as *Amoeba* or *Pelomyxa*) are temporary tubular extensions of clear outer protoplasm (or hyaloplasm), exhibiting cyclic protoplasmic flow (Jahn and Bovee, 1965). Larger lobopodia commonly have a core of actively flowing granular endoplasm. Granular endoplasm and clear hyaloplasm are separated by an active transition zone rather than by a sharp boundary. Lobopodia are often simple; they may ramify but almost never anastomose (Leidy, 1879). They may become pointed and tapering and may even coil in response to sudden environmental changes such as in temporary flotation (Bovee, 1964; Adshead, unpublished data).

(2) Filopodia protrude as slender ectoplasmic strands from the mass of cytoplasm at the mouth of testate amoebas, including foraminifera. They are

strong, move vigorously and quickly, fork sharply, but rarely anastomose other than about encountered food particles (Leidy, 1879; also Plate 2, Fig. 1). Although filopodia were previously thought to be confined to testaceans, this study and observations on *Astrorhiza limicola* (a large arenaceous foraminifer) by Buchanan and Hedley (1960) suggest that filopodia may reflect a specific physiological state of the organism, and in fact occur in many sarcodine groups. Filopodia are distinctly not adhesive or "sticky," and are usually seen in actively moving or nonfeeding organisms. The finely granular protoplasm lacks conspicuous granules or vacuoles. Testate forms with filopodia frequently assume an erect position in movement, with relatively few pseudopodia diverging from the mouth of the shell. A distal pseudopodial branch may bend sharply, and the bent part may vibrate slowly in a remarkable manner, considering the distance from the test and the control systems involved (Adshead, unpublished data), or a branch may suddenly contract in a serpentine manner (Leidy, 1879). Bardele (1972) also described filopodia in the stalked stage of the pseudoheliozoan *Clathrulina elegans*.

(3) Pharopodia (Allen, 1968) are sheetlike pseudopodia, also described as lamellar cytoplasm by Vasiliev and Gelfand (1973), in referring to similar structures which occur in attaching or moving fibroblast cells in vertebrate tissue cultures. In globigerinids, a pharopodium may spread out in advance of the branching filopodia (Plate 2, Fig. 1), displaying a wavy surface which would be seen to greatest advantage with a scanning electron microscope.

(4) Reticulopodia (=rhizopodia) are delicate, filamentous, constantly branching and anastomosing pseudopodia showing active bidirectional streaming of coarser granular contents. The reticulopodia ramify initially, then anastomose freely to form an intricate, mobile, feeding network. The granular contents (described by Arnold, 1953, for *Allogromia*, and also by Leidy, 1879, and by Jepps, 1942, for *Polystomella*) may vary considerably with environmental changes, and are in constant motion in opposite directions except in the finest branches. Leidy described the granules as follows: "In the larger threads, the granules are immersed and near together; in the smallest threads they are in single rows, more or less widely separated, and thicker than the threads, so that these appear like strings of minute beads." These coarser, streaming granular contents (Pl. 4, Fig. 1; Pl. 5, Fig. 4) are characteristic of both reticulopodia and axopodia. Each reticulopod operates by "remote control," and may be rapidly spiralled or bent at any point along its length. Foraminifera which develop reticulate feeding nets (well illustrated with scanning electron photomicrographs by Marszalek, 1969, for the benthic *Iridia*) tend to settle in one position for long periods, building up small piles of detritus around the periphery (distal to the test). Spindlelike accumulations of protoplasm may occur, groups of which may join to form satellite centers for secondary nets (clearly seen in a

---

→

PLATE 1

Living, floating globigerinid with yellowish zooxanthellae (probably chrysomonads) clustered over the test and spread out among the axopodia. These zooxanthellae were light sensitive, and moved out from the test only when light transmitted by the microscope was kept at moderate to dim levels. (about ×470).

PLATE 2

Benthic globigerinids

1 Living, mature globigerinid moving on a substrate. Notice the sheet of lamellar cytoplasm (arrow), or pharopodium, which is continuous from the outer forked tips of both the smooth and varicose filopodia. Spines appear to have been resorbed. (×625)

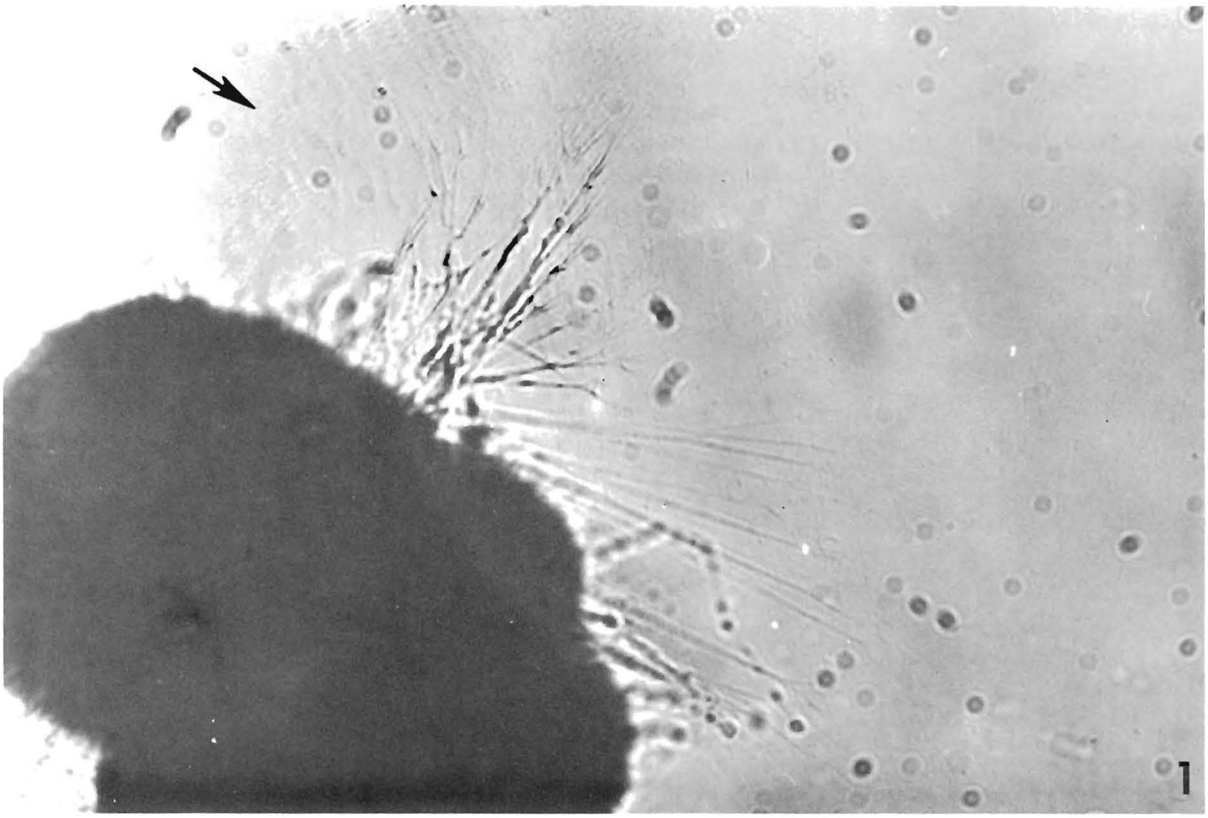
2 Same specimen as in Figure 1, rotating on a substrate. For this type of movement reticulopodia cluster together in small waves similar to those seen in "*Orbulina*" (Pl. 8, Figs. 1–3). (×440)

PLATE 3

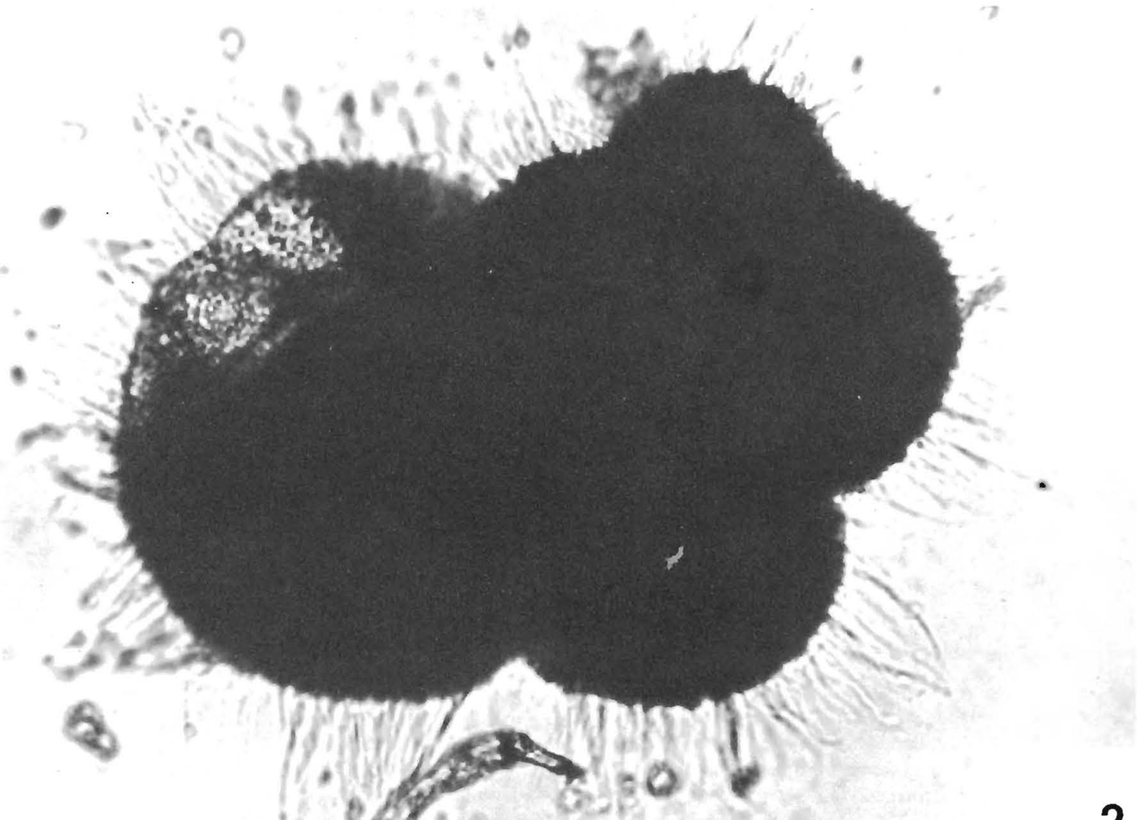
Benthic globigerinids

1 *Globigerina bulloides* moving on a substrate toward the upper left corner, leaving a trail of detritus and possibly mucus behind. Filopodia and reticulopodia are used in this movement. (×365)

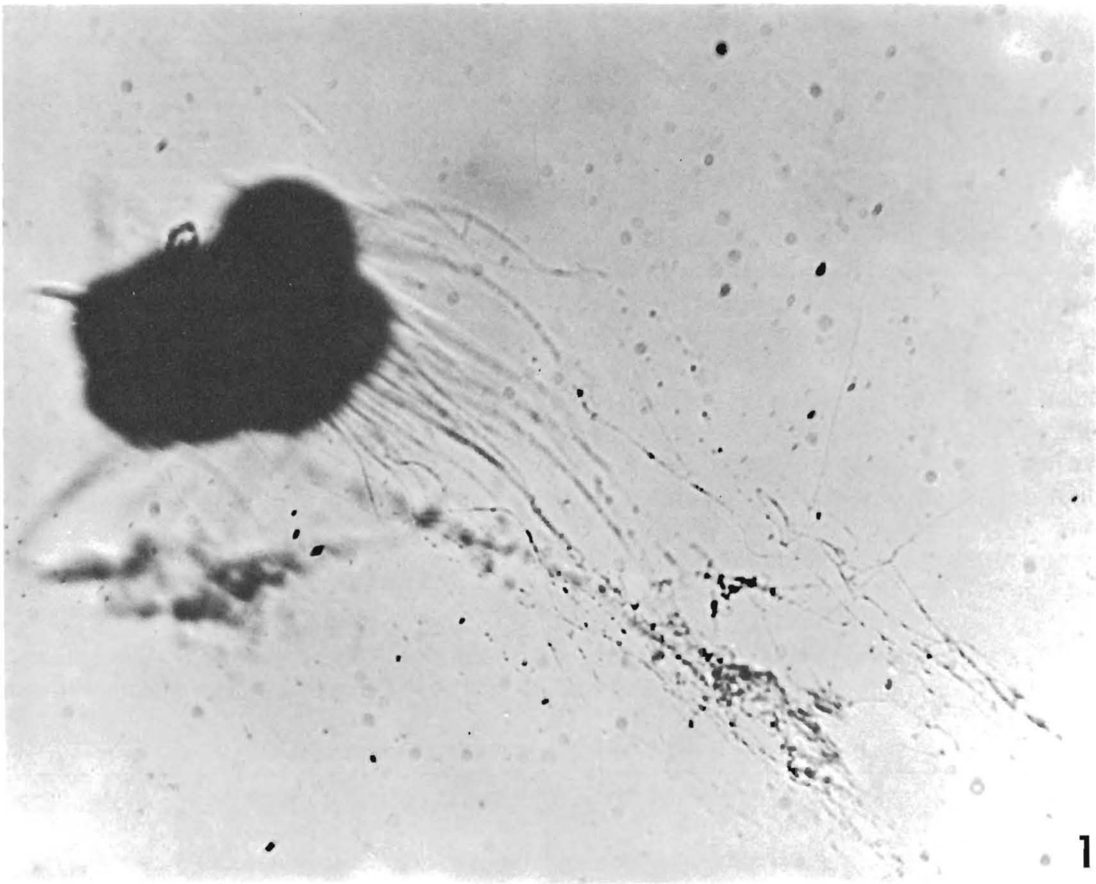
2, 3 Closeup of globigerinids rotating on a substrate. Pseudopodia tend to form waves, and occasionally the tips expand to form flame-shaped swellings. (×500)



1



2



1

2

3

, p. 68–
ne vicin-
, Contr.
ossi, R.,
Riv. Ital-
nic Fora-
. Foram.
a *pachy-*
20.
sediments
Geol. Hel-
THIEU, G.,
an, *in* Tur-
: New Ha-
ion and the
: Bull. Am.
coiling ratio
): Micropa-
of the fora-
Pliocene of
International
p. 143–156.
pachyderma
west Pacific
ra in surface
Conf. Plank-
2, p. 307–322.
a (Ehrenberg)
. Foram. Re-
: foraminiferal
Leg 21: Deep
globoquadrina
rginal and cen-
interpretation:
ene planktonic
nd Italian Stra-
57 (Protozoa 8),
tonic foraminif-
: Internat. Conf.
oc., v. 1, p. 921–
achyderma (Eh-
Northeastern Pa-
s Bull., v. 57, p.
st of *Globigerina*
., and Saito, T.
d papers in hono
leontology Press

specimen of *Shepheardella* spread out among sand grains in a petri dish).

(5) Axopodia are long, radiate, tapering extensions of viscous, actively granular rheoplasm surrounding axial cores which are birefringent in polarized light. The cores are composed of microtubules arranged in precise and specific patterns. Axopodia are temporary structures, and may often be rapidly extended or retracted as in heliozoans (Pl. 10, Fig. 2). The axopodia appear to help support flotation, and provide a large surface area for food uptake, waste removal, and metabolic exchange with the water. Axopodia are quite flexible under slight stress (may be elastically deformed with a glass probe), yet are sufficiently vibratile to serve in a minor locomotor capacity (Pl. 10, Fig. 1). In heliozoans, axopodia are very sensitive, and may function in food capture by gripping and enveloping prey organisms. In some foraminiferans, radiolarians, and acantharians the role appears to be more passive.

Contrary to popular opinion, which laid great stress on the importance of axopodia in classifying Sarcodina for many years, axopodia appear to have developed in planktonic foraminifera, as well as in heliozoans, radiolarians, and acantharians. This problem was considered briefly in an earlier paper (Adshead, 1967b). In addition to axopodia developing in planktonic species, they may also occur in some stalked forms. Christiansen (1958, p. 32) described a strange foraminiferan, *Marsipella arenaria*, in which a tubelike arenaceous test was anchored in the mud by pseudopodia attached to sand grains in the mud. The 18 x 0.5 mm tube stood upright, and thin "threads" which Christiansen thought might be keratinlike radiated out in the water for about 4.5 mm. These "threads" could very well qualify as axopodia if they showed orderly axial arrangements of microtubules in cross-sections of axopodia viewed in the electron microscope.

ASPECTS OF CYTOPLASMIC MOTILITY IN PLANKTONIC SARCODINA

Grell (1973) noted that all protoplasm has motility and that intracellular cytoplasmic streaming and lo-

→

PLATE 4

Young, planktonic globigerinids, all with extended, tenuous, highly flexible axopodia, some of considerable length.

1 Numerous long, granular axopodia showing the beads-on-a-string appearance typical of reticulopodia and young axopodia. (×210)

2 Several axopodia fused to form a temporary common tip. During fusion granular contents move from one axopodium to another, then the axopodia separate again. The membrane phenomena involved in this behavior would be particularly interesting to investigate. (×200)

3 Globigerinid with axopodia tangled by transfer, showing the extreme flexibility of these structures in young specimens. (× 210)

4 *Globigerina bulloides* with extended axopodia, slightly tangled at the ends to show the remarkable length (over 10× the test diameter) attained by globigerinid axopodia, much greater than the length of spines, which develop later. (×200)

PLATE 5

1–3 Young globigerinid spines, showing a contracting motile tip with granular contents at the end of one spine (arrow). The tip is pulled back onto the spine, and the contents move along the surface of the calcified core (arrows). (×600)

4 Numerous axopodia with abundant granular contents, typical of a young, actively metabolizing and calcifying specimen of *Globigerina bulloides*. (×200)

5 Slender spines with retracted tips, interspersed with reticulopodia in a globigerinid with numerous extracellular zooxanthellae (round variety). (×230)

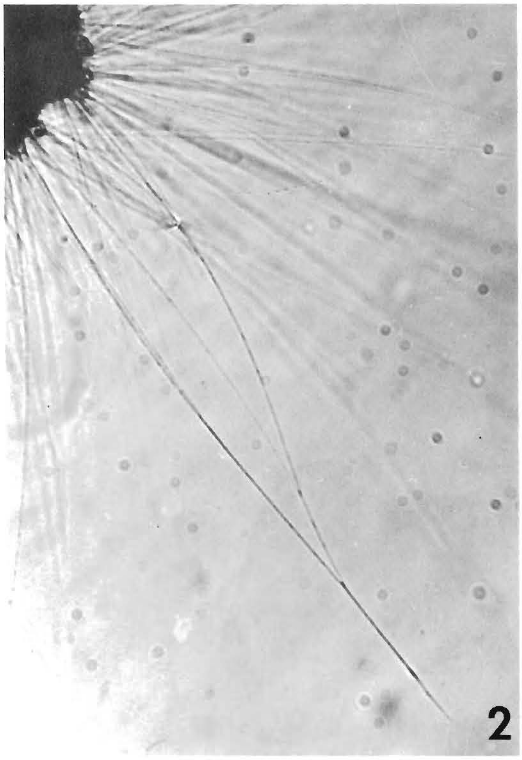
PLATE 6

Spine formation in *Globigerina bulloides*

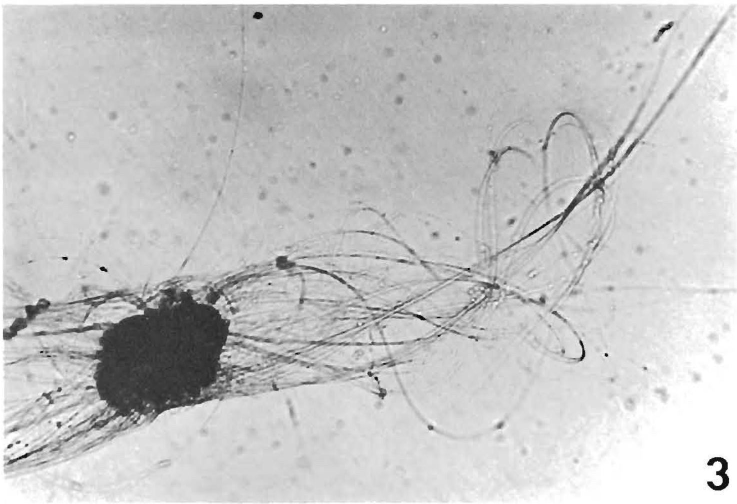
1–3 Spines with motile, retractable pseudopodial tips which probe the surrounding water and may fuse temporarily (Fig. 2, arrow). Globigerinids and other planktonic Sarcodina use such sticky tips to enable them to roll along a substrate in a slight current. Calcification appears to occur in a gradient, with active calcification taking place distally along the axial core of the forming spines. The spines are brittle, breaking rather than bending, and are much shorter than axopodia (relative to the test diameter) and less numerous. (×600)

4 Specimen of *Globigerina bulloides* with developing spines. The banner-like pseudopodial tips are visible at the ends of some of the spines. (×210)

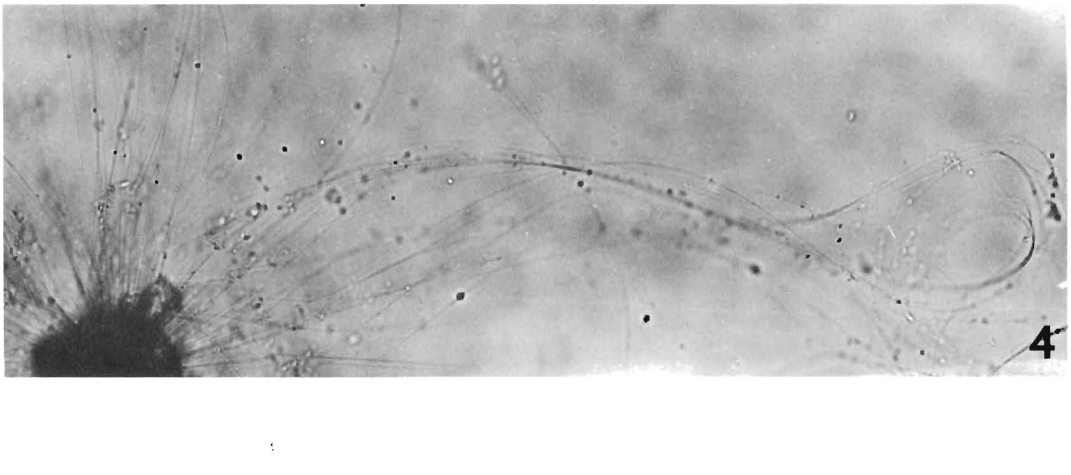
1



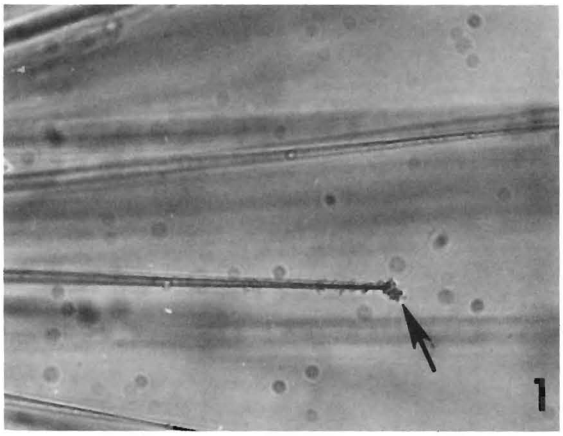
2



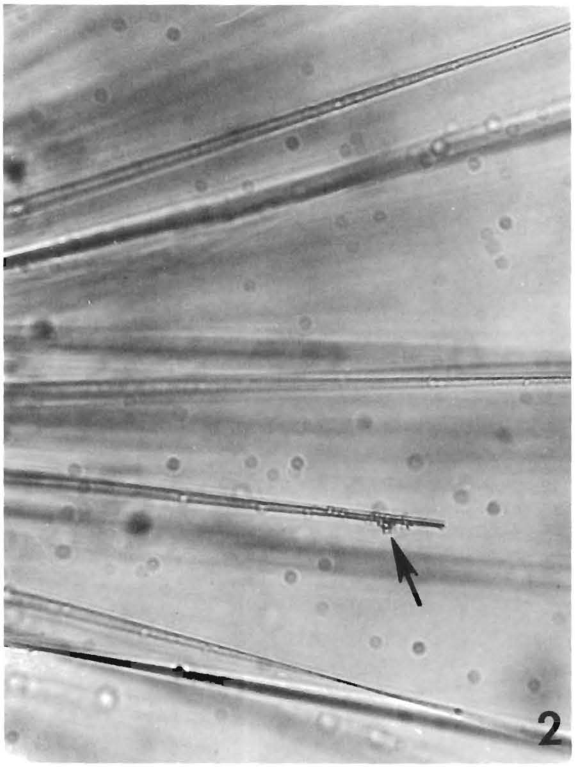
3

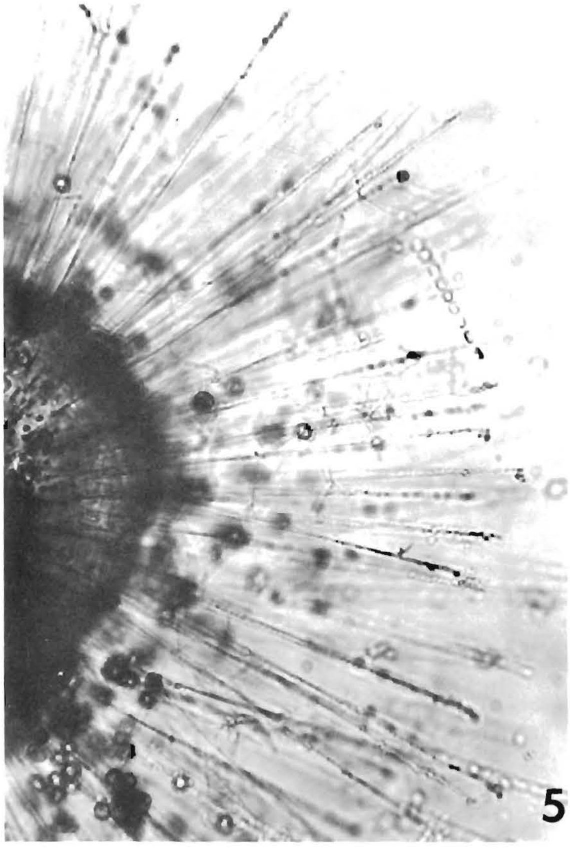


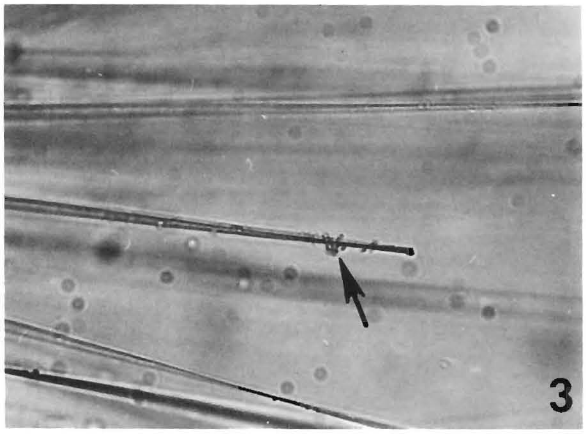
4


1

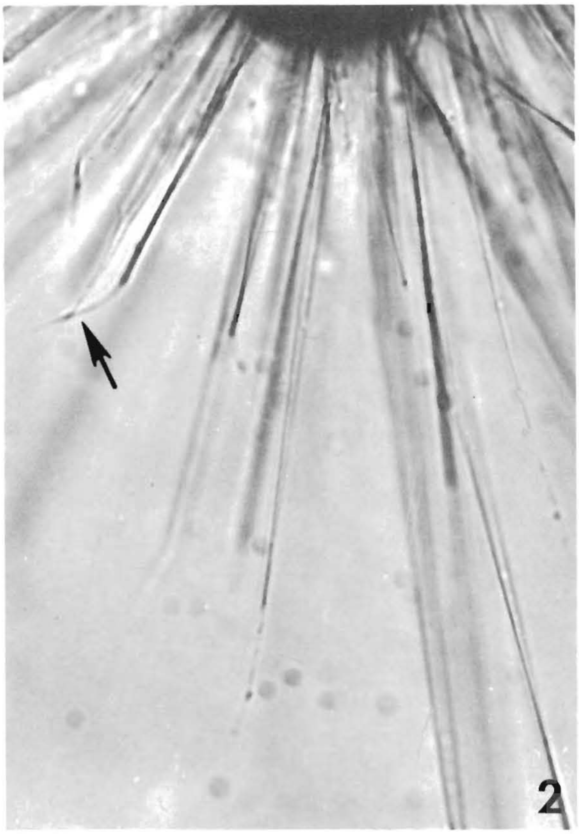

4


2


5

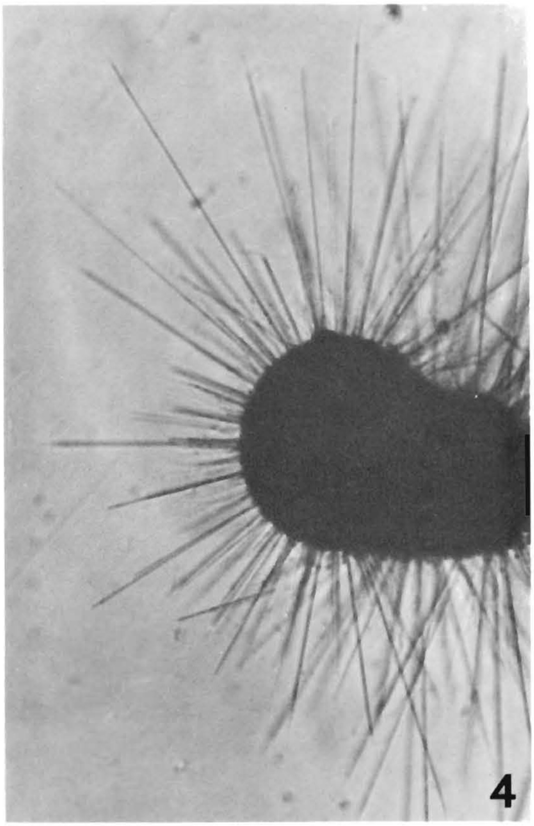

3

1

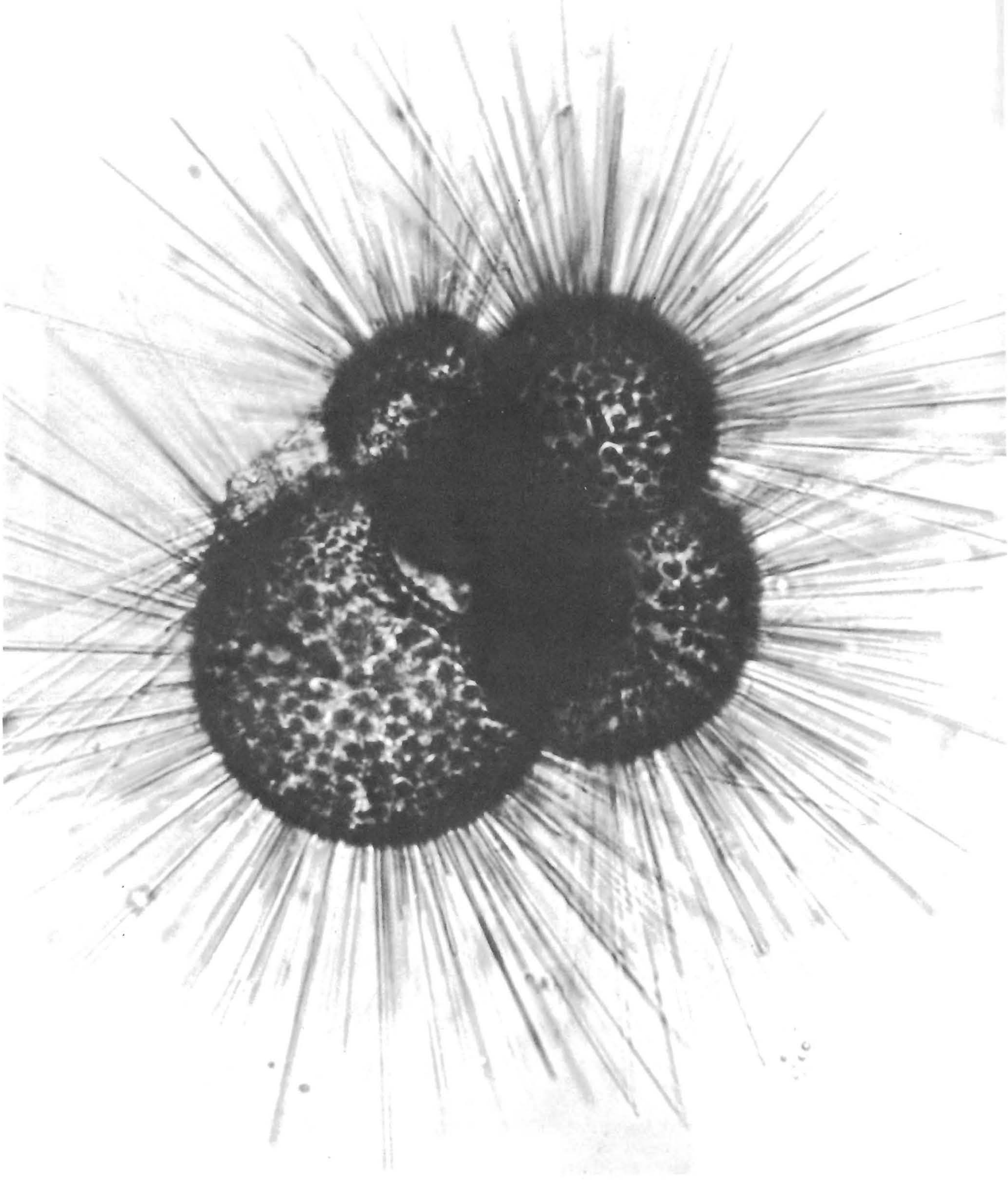


2

3



4



comotion are both common to most Protozoa; however, there are considerable differences in manner and amount of cytoplasmic motility among different groups.

Foraminifera utilize pseudopodia to effect locomotion, but also display a continuous bidirectional streaming of cytoplasm in pseudopodia which is typical of planktonic Sarcodina in general. Such streaming is considered to be a result of a two-layered antithetical flow with saltation of contained particles (Tilney, 1971; Edds, 1975a), and is rarely seen in cells of higher organisms except nerve cells, where flow is at a much slower rate (McGee-Russell and Allen, 1971; Berlinrood and others, 1972; Ochs, 1972). Although Doflein (1916) coined the term "rheoplasm" for the outer layer of protoplasm (showing flow and counterflow) which he observed in heliozoan axopodia, these same conditions may also be observed to varying degrees with the light microscope in the various pseudopodia of foraminiferans, acantharians, and radiolarians. Bardele (1976, p. 191) has provided a clear description of the movement of granules in axopodia of centrohelidan heliozoans, a description which could well be applied to the other groups mentioned above.

Rheoplasm and its occurrence in Sarcodina have yet to be adequately characterized or defined, although progress has been made with the factors governing motility. Edds (1975b) showed that cytoplasmic motility in *Echinosphaerium* was probably due to the presence of two types of microfilaments, the thin filaments of actin and thicker filaments which could be aggregated myosin. Actin and myosin, which form the basis for striated muscle in advanced organisms, have also been implicated in non-muscle motility of many lower organisms including amoebae in recent years (Pollard and Weihing, 1974; Mannherz and Goody, 1976). The microtubular systems earlier credited with an active role in motility probably serve more of a support function. Edds (1975a) showed that he could substitute a thin glass rod for the microtubular complex in heliozoan without altering particle motion.

An additional characteristic which typifies planktonic sarcodine pseudopodia is the often "sticky" nature of the rheoplasm. Development of feeding nets in the benthic foraminifer *Astrorhiza* was associated with a marked and tenacious adhesiveness of the ramifying pseudopodia (Buchanan and Hedley, 1960). This physiological state contrasted sharply with a second state in which there was no adhesive property (as noted above in defining filopodia). Williams and Roth (1973) found that fusion occurred in association with feeding and other stimuli in several species of heliozoan, and apparently involved an interaction between "newly formed or denuded cell surface membranes." Vollett and Roth (1972) had shown that 5 millimolar (mM) $CaCl_2$ and cold (4°C) temperatures had a similar effect on *Echinosphaerium*, resulting in an alignment, apposition, and fusion of plasma membranes between multiple organisms.

Planktonic representatives of the sarcodine groups can utilize the sticky tips of axopodia or the motile tips which extend from spines to roll along contacted surfaces (Pl. 6, Figs. 1–4; Pl. 8, Fig. 4; Pl. 4, Fig. 3). When pseudopodia vary in form and behavior (physiological state) it appears to be the rheoplasm that is the chief variant.

Although both adhesive and nonadhesive states have been observed to occur in response to environmental changes in benthic and planktonic foraminifera, the ultrastructural and biochemical bases for the switches have not been clarified. The rheoplasm must have certain unique properties which could be detected using recently available techniques. A freeze-etch study of the membrane in both states, using surface replica techniques as well as standard freeze-fracture methods, would probably contribute a great deal to our understanding of reversible adhesiveness in rheoplasm. Vollett and Roth (1974) have recently implicated new cell-surface membrane (formed in the presence of calcium or magnesium ions) in cell fusion of *Echinosphaerium*. Roth, Vollet, and Davidson (1975) further found that specific receptor sites on the axopodial cell surface were involved in axopodial responses to external stimuli.

OBSERVATIONS

Planktonic-Benthic Behavior of Globigerinids

Young, healthy globigerinids are surprisingly active creatures. Newly collected specimens may glide about on the bottom of culture dishes (Pl. 3, Fig. 1) or set up an active reticulopodial feeding net similar to that

←

PLATE 7

Mature specimen of *Globigerina bulloides* with extended spines and hispid test structure. (×500).

described by Marszalek (1969) for *Iridia*, and settle in one place for several days.

Such metabolically active globigerinids will commonly extend slender axopodia to lengths up to ten times the test diameter (Pl. 1; Pl. 3, Figs. 1–4) and float free in the water. Specimens which come together accidentally may stick together for varying periods of time by fusion of axopodia. While the axopodia are joined they may exchange granular contents by streaming, then separate again. Floating specimens coming into contact with surfaces, such as the wall of the culture dish, can control their rolling motion in a slight current by alternately gripping and releasing available substrates using the sticky tips of axopodia. Similar behavior is seen in heliozoans, radiolarians, and acantharians, as noted earlier.

Heavily calcified mature specimens were observed to resorb calcified axial cores of spines and sink to the bottom of culture dishes. There they were able to feed and move about with slender pseudopodia for extended periods of time. Once such mature individuals became benthic, however, they were unable to resume floating in cultures, remaining benthic until they died. From physiological and behavioral changes of cultured specimens, it seems likely that benthic stages may, in fact, occur in a number of globigerinid life cycles and may be more common than is now supposed.

VARIABILITY OF GLOBIGERINID PSEUDOPODIA

Pseudopodia of globigerinids are surprisingly variable in form, changing continuously from filopodia and pharopodia used in benthic locomotion, to motile anastomosing, reticulopodial feeding networks on a suitable substrate. In young, metabolically active globigerinids the reticulopodia extending into the overlying water develop into axopodia, enabling the foraminiferan to float free. Stages in the transition from axopodia to spines are unclear, and will be discussed later. The transition from motile filopodia and reticulopodia, to axopodia, to calcified spines, and finally resorption of these spines and resumption of a benthic existence in some mature globigerinids and orbulinids presents a complex sequence.

When anastomosing reticulopodia occur in globigerinids they are similar to those found in benthic foraminifera. They normally occur in healthy, young individuals which have accidentally lost their pseudopodia, as in heavily calcified older individuals which cannot replace lost or resorbed axopodia and are confined to a benthic existence. Reticulopodia are also seen in older specimens, interspersed among the spines or resorbing axopodia (Pl. 5, Fig. 5). Reticulopodia often form feeding nets which extend like mooring lines from the test surface to the substrate some distance away (best illustrated for the benthic *Iridia* by Marzalek, 1969). The "lines" may anastomose along their full length, are constantly changing and branching, with active bidirectional flow of granular contents, and emanate from test pores. Feeding-net reticulopodia are relatively stable structures, firmly attached distally. They can withstand stretching with a glass probe, simply tearing loose from the substrate when the force becomes too great. Sometimes reticulopodia are fairly short, radiating in waves (Pl. 2, Fig. 2; Pl. 3, Figs. 2, 3), in globigerinids which are rotating on a surface. Jepps (1942, p. 624) captured the intense activity seen in the reticulopodia of the benthic foraminifer *Polystomella*. "They may be shot out a short distance into the water like little rockets, and with the granules chasing up and down, wave about like minute feelers, bending, undulating, quivering, and putting out side branches which meet and fuse and so establish the reticulum."

Net-forming species can concentrate their pseudopodia for active movement on a substrate (Pl. 3, Fig. 1), but usually do so only when strongly stimulated by environmental factors. Globigerinids exhibiting directional movement on a substrate sometimes developed filopodia (Pl. 2, Fig. 1) similar to those described by Berrend (1964, p. 435). The actual movement involved simple, branching filopodia merging into a ruffled sheet of protoplasm (pharopodium of Allen, 1968), which spread out in advance of the moving globigerinid (Pl.

→

PLATE 8

Orbulinid pseudopodia

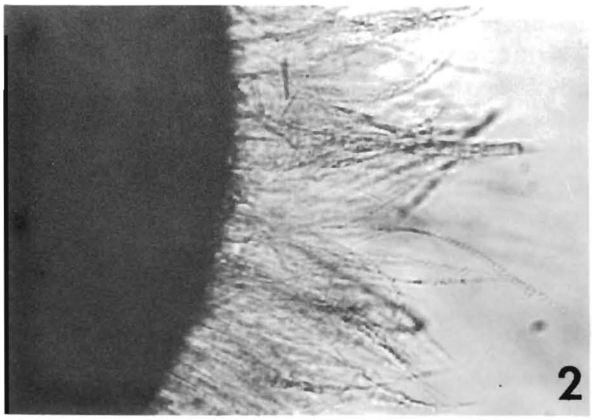
1, 2 Cone- or wave-shaped accumulations of reticulopodia which are used by newly collected orbulinids to roll on a substrate during recovery from collection shock and before renewed flotation. (Fig. 1, ×450, Figure 2, ca. ×300).

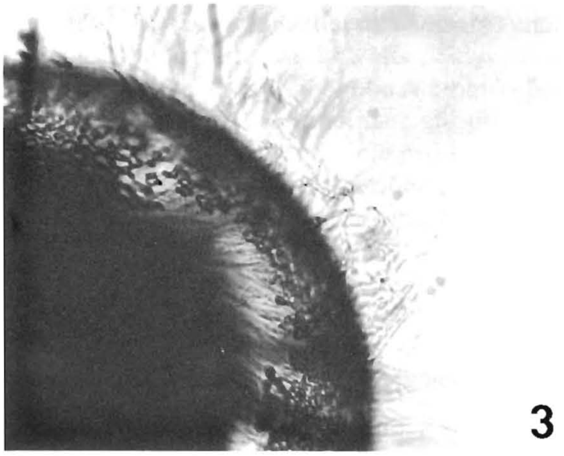
3 Reticulopodia in a recovering, damaged orbulinid, showing the origin of pseudopodia within the test. (×350)

4 Fusing axopodial tips of floating orbulinid. Notice tendency of axopodia to twist. (×600)

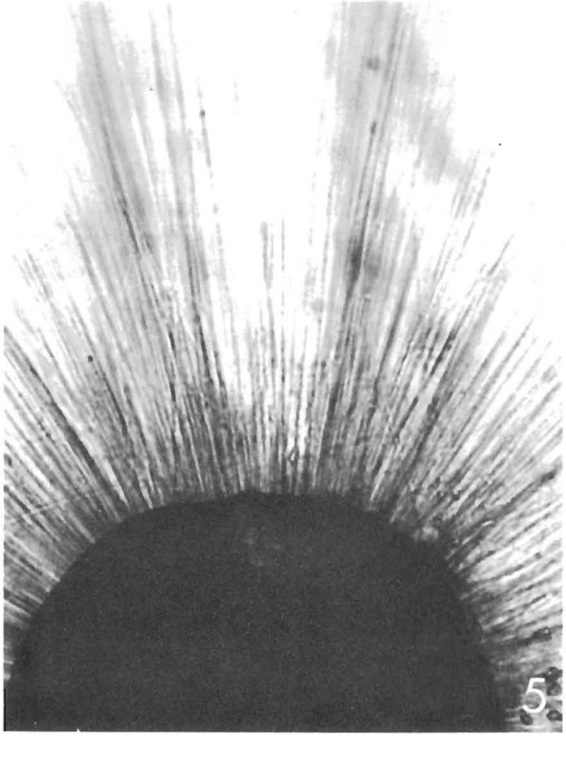
5 Floating orbulinid with numerous long axopodia. (×300)


1


2


3


4


5

2, Fig. 1). Globigerinids moving across a substrate often left a trail, possibly mucous or secretory in nature (Pl. 3, Fig. 1). Arnold (1953) described similar movement in *Allogromia laticollaris* as follows: "Through mechanisms which are still completely baffling to the biologist, the organism is able to concentrate its pseudopodial effort in one direction and move toward the attached ends of these, while simultaneously withdrawing the pseudopodia which were stretched out behind. As a general rule the test remains in a fairly upright position above the moving mass of protoplasm, just as a snail does as the snail moves about."

Allogromia has a particularly labile microtubule complement (McGee-Russell and Allen, 1971) in its pseudopodia, which allows for such movement. Possibly globigerinid pseudopodia have similarly labile microtubules during such periods of benthic activity. Globigerinids and orbulinids moving on a surface are also able to extend short reticulopodia which function in slightly conical waves to produce a rotating movement (Pl. 2, Fig. 2; Pl. 3, Figs. 2, 3).

Reticulopodia in young globigerinids commonly develop within a few days or sooner into axopodia. Development of the supporting microtubular axial complex lengthens axopodia up to ten times the test diameter in length. The delicate axial core of axopodia is remarkably flexible in young specimens (Pl. 4, Figs. 3, 4), supporting the extremely long, tenuous pseudopodia which tend to curve distally due to their own weight (Pl. 4, Figs. 1, 2). The granular components of young axopodia are often larger than the axopodial diameter, and resemble irregular beads on a slender string (Pl. 4, Fig. 1; Pl. 5, Fig. 4). Axopodia are readily regenerated following loss by an actively metabolizing young foraminifer. They may be badly tangled in transfer, and will slowly return to their original form (Pl. 4, Fig. 3). Floating globigerinids in cultures roll actively up and down in their medium, with axopodia curving into the currents.

The great length of the numerous axopodia in young specimens (Pl. 4, Fig. 4) greatly increases the cytoplasmic surface exposed for nutrient and waste exchange. In addition, pseudopodia help provide functional support and probably some buoyancy. Specimens under observation occasionally release air bubbles, which may also be associated with the buoyancy mechanism in globigerinids.

Although globigerinids are wonderfully pliant in their early stages and can tolerate considerable abuse, they do not seem able to rebuild a damaged final chamber. A damaged specimen can simply withdraw the cytoplasm into the remaining portion of the broken chamber, extend new axopodia directly from the cell surface, and continue to metabolize and float normally. Observation of such accidents leaves no doubt as to the origin of the axopodia, and their true pseudopodial nature is clear. They are definitely not spines. The transition from axopodia to spines is complex and difficult to resolve with the light microscope.

Spine Development and Associated Behavioral Changes of Globigerinids

As secondary calcification of the test proceeds, the appearance of the organisms changes considerably. There is a marked decrease in numbers of axopodia, which are replaced by fewer shorter, blunter and thicker, developing spines (Pl. 4, Fig. 1; Pl. 5, Fig. 4 vs. Pl. 6, Fig. 4).

The hardened cores of spines appear to grow outwards at the tip. An intermediate stage in calcification is visible at the distal end of the core, grading into the clear protoplasm at the tip. During active spine growth the protoplasm extends beyond the tapering calcite tip while retaining the normal bidirectional movement of contents. The protoplasmic extensions (Pl. 6, Figs. 1–3) move in an exploratory manner at the tip of each spine, greatly extending the feeding and exchange capacity of the floating globigerinid in the absence of axopodia. The tips anastomose only rarely, when they contact other exploring tips (Pl. 6, Fig. 2 arrow), because of the distance between the spines. Streaming motile extensions up to one-third the length of the calcified axial cores were seen in one floating globigerinid with long spines.

The motile tips are sensitive, withdrawing quite rapidly (in a visible motion) when disturbed or damaged in any way. They can then be seen initially as irregular buildups near the tip of the core (Pl. 5, Fig. 1) which subsequently move back along the spine using the calcified core as a substrate (Pl. 5, Figs. 2, 3).

There is a tendency in both axopodia (Pl. 8, Fig. 4) and spines (Pl. 6, Figs. 1, 3) for the protoplasm to appear twisted about the axial core, which itself appears somewhat flattened and tapering. However, once the riblike nature of the outer edges of the calcified core becomes visible, the spiralling is no longer so obvious. Doflein (1916) described a similar spiralling of protoplasm about the axial cores of certain heliozoan axopodia.

As calcification proceeds, the spines become brittle and may be broken in transfer, rather than tangled as with axopodia. Orbulinid axopodia are usually resorbed as the internal globigerinid is resorbed. In globigerinids, development continues as long as the specimen is actively metabolizing and not heavily calcified. Spines are usually much shorter than the earlier axopodia possibly in part due to breakage, but also because the heavier calcified cores cannot be supported as far out from the test as can the delicate microtubular cores of axopodia. With time, sharply tapering spine ends appear blunter, and the bases become wider and heavier. The granular contents of the protoplasm covering the spines are greatly decreased in quantity and variety of form (Pl. 5, Figs. 1–3 vs. 4) and seem to be restricted largely to mitochondria, vacuoles, and small particles quite unlike the irregular food granules transported by axopodia and reticulopodia at an earlier stage. Possibly the food requirements are greatly reduced at this stage, as metabolism slows down and the creature matures. Also, because test pores are slowly filled in, the size of particle which can be transported into the test probably decreases at this time, with the exception of particles entering through the aperture.

Bé (1965) showed that pores of *Globigerinoides sacculifer* are gradually sealed by euhedral calcite. Because similar closing was observed in thin sections of *Globigerina bulloides* (Adshead and Stapleton, unpublished data), it is quite likely that axopodia are gradually resorbed and replaced by growing spines. Protoplasm is still able to move onto the surface of the test and form the pseudopodial structures in which spines develop, possibly involving microtubular axonemes as an organic matrix for calcification. Clarification of the sequential stages in spine development will require a scanning electron microscope study of specimens in culture. The process could not be clearly visualized at the test surface using the light microscope, owing to depth of field and resolution restrictions at high magnifications.

When calcification has advanced sufficiently in mature globigerinids, the organisms apparently drift down in the water column (falling to the dish bottom in cultures). The spines, being much shorter and less numerous, may not be adequate to support flotation of the heavily calcified test beyond a certain density, even when combined with the internal vesicular system suggested by Lee and others (1965), and Anderson and Bé (1976). It is also likely that the extensive and constant feeding seen in healthy young specimens with axopodia is essential to provide the gases involved in the buoyancy mechanism.

At some point in the maturation process, globigerinids may die and fall to the bottom with the spines still intact, or they may resorb the spines and fall to the bottom. Globigerinids with resorbed spines can continue to move and feed benthically, but they cannot replace spines and resume flotation as could younger specimens following repair of damaged axopodia. Accordingly, such mature specimens are apparently not suitable for starting cultures.

Development and Pseudopodia of Orbulinid and Biorbulinid Individuals

Occasionally a recently collected floating globigerinid lays down an orbulinid sphere amongst the bases of extended axopodia (Adshead, 1967a). For about three weeks such an individual passes through a definite developmental sequence. Initially the clear, smooth sphere floats on the long, actively streaming axopodia (Pl. 8, Fig. 4), while the enclosed globigerinid is resorbed and secondary calcification of the outer sphere proceeds.

When the test has become thick and opaque, axopodia are apparently resorbed and the shell-heavy orbulinid drops to the bottom of the culture dish. Such a descent of mature specimens in the ocean would probably explain the occurrence of mature heavily calcified globigerinids and orbulinids relatively deep in the water column (300–2,000 m), although Bé (1965) thought that such shell thickening might be an "adaptation to increasingly deeper habitats."

Specimens broken early in the developmental sequence (for example, Pl. 8, Fig. 3) have shown that pseudopodia originate initially from the parent globigerinid inside the sphere. Some aspects of the maturation process are illustrated in Pl. 9, Figs. 1–6. Release of gametes as described by Le Calvez (1936), although not observed in my cultures, may be triggered only by specific stimuli which were not present. Rarely, two globigerinids may fuse prior to secretion of the orbulinid spheres, resulting in the formation of a biorbulinid structure. The two united specimens may calcify at different rates, that is, one sphere may lag behind the other as it passes through the developmental sequence outlined above. Such a lag between the two halves suggests that biorbulinid formation may be accidental.

When orbulinid axopodia are broken off in plankton tows, short reticulopodia may emerge from the test. These reticulopodia function in wavelike groups (Pl. 8, Figs. 1, 2) similar to those seen in mature globigerinids rotating on a surface (Pl. 2, Fig. 2; Pl. 3, Figs. 2, 3). In the spherical orbulinids, however, the "waves" enable the protist to roll actively on a substrate.

PSEUDOPODIA OF HELIOZOANS

Heliozoans develop axopodia which normally support flotation (Pl. 10, Fig. 1), but can serve as mooring lines (similar in effect to the reticulopodial feeding net of foraminiferans) to attach the creatures to a substrate. The attached axopodia are so firmly anchored that they can be pulled aside along their length, but can be moved from position only by tearing them loose. Although heliozoan axopodia also exhibit bidirectional flow of protoplasm and contents (mitochondria, vacuoles, and dense bodies), they do not have the restrictions imposed by the calcareous test of globigerinids and routinely utilize whole food. Accordingly, heliozoan axopodia lack the coarse, granular contents seen in axopodia of young globigerinids. Heliozoan axopodia do contain fine, regular granules which exhibit saltatory movement (Rebhun, 1972; Edds, 1975a) similar to that seen in globigerinids. The refractile granules found in centrohelidan axopodia were termed "kinetocysts" by Bardele (1976), who suggested that these extrusive organelles were "compound motile mucocysts" which functioned in food trapping.

Heliozoan axopodia are often extremely sensitive (Bardele, 1975) retracting readily when irritated or on contact with prey organisms. Two methods of feeding have been described for heliozoans. One method, described by Kitching (1964) and Ockleford and Tucker (1973) for *Actinophrys sol,* involves an axopodium holding the prey and rapidly contracting to deposit the food organism near the cell body, which sends a food-cup forming pseudopodial outgrowth to engulf the prey and draw it into the cell body. Another method described by Mackinnon and Hawes (1961) for *Echinosphaerium* (=*Actinosphaerium*) is initiated when a flagellate contacts several axopodia which immediately bend and contract to surround the organism and draw it in toward the cell body (Pl. 10, Fig. 2). The axopodia continue the enveloping process to form an

→

PLATE 9

Orbulinid axopodia

1–3 Long tenuous axopodia of a recently formed orbulinid, flexible and containing granules (although less than in young globigerinids). Figure 3 shows two fused tips separating, joined only by slender strands of protoplasm. (Fig. 1, ×200, Figs. 2, 3, ×300)

4 Axopodia appear to have developed calcified axial cores, being thicker and more brittle than in Figs. 1–3 (×300)

5 Axopodia towards the end of the three-week developmental period, being resorbed as secondary calcification of the test proceeds. (×450)

6 Resorption of axopodia in a hispid, well-developed orbulinid. At this stage, the creatures fall to the bottom of the culture dish, being heavily calcified and greatly slowed metabolically. According to LeCalvez (1936), gamete release probably occurs at about this stage. (×350)

PLATE 10

Heliozoan axopodia

1 *Echinosphaerium nucleofilum* floating in culture with extended, flexible axopodia having bidirectional movement of finely granular contents. Upper axopodia are gripping a pile of detritus. (×650)

2 *Echinosphaerium* capturing a flagellated food organism. Axopodia bend and are rapidly retracted following contact, pulling the food organism into the cell body. Axopodia at this point are irregular and distorted (arrow) almost like reticulopodia as they surround the prey and form a food vacuole. (×2,000)

3 As the food vacuole is being taken into the cell body, micropseudopodia (arrow) appear, radiating from the surface of the vacuole. Their function is not clear. (×2,000)

PLATE 11

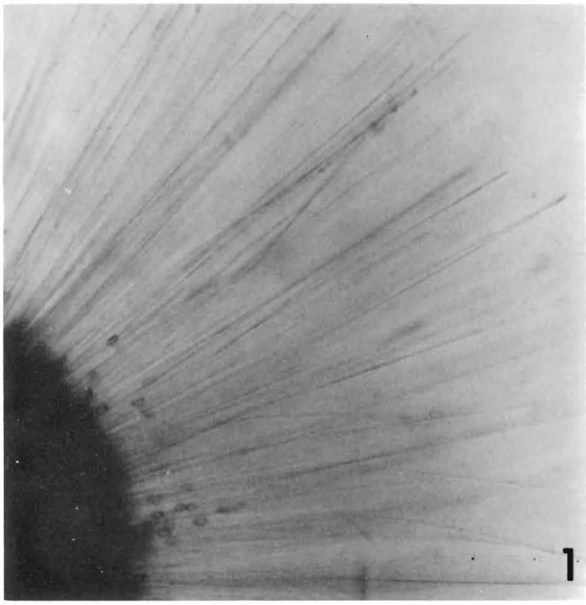
Acantharian pseudopodia and myofrisks

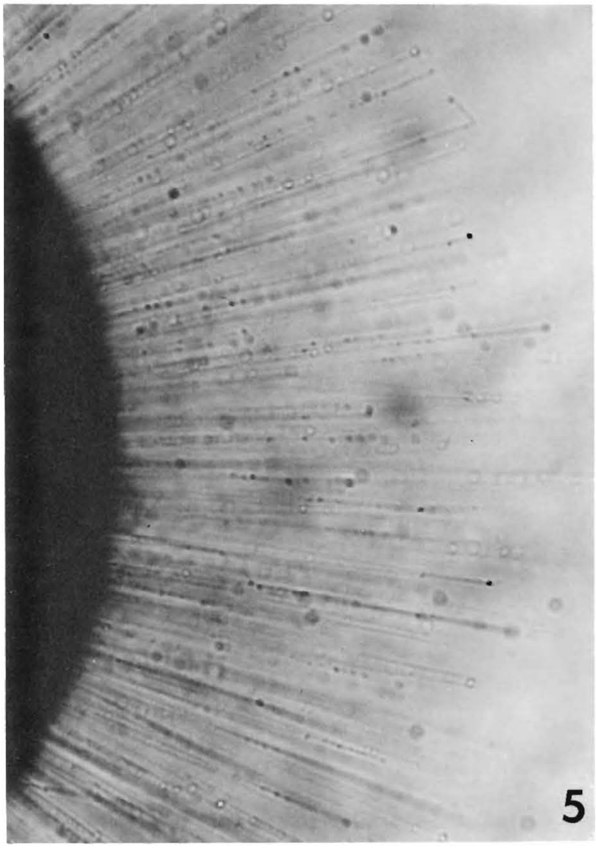
1 Acantharian with extended axopodia (arrow), and myofrisks extended along the spines. (×500)

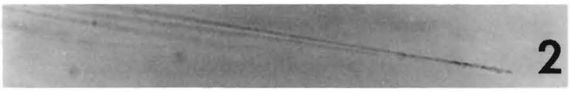
2 Acantharian with myofrisk extended almost to end of spine (arrow). (×500)

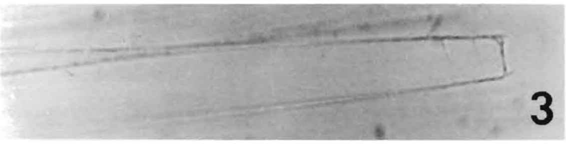
3 Acantharian spine showing an unusual variety of spidery filopodium (arrow number 1) which literally climbs rapidly up and down the spines. The motion is unlike that seen in any other pseudopodia observed. A sticky pseudopodial tip (arrow number 2) is doubled over at the tip of the same spine. (×500)

4 Acantharian which had just retracted by pulling in the myofrisks along the spines. (×250)

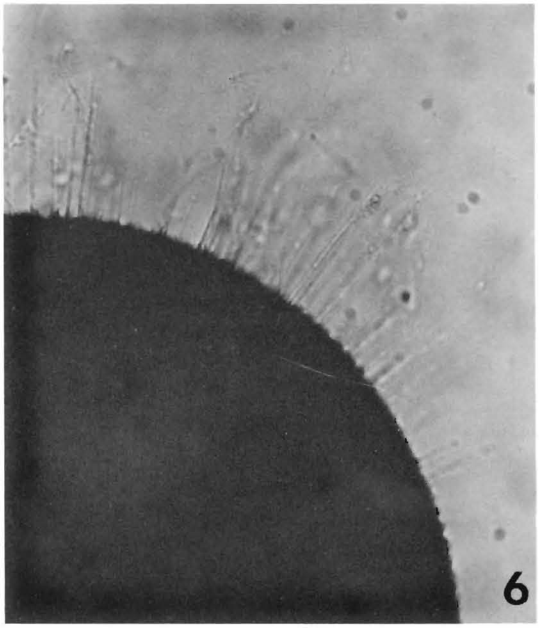

1

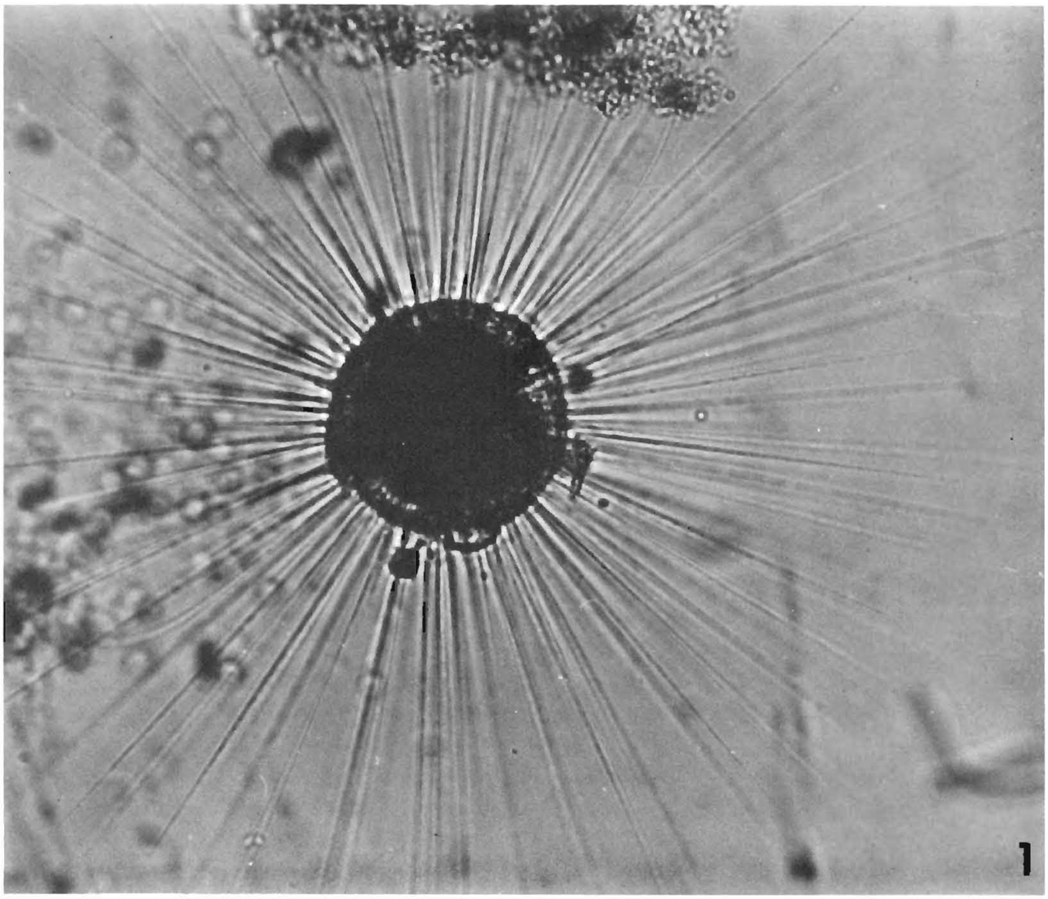

5


2


3

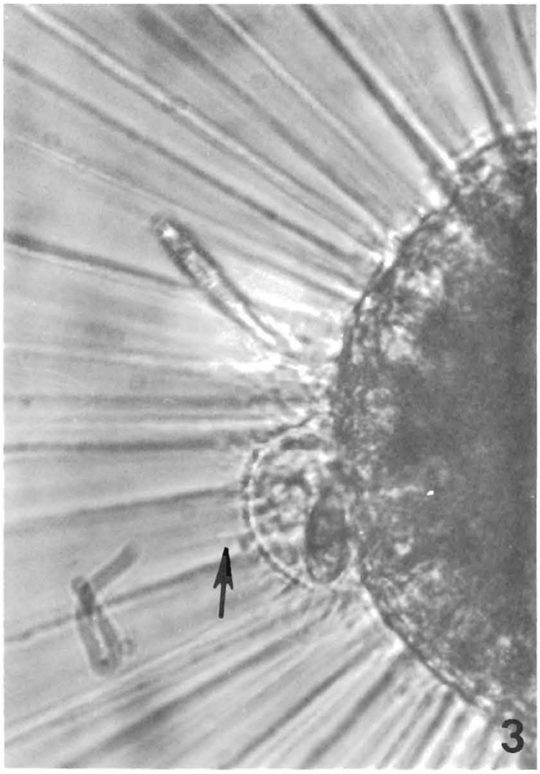

4


6

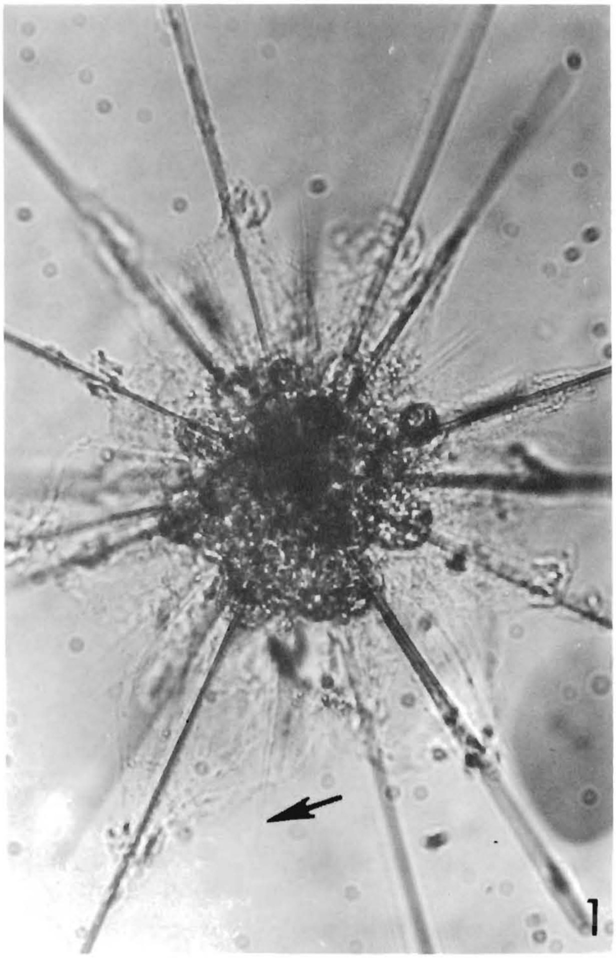


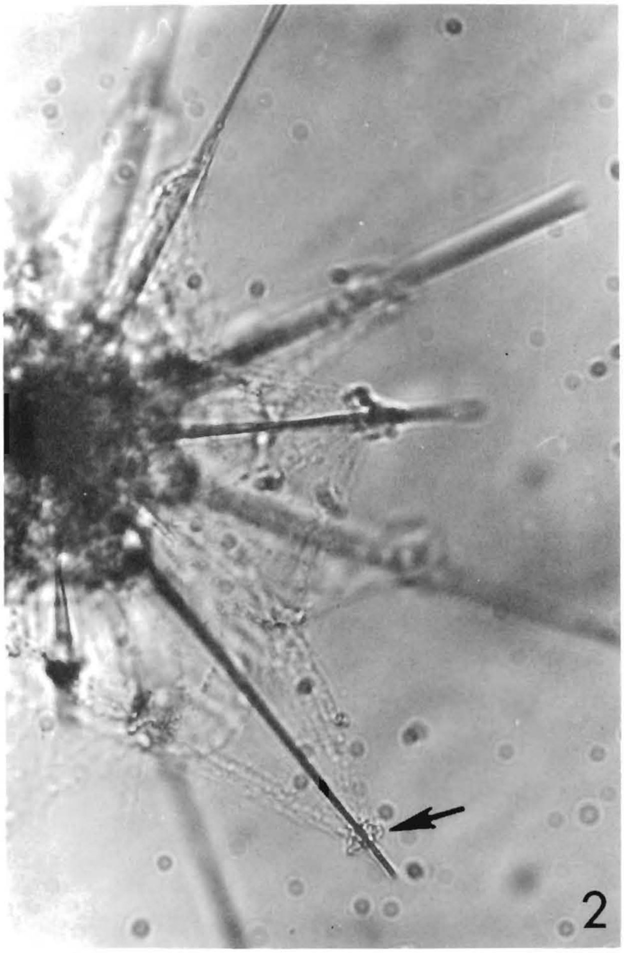
1

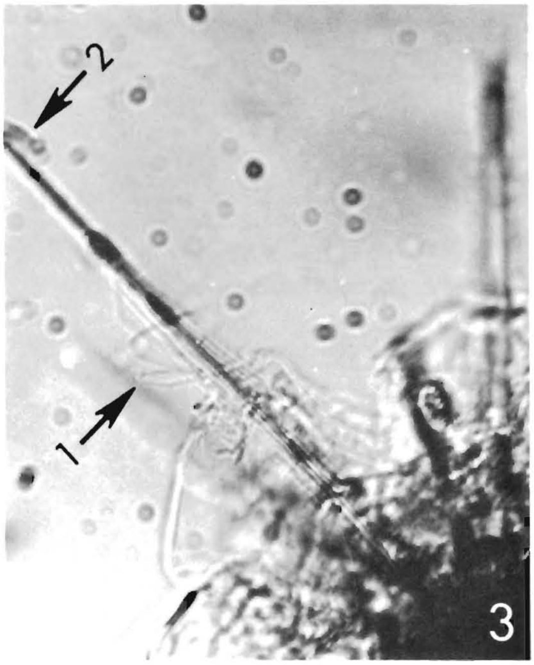
2

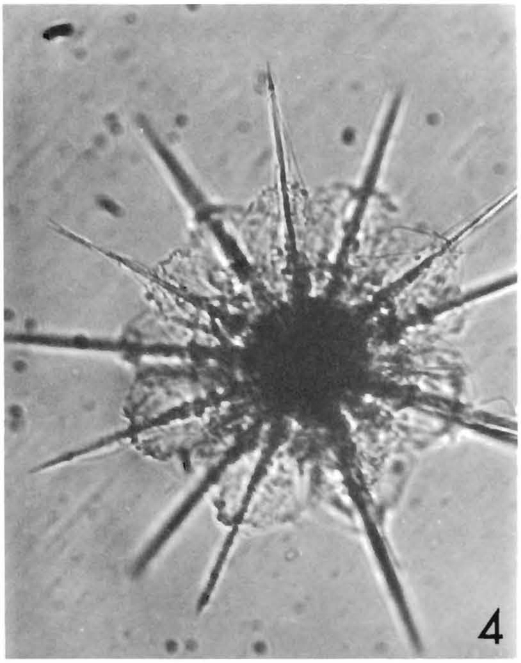


3


1


2


2
1
3


4

external vacuole, which is then pulled into the cell body. As the vacuole is retracted, numerous fine processes appear, radiating from the surface of the vacuoles (Pl. 10, Fig. 3). A remarkably similar process was described by Wetzel and Wollman (1972) in the thyroid cells of the rat, which when stimulated engulf colloid from the lumen and pull it into the cell in an externally formed vacuole with "microvilli" on the surface!

Axopodial retraction in *Heterophrys marina* takes less than 20 milliseconds (Davidson, 1973), whereas re-extension takes 2–3 minutes. Axopodia may be withdrawn singly, in groups, or simultaneously depending on the stimulus. Heliozoans can also use axopodial tips, as do globigerinids, acantharians, and radiolarians, to control rolling along a substrate with the current (Watters, 1968). In the process, they grip and release the surface with alternating axopodial tips.

PSEUDOPODIA OF ACANTHARIANS

Acantharians develop reticulopodia, fine axopodia, and a unique type of spidery filopodia which literally climb very rapidly up and down the spines (Pl. 11, Fig. 3), as well as rounded or blunt pseudopodial tips on the spines (Pl. 11, Fig. 3).

In addition, acantharians possess myofrisks, bundles of specialized fibers connecting the cell body with the spines (Pl. 11, Figs. 1–3) and providing these primitive protists with a coordinated, hydrostatic control system. When an acantharian is irritated, the myofrisks appear to contract almost in unison, pulling the bulk of the extended cell body down the spines and away from the stimulus (somewhat like an opening umbrella). The effect of such contraction can be seen in comparing Figures 1, 2, and 4 of Plate 11. Cheissin and Poljansky (1963) referred to the hydrostatic nature of this remarkable apparatus, found only in acantharians. Febvre (1971), who at that time doubted the functional nature of the myonemes, apparently did not observe such contraction in his study of acantharians. More recently, Febvre and Febvre-Chevalier (pers. comm.) have recorded some of the behavior of acantharians using quite spectacular cinemicrography. Their results should rapidly advance our understanding of these creatures.

PSEUDOPODIA OF RADIOLARIANS

Radiolarians as well as acantharians were kept alive using the technique of Adshead (1967a). Some living, floating specimens with ornately branching spines seemed to utilize a frothy cytoplasm to remain afloat, as no axopodia were visible. Other specimens (Pl. 12) possess axopodia which extend to varying degrees (see also Adshead, 1967a). Axopodia of radiolarians are usually extremely fine and clear, with only small amounts of granular contents, and are more similar to axopodia of acantharians than to those of foraminiferans or heliozoans. The axopodia are far more numerous than the spines, and also have pseudopodial tips that can be used in rolling on a substrate.

There is very little information available on behavior of axopodia in radiolarians, although they appear to be relatively short, stable, supporting structures. *Thalassicolla,* a large radiolarian with no shell, has a protective gelatinous capsule traversed by pseudopodia of an unusual nature, which can be extended beyond the capsule for feeding, or retracted when disturbed.

ZOOXANTHELLAE

External zooxanthellae were commonly encountered in actively metabolizing, healthy young globigerinids and newly formed orbulinids, often in great numbers. The symbionts (apparently chrysomonad algae), were yellow orange in color and quite light sensitive, clustering over the test in intense light, and spreading out along the axopodia in moderate-dim microscope light (Pl. 1). Occasionally a round green algal symbiont was found in globigerinids. The zooxanthellae were most numerous in actively calcifying globigerinids and early orbulinid phases.

DISCUSSION

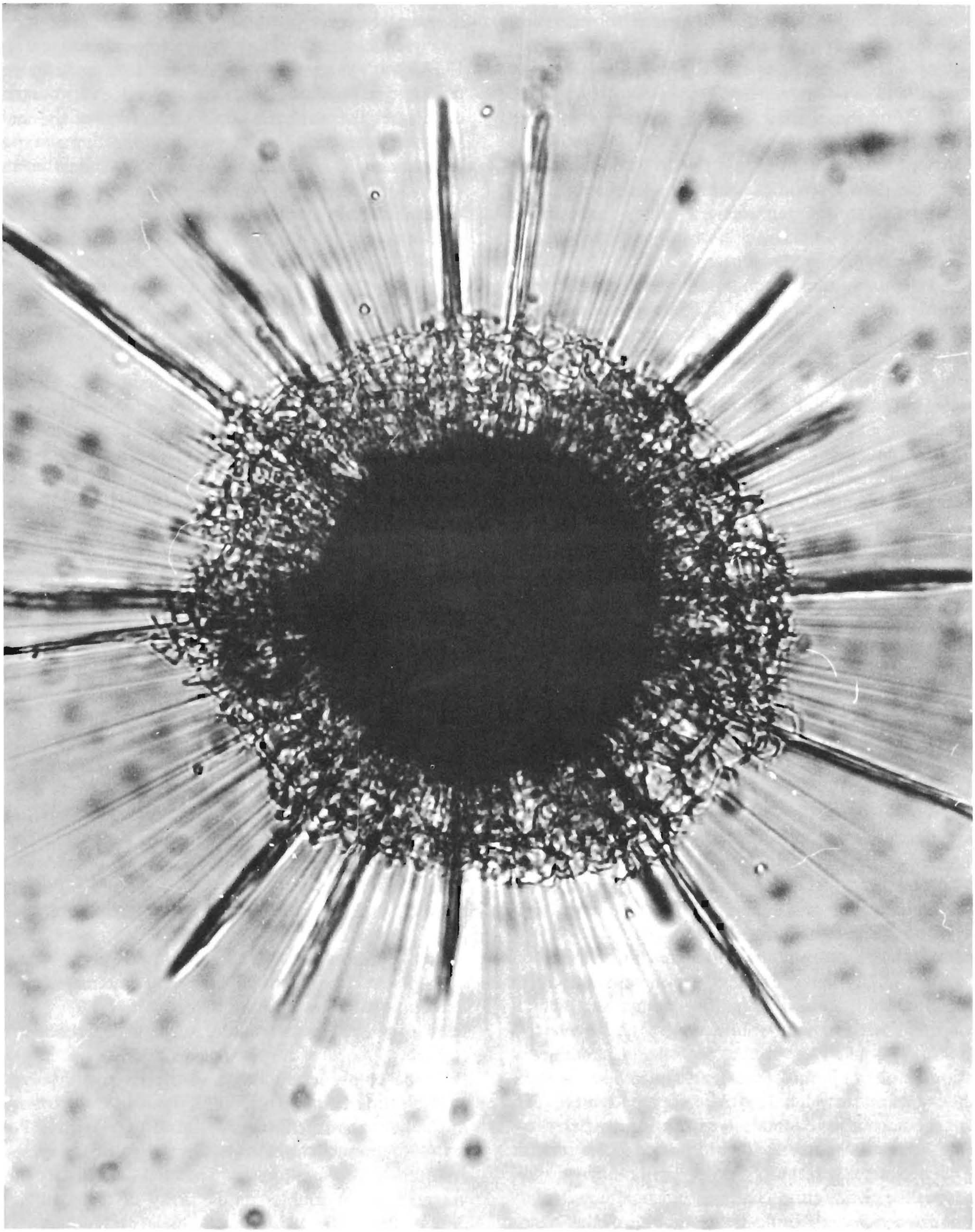
PRESERVATION OF SARCODINA FOR ULTRASTRUCTURAL STUDIES OF PSEUDOPODIA

The remarkable and unexpected adaptiveness of planktonic foraminifera is due largely to their ability to employ a wide variety of pseudopodial structures in response to environmental changes. Probably globigerinids are the most diverse representatives of the planktonic Sarcodina, in view of the ease with which

→

PLATE 12

Floating radiolarian with extended spines and axopodia. (×500).



some species can switch from a planktonic existence to a benthic one similar to that of benthic foraminiferal species. Although all planktonic Sarcodina are apparently able to roll on a substrate, and heliozoans may attach, there is so far no record of such a reversibility as that found in globigerinids.

When this study was initiated (1964–66) electron microscopists were only beginning to turn their attention to the pseudopodia of heliozoans (Kitching, 1964) and some benthic foraminifera (Hedley and others, 1967). Prior to that time, preservation methods were inadequate for dealing with such sensitive organisms, and particularly their pseudopodial extensions. Glutaraldehyde was introduced by Sabatini and others (1963) as a superior fixative for protein, commonly used prior to osmium tetroxide in fixation procedures. Without a glutaraldehyde prefix, the microtubules supporting exposed pseudopodia are irreversibly damaged by osmium, although some remarkably good pictures of microtubules in the oral capsule of osmium-fixed *Gromia* were obtained by Hedley and Bertaud (1962). There is still controversy concerning the effects of fixatives on cells and their organelles. The only acceptable criterion is comparison of fixed cells with their healthy, living state by monitoring fixation.

McGee-Russell and Allan (1971) used extremely high levels (38%) of $MgCl_2$ to stabilize an extremely labile class of microtubules in the benthic foraminifer *Allogromia*. Earlier workers had failed to find microtubules in *Allogromia*, although their presence had been indicated by rigidity and positive birefringence in the living specimens. However, the levels of $MgCl_2$ used proved quite disastrous to specimens of the marine heliozoan *Heterophrys* (Bardele, 1975) and the planktonic foraminifer *Globigerinoides ruber* (Adshead, unpublished data), causing total breakdown in *Heterophrys* and loss of axopodia in *Globigerinoides*.

Although Mg^{2+} served to stabilize heliozoan axopodial microtubules at concentrations of 0.07–10 millimolar (mM), Shigenaka and others (1974) found that concentrations above 12 mM resulted in degradation of axopodia. A similar divalent cation sensitivity was encountered in gill cilia of freshwater mussels, which responded with a rigid "shock-stop" (Adshead and others, 1974) when exposed to Mg^{2+} and Ca^{2+} concentrations of 2.5–100 mM (Adshead and others, unpublished data). Although the cilia appeared intact, all signs of normal axonemal structure (as revealed by ultrathin sections, freeze-fracture, and ciliary spreading techniques) were lost.

Bardele (1975) found that Ca^{2+} also affected *Heterophrys* axopodia during fixation, unless the heliozoans were placed in a calcium-free artificial seawater medium containing 10 millimolar (mM) ethyleneglycolbis (β-aminoethyl ether) N_1N^1 tetraacetic acid (= EGTA) to chelate any free calcium ions prior to glutaraldehyde fixation. This selective removal of extracellular Ca^{2+} resulted in superior fixation of the most sensitive axopodia. Addition of a supporting slurry of 0.8 percent agar after fixation helped Anderson and Bé (1976) to protect *Globigerinoides sacculifer* through the rigors of uranyl acetate postfixation (decalcification) dehydration and embedding. However, decalcified specimens should routinely be compared with *intact* fixed specimens to determine losses resulting from decalcification. Adshead, Cachon and Cachon (manuscript in preparation) have recently perfected a fixation technique which protects even the most sensitive pseudopodia of globigerinids. The technique can be used for specimens intended for either transmission or scanning electron microscopy, and should allow greater success in studying ultrastructural aspects of the developmental stages and physiological states of globigerinids and other planktonic Sarcodina.

Microtubule Support for Pseudopodia

Prior to use of the electron microscope, Doflein (1916) had described a clear, thicker supporting core (stereoplasm), overlain by streaming, miscible, granular rheoplasm in heliozoan axopodia. Similar rheoplasm served in foraminifera to build up a reticulum, and Doflein maintained that the only difference between reticulopodia and axopodia was due to a change in state of the internal material of reticulopods. Light microscope studies of globigerinids strongly supported Doflein's hypothesis. And modern electron microscopic investigations of heliozoans (Kitching, 1964; Tilney and Porter, 1965; Roth and others, 1970), radiolarians (Cachon and Cachon, 1971), and benthic foraminifera (Hedley and others, 1967; Marszalek, 1969) show the ultrastructural basis for the earlier observations. Pseudopodia in rheoplasmic Sarcodina (all those exhibiting stickiness of the outer granular layer) have been found to contain axial microtubule concentrations of a more or less ordered nature depending on the type of pseudopodium and the species involved.

Microtubules have been described in the axopodia of the heliozoan *Echinosphaerium* by Tilney and Porter (1965), and Roth and others (1970). In this heliozoan, the elaborate, birefringent axial core or axoneme consists of a "double-spiral" array of microtubules, first described by Kitching (1964) for *Actinophrys*.

Kitching noted that the microtubules resemble "those of cilia except that they are arranged in two interposed spirals, instead of a ring within which there are two central fibers." The precise axoneme structure is maintained by the linakge structures or bridges which bind adjacent microtubules into specific patterns (Roth and others, 1970). Circulating in the cytoplasm between the limiting plasma membrane and the axial core of axopodia are mitochondria, dense bodies, vacuoles and in *Heterophrys*, specialized organelles termed kinetocysts by Bardele (1975). Tilney and Porter (1965, p. 337) emphasized the support function of axopodial microtubules as follows:

> "Since in other biological systems the plasma membrane is not recognized as a rigid form-producing structure but instead as a limiting membrane of extremely low elasticity, it is evident that support of a relatively rigid cell process, 100 times longer than wide, must reside in the axial rod or bundle of microtubules."

Shigenaka and others (1971) showed that the heliozoan axopodium has three regions, based on differing reactions to dilute urea (0.15 Molar). The basal part is most stable, having the most defined structure, numerous links, and many microtubules. Lability increases distally along the axopodium out to the sensitive tip, which has relatively few loosely ordered microtubules. This distal lability allows the frequent and rapid retraction of pseudopodial tips, which are normally involved in feeding and response to stimuli (Pl. 10, Fig. 2). Bardele (1975) suggested that heliozoan axopodia might function on the basis of mechanical or chemical stimuli causing changes in membrane permeability to allow a sudden influx of Ca^{2+} (or other divalent cations present in excess). Such an alteration in microenvironment along the length of the axoneme could cause "instantaneous microtubule disassembly during rapid contraction."

The only information on radiolarian axopodial fine structure comes from the French laboratories of Hollande and others (1965, 1970) and of Cachon and Cachon (1971, 1972a, b, c; Cachon and others, 1973). They demonstrated the presence of a surprising paddle-wheel configuration of microtubules in cross sections of the axoneme of nassellairian radiolarians, and showed the variations found in other groups as well. In 1975, Cachon and Cachon discovered a remarkably orderly series of arms along the pseudopodial microtubules of the shell-free radiolarian *Thalassicolla nucleata* Huxley.

Pseudopodial microtubules were demonstrated in ultrastructural studies of several species of benthic foraminifera which lack the calcareous test found in most foraminifera, and were therefore easier to study. Hedley and others (1967) were the first workers to demonstrate pseudopodial microtubules in a benthic foraminifera (*Shepheardella taeniformis*). Marszalek (1969) used transmission and scanning electron microscopy to show that the rigidity attained by reticulose pseudopodia in *Iridia diaphana* was due to the presence of numerous microtubules. Although Marszalek could find closely packed microtubules (connected with fine bridges) throughout a given reticulopodium, microtubules more commonly occurred in discrete groups, running along or parallel to the long axis. Hottinger and Dreher (1974) found a similar grouping of microtubules showing connecting bridges in *Operculina ammonoides*.

The ultrastructure of planktonic foraminiferal pseudopodia has not been adequately studied to date due to the scarcity of living specimens in established cultures, and the firmly held belief that axopodia do not develop in the Foraminiferida. Axopodia were used by taxonomists for a long time, to separate Sarcodina having them from those which did not. Because the only living foraminifera studied earlier were benthic, it was believed that only reticulopodia formed in the Foraminiferida. Adshead (1967b) reported that axopodia do develop in healthy, young, globigerinids (for example, *Globigerina bulloides*), and in fact appear as part of a developmental sequence whose ultrastructure would be of considerable interest to students of primitive motility. These developmental stages are presently being studied by Adshead, Cachon and Cachon.

The major inadequacy of published ultrastructural studies of globigerinids to date (Febvre-Chevalier, 1971; Anderson and Bé, 1976) has been their restriction to more mature specimens having distinct spines. Also, Anderson and Bé seem to have concentrated on one specimen of *Globigerinoides sacculifer*, which cannot be considered a representative sample, especially in organisms having complex developmental sequences.

Fixation techniques have been a limiting factor, there being no real precedent for adequate globigerinid fixation (as mentioned earlier). Amongst planktonic Sarcodina which have been studied, heliozoans (although sensitive) lack a test, and radiolarians are siliceous. Decalcification procedures used in both published studies of globigerinid ultrastructure (that is, Febvre-Chevalier, 1971; Anderson and Bé, 1976) might have damaged delicate peripheral structures and pseudopodia. Such damage could lead to wrong or misleading interpretations of results due to a lack of control specimens for comparison.

Febvre-Chevalier (1971, p. 217) found a somewhat orderly microtubular core in what she termed filopodia of *Globigerina bulloides*. The slightly wavy core actually resembled that of axopodia in the very sensitive heliozoan *Heterophrys* discussed by Bardele (1975, p. 94). Febvre-Chevalier may have sectioned a reticulopodium (filopodium) similar to those seen among the base of spines in mature specimens (Pl. 5, Fig. 5), or may in fact have encountered an axopodium which was in a transition stage or had been slightly altered during fixation. Her work was careful and thorough, and is still the only available reference on ultrastructure of *Globigerina bulloides*.

Anderson and Bé (1976) found only a network of rhizopodia (= *reticulopodia*) in their specimen of *Globigerinoides sacculifer*, and were unable to demonstrate microtubule distribution in these pseudopodia. If *Globigerina* and *Globigerinoides* have comparable pseudopodial development, their specimen of *Globigerinoides* might correspond to that of *Globigerina* shown in Plate 6, Figure 4, possibly having reticulopodia similar to those seen in Plate 5, Figure 5.

BIDIRECTIONAL STREAMING OF PROTOPLASM

Bidirectional filamentous movement of protoplasm was described in the 19th century in foraminiferans, radiolarians, heliozoans, some testate amoebae with filose pseudopodia, and certain proteomyxans (affinities uncertain, probably related to heliozoans). Protoplasmic streaming in extensive and relatively large pseudopodial networks of foraminifera have been studied most frequently by light microscopy. Jepps (1942) and Arnold (1953) presented some of the most aesthetically pleasing descriptions of streaming in the benthic foraminifera, while Allen (1964) was more biophysically oriented. The "granular" nature of the cytoplasm which composes reticulopodia and axopodia in foraminiferans and heliozoans enhances observation of streaming in these organisms.

Although the mechanism in all cases appears to be similar, there has been considerable controversy concerning bidirectional streaming for some years. Tilney (1971) emphasized that two distinguishing features of bidirectional streaming were (1) specificity of particles moved (not indiscriminate movement of cytoplasm in a stream, as in *Amoeba, Nitella*, and *Physarum*), and (2) movement of particles in rigidly defined tracks (saltatory movement of particles). Edds (1975b) and Bardele (1976) have implicated microfibrillar systems (actin and myosin) in the streaming mechanism of heliozoans.

SPINE DEVELOPMENT RELATIVE TO CALCIFICATION IN GLOBIGERINIDS

There appear to be two possible explanations for the differences seen between the long, tenuous axopodia of young specimens, and the shorter, blunter, calcifying extensions with motile tips found in maturing specimens with considerable secondary calcification. Either (1) some axopodia develop calcified axial cores (Cachon and Cachon, 1972a, suggested a possible role of axopodia in silica deposition in radiolarians), or (2) axopodia are withdrawn as the spine extensions are built outward from the test.

Because spines are considerably less numerous than young axopodia (compare Pl. 5, Fig. 4; Pl. 6, Fig. 2), they may be a different phenomenon. Owen (1868) noted that pseudopodia extended from the foramina, whereas spines originated on the test around openings. Bé and Hemleben (1970) referred also to spines "from internal chambers protruding through some of the pores."

Adshead and Jongebloed (paper in preparation) have recently made a scanning electron microscope (SEM) study of living globigerinids in cultures, looking at all the stages of pseudopodial and spine development at the test level. The results help to clarify pseudopodia-spine-test interactions in development by providing a depth of field that is lacking at high power in light microscopes, and a third dimension that is lacking in transmission electron microscopy. Hemleben (1969) has used SEM most effectively on planktonic foraminifera which were alive but lacking the extensive pseudopodial development seen in cultured specimens which have been allowed to recover from collection shock.

Any interpretations based on newly collected specimens will inevitably be incomplete, as are interpretations which fail to take into account the evidence of spine development in calcifying tests. The important question concerns the true nature of spines: are they calcified axopodia or independent structures? If they are independent, is there a correlation between the structures, that is, must the globigerinid resorb axopodia to provide a pool of materials with which to form spines? Or can the two structures occur concurrently as suggested by some observations?

Globigerinids with calcifying spines have been observed to have motile, streaming protoplasmic extensions up to one-third the length of the calcified axial cores (Pl. 6, Figs. 1–3). It may have been such extensions which Bé (pers. comm., 1966) referred to as resembling flags, because in a floating specimen they do bear a similarity to banners flying from standards. Bé believed then that the pseudopodial tips might emanate from within hollow spines, but was restricted by the limitations of the binocular microscope in this observation. Lipps (1966) also referred to the pseudopodial extensions from globigerinid spines.

Mature, heavily calcified specimens of *Globigerina bulloides* may lose both axopodia and spines, fall to the bottom of culture dishes, and lead a benthic existence. Parker (1962) noted that often young specimens have spines and older ones do not. Bé (1960a) pointed out that spines are present in juveniles of many globigerinids, but are reduced in numbers or lost completely in later stages. Bé stated (1965, p. 377):

> "The absence of spines at some stage or throughout the life cycle of these species is real and not due to breakage during plankton-towing, because in the latter event the broken spine bases would be apparent."

My observations suggest that the spines are in fact resorbed by some globigerinids and orbulinids as the specimens calcify and mature (illustrated for orbulinids in Pl. 9), perhaps prior to assuming a benthic lifestyle in some species. Hemleben (1969) believed that globigerinids could resorb spines.

Radiolarians exhibit axopodia in addition to spines (Pl. 12); a similar situation may exist in globigerinids also.

Secondary calcification of the globigerinid test occurs at different rates in different specimens and culture conditions. All degrees of calcification have been found in cultured specimens (depth of culture medium a few centimeters), although Bé (1965) stated that calcification could be related to depth in the water column, that is, "most living planktonic foraminifera thicken their tests in adaptation to increasingly deeper habitats." In fact, in the same way that the maturing foraminiferan thickens and falls to the bottom of culture dishes, in nature such dense specimens would have resorbed spines (or be in the process of doing so), would be falling in the water column, and therefore would be collected at greater depths. Buoyancy would no longer be vital at this stage of maturity, where metabolism has apparently slowed and food exchange is drastically reduced. The reduced requirement for particulate food is clearly reflected in the reduced surface area of mature individuals (which have relatively few, shorter spines) compared to the surface area of young, actively metabolizing specimens, with thin tests and numerous lengthy axopodia or young spines.

CULTURING PLANKTONIC SARCODINA

The planktonic mode of life has been achieved by a remarkable variety of Sarcodina. Some of the groups represented are entirely planktonic, some are planktonic for only part of the life cycle. In most representatives the life cycle is quite complex, involving an alternation of sexual and asexual generations. Complete life cycles are poorly known or not at all for many groups, including all of the planktonic foraminiferans, due to the complexity of the life cycle. Because specific stimuli are required to trigger each generation, these stimuli must be recognized by researchers before life cycles can be completed in cultures.

The problem has been overcome for a number of benthic foraminiferans after years of effort by many workers. Sliter (1965) was able to show that *Rosalina globularis* was in fact the correct identity for the species which Myers (1943) had described in such exquisite detail as *Tretomphalus bulloides*. That study was complicated by the unusual reproductive float chamber which enables *Rosalina* to utilize effectively both the benthic and the planktonic habitats.

Planktonic foraminiferans have been less accessible and have quite different maintenance requirements than benthic foraminiferans. Because of this, no one had kept foraminifera in cultures prior to 1964–66 (Adshead, 1967a), although there had been interest in the problem for some time (Bé and Ericson, 1963).

In order to determine an organism's specific living requirements it is essential to watch the organism for long hours to learn something about its behavior and its responses to environmental change in reasonably "natural" cultures. Such studies are painstaking, require much patience and may at first seem like "soft" science. Yet with the resulting knowledge it is possible to undertake ultrastructural and ecological studies that actually can be correlated to the life of the organism. Without such knowledge, ultrastructural and often ecological studies will tend to be interpreted out of context, and can have only limited value.

Sliter (1965), knowing the careful descriptive work of Myers (1943) and others on *Tretomphalus*, was able to show its true life relations, and found that only minor temperature changes were required in his established culture conditions to induce gametogenesis.

My observations of *Globigerina bulloides* and other globigerinids in culture (1967a) support Bandy (1966) and Hofker (1967) in the claim that the orbulinid phase (reported by Le Calvez, 1936, to produce gametes) does in fact occur periodically in several globigerinid species. However, orbulinids obviously do not occur in all globigerinid life cycles. Species-specific differences in life cycles were described by Grell (1973) in benthic foraminifera. There is no reason to expect that planktonic species will be simpler, as Bé and Anderson (1976) have pointed out. The possible occurrence of benthic stages in the life cycle, as described by Christiansen (1965) for *Globigerinoides rubra*, is a further complicating factor, which may have to be considered in attempting to determine some globigerinid life cycles.

In their admirable description of gametogenesis in *Hastigerina pelagica*, Bé and Anderson (1976, p. 890) made the surprising claim that planktonic foraminifera had not been studied in cultures prior to their work. "The delicate nature of the latter group (planktonics) frustrated previous attempts to study them in culture." Anderson and Bé (1976, p. 1) again declared that "Despite the effort of numerous investigators during the past decade, no successful laboratory cultures have been achieved to date."

Despite considerable progress in studying living planktonic foraminiferans, we are still ignorant of many very basic details in the development and life cycles of globigerinids. It would be most constructive if researchers describing observations of living globigerinids would clearly define the term "cultures" as it applies to their studies. Then ensuing workers can better evaluate their own contributions. The fact that organisms cannot be reared through *all* of a complex life cycle does *not* negate observations on specimens reared through a part of that life cycle. This is particularly true, for example, when *Orbulina universa* is still being used as a valid taxon, 14 years after Bandy (1966) and Hofker (1967), using fossil evidence had urged that orbulinid spheres be recognized as reproductive stages in several genera and species of globigerinids (discussed later). Adshead's repeated observation of the globigerinid-to-orbulinid transition in cultures has reinforced their findings by showing that the sequence occurs regularly in some recent globigerinids at least. The actual mechanisms for this remarkable occurrence are still not clear.

Most important, whether one "maintains" or "cultures" globigerinids through all or part of the life cycle, careful observations of many healthy, floating and developing globigerinids (including occasional transitions to orbulinid or rarely biorbulinid stages) can be extremely useful. In fact, such studies should soon enable us to achieve complete life cycles in culture.

PLANKTONIC AND BENTHIC BEHAVIOR OF GLOBIGERINIDS

Foraminifera are usually considered to be either planktonic or benthic, except such rotaliids as *Rosalina* with its "*Tretomphalus*" floating stage. Nonetheless, globigerinids in culture are well adapted to assume a benthic mode of existence after damage in young specimens, and commonly also in mature specimens with resorbed spines. The frequency of such observations in cultures suggested a definite role in the natural environment for this ability of globigerinids to revert to a benthic existence.

Murray (1897) established the planktonic life style of some foraminifera (using specimens collected in drinking glasses from surface water) during a cruise of the *Challenger*. Murray was one of the earliest workers (except Owen, 1868) to observe undamaged living planktonic foraminifera. His unusual collection method resulted from a dispute over the natural habitat of globigerinids (sea surface vs. sea floor) and the contention of other biologists that globigerinids collected in surface tows with a plankton net had originated instead from sediment contaminants on deck.

The planktonic nature of globigerinids has since been so firmly established that many workers today tend to dismiss as contaminants rose bengal-stained specimens (Walton, 1952) of globigerinids found in bottom sediments (Green, 1960; Phleger, 1954, 1960). However, Christiansen (1965) described a benthic stage in the life cycle of *Globigerinoides ruber* collected in bottom mud from a depth of 200 m in the Gulf of Naples. The benthic stage, living in mud houses, was microspheric and multinucleate, whereas specimens from plankton tows were megalospheric and uninucleate. *Globigerinoides ruber* is thus apparently one species of *Globigerinoides* which omits an orbulinid phase. Other species [*G. triloba sacculifera* (Brady) and *G. conglobata*] were found inside orbulinid chambers by Rhumbler (1911), Bandy (1966), and Hofker (1967).

Bé's study (1960b) of Arctic *Globigerina pachyderma* disclosed the presence of the terminal (mature) form in bottom sediments, while the juvenile was collected from near-surface waters. Bé did not indicate whether any of the bottom forms were alive. Green (1960) found more stained *G. pachyderma* in surface layers of Arctic bottom sediments than any accepted benthic species. Although Green attempted to explain away this occurrence, it is possible that these globigerinids also adopt a benthic existence following secondary calcification, much as is seen in cultured specimens of *G. bulloides*.

The importance of such an adaptation to population studies is immediately obvious. Accordingly, it seems important to consider the distribution of living benthic globigerinids and the role which a temporary benthic existence might play in the life cycle of many planktonic foraminiferans. It is essential to remain flexible in observing cultures of organisms with such complex life cycles, especially when the behavior and relations of the whole group are so poorly known.

ORBULINID PHASES IN LIFE CYCLES OF GLOBIGERINIDS

Observation of the formation of orbulinid phases from globigerinids in cultures as described by Adshead (1967a), following the work of Rhumbler (1911) and accompanying the study of fossil specimens by Bandy (1966) and Hofker (1967), should have been adequate to eliminate the use of "*Orbulina*" as a taxon. Yet as recently as 1976, Hecht and others used the taxon freely.

Bandy (1966) showed that *Orbulina universa* is in fact a final spherical float chamber associated with different species and genera of globigerinids, and concluded that modern "*Orbulina*" has had a multiple origin from different globigerinids. Hofker (1967) supported Bandy's view and enlarged it to include *Biorbulina*, which was observed in my cultures to form from two globigerinids attached to each other, with the two lobes developing at different rates. Hofker believed that his observations:

> ". . . clearly prove that *Orbulina* is a stage with surrounding bulla of quite different species which even may belong to different genera of planktonic Foraminifera. This also can be said about *Candorbulina* and *Biorbulina* so that as a genus *Orbulina* and its allies lose all biological meaning. We can only say that from a certain geologic time on, circumstances became such, that the forming of embracing bullae became possible for several planktonic species."

Owen (1868), observing the similarity of internal chambers of "*Orbulina*" to *Globigerina*, and the close resemblance between the varying test surfaces (with and without spines), preceded the foregoing by nearly a century. Owen's solution was to make "*Orbulina*" a subgenus of *Globigerina*, because he was unaware of the possible reproductive role suggested by Le Calvez (1936). Since then several workers including Parker (1962) have suggested that "*Orbulina*" is indeed characteristic of a number of genera and species of globigerinids. Observation of gamete release and fusion, followed by development of new globigerinids in cultures, would be desirable final proof of the function of "*Orbulina*" as a reproductive float chamber.

ZOOXANTHELLAE AND CALCIFICATION

One of the earliest attempts to capture the dynamic essence of living planktonic foraminifera and their algal symbionts was by J. Murray (1897).

> "In *Globigerina bulloides* . . . the yellow-orange colour of the sarcode is due to the presence of numerous oval-shaped xanthidae or 'yellow cells', similar to those found in the Radiolaria. When the sarcode with these 'yellow cells' flows out of the foramina, and mounts between the numerous spines outside the shell, the whole presents a very striking object under the microscope; the transparent sarcode can be seen running up and down the long silk-like spines, and the 'yellow cells', seated at the base of these spines, quite obscure the body of the shell."

External zooxanthellae were commonly encountered in actively metabolizing, healthy young globigerinids and newly formed orbulinids in my cultures, often in great numbers. The symbionts, apparently chrysomonad algae, were yellow orange in color and were quite light sensitive, clustering over the test in specimens exposed to intense light, and spreading out along the axopodia in moderate-dim microscope light (Pl. 1).

Rhumbler (1911, p. 245) illustrated zooxanthellae which were similar to those described by J. Murray (1897) and to those seen in this study also. Anderson and Bé (1976) observed dynoflagellate symbionts in *Globigerinoides* which moved into the distal chamber at night and out along the spines by day.

J. W. Murray (1973) referred to the role of zooxanthellae in increasing the rate of test calcification by enabling the foraminiferan to take up calcium more efficiently. Similar reports have been made concerning the algal symbionts of coral for many years by Goreau (1961), Pearse and Muscatine (1971), and others. Pearse and Muscatine found that although calcification rates in a branching coral (*Acropora*) are highest in the tips, zooxanthellae are most numerous near the base. By means of radioactive tagging experiments they showed that coral calcification rates were enhanced by translocation of the organic products of algal photosynthesis from symbionts in lower parts of the branch to the growing tip. Because the zooxanthellae were most common and numerous in actively calcifying specimens of *Globigerina bulloides* (and young orbulinid phases), it appears that they may be involved in calcification in these organisms also.

CONCLUSION

None of the planktonic Sarcodina show the remarkable diversity of pseudopodial structures observed in globigerinids. Sandon (1963), although unaware of the variability of globigerinid pseudopodia, was well aware of "all the varied activities (of which flow is only one) of all the different kinds of pseudopodia found among the *Sarcodina*, among which those of the *Foraminifera* are perhaps the most remarkable."

Globigerinids can move or feed on a substrate with filopodia, reticulopodia, and pharopodia. They can float on long, tenuous axopodia or spines with motile protoplasm and extended pseudopodial tips. When axopodia are damaged, globigerinids and orbulinids can revert to a benthic existence while they recover.

The ultrastructural basis of these globigerinid pseudopodia is almost unknown. Even in heliozoans, whose basic axopodial structure is well known, there is no information on the ultrastructural changes which occur in axopodia during feeding or attachment to a substrate, and the mechanisms are entirely theoretical (Roth and others, 1970; Bardele, 1976). Acantharians have a remarkable diversity of pseudopodia (the "spidery" filopodia have not been described at all), and although radiolarians are beginning to be studied (following the breakthrough studies of Cachon and Cachon), correlation of structure with behavior and environmental change has yet to be made. In addition, the mechanism underlying alterations in surface "stickiness" in response to environmental change is only beginning to be clarified (Vollett and Roth, 1972, 1974).

Much of the effort in primitive motility to date has been directed toward lobate amoebas and slime moulds. Planktonic Sarcodina have been generally neglected, often because of technical difficulties which are only beginning to be overcome. Yet these delicate, often beautiful creatures could hold the key to many of the problems of primitive motility. Simple exaggerations which occur in some systems, such as the arms extending from microtubules in *Thalassicolla* (Cachon and Cachon, 1975), may allow isolation of elusive factors once culture methods are perfected. The methods needed for analyzing these systems are available now.

We should not close our minds as to what might be found when sophisticated techniques are applied to the unexpectedly dynamic planktonic Sarcodina, whose living cytoplasmic aspects are not nearly as familiar as their exquisite skeletons.

REFERENCES

ADSHEAD, P. C., 1966, Observations on living planktonic foraminifera in cultures, (abs.): Am. Assoc. Petroleum Geologists Bull., v. 50, p. 642–643.

———, 1967a, Collection and laboratory maintenance of living planktonic foraminifera: Micropaleontology, v. 13, no. 1, p. 32–40.

———, 1967b, Taxonomic significance of axopodial development in living planktonic Foraminiferida and other *Sarcodina*: Jour. Protozoology, v. 14, Suppl., p. 31.

ADSHEAD, P. C., MARTINEZ, J. R., KILBURN, K. H., and HESS, R. A., 1974, Ciliary inhibition and axonemal microtubule alterations in freshwater mussels: New York Acad. Sci. Ann., v. 253, p. 192–212.

ALLEN, R. D., 1964, Cytoplasmic streaming and locomotion in marine Foraminifera, *in* Allen, R. D. and Kamiya, N., eds., Primitive motile systems in cell biology: New York, Academic Press, p. 407–432.

———, 1968, Differences of a fundamental nature among several types of amoeboid movement, *in* Symposium on Aspects of cell motility: Soc. Exptl. Biology, v. 22, p. 151–168.

ANDERSON, O. R., and BÉ, A. W. H., 1976, The ultrastructure of a planktonic foraminifer, *Globigerinoides sacculifer* (Brady), and its symbiotic dinoflagellates: Jour. Foram. Research, v. 6, p. 1–21.

ARNOLD, Z. M., 1953, An introduction to the study of movement and dispersal in *Allogromia laticollaris* Arnold: Cushman Found. Foram. Research, Contr., v. 4, pp. 15–21.

———, 1954, Culture methods in the study of living Foraminifera: Jour. Paleontology, v. 28, p. 404–416.

———, 1964, Biological observations on the foraminifer *Spiroloculina hyalina* Schulze: California Univ. Pubs. Zoology, v. 72, p. 1–78.

BANDY, O. L., 1966, Restrictions on the "*Orbulina*" datum: Micropaleontology, v. 12, no. 1, p. 79–86.

BARDELE, C. L. F., 1972, Cell cycle, morphogenesis, and ultrastructure in the pseudoheliozoan *Clathrulina elegans*: Zeitschr. Zellforschung, v. 130, p. 219–242.

———, 1975, The fine structure of the centrohelidan heliozoan *Heterophrys marina*: Cell Tissue Research, v. 161, p. 85–102.

———, 1976, Particle movement in heliozoan axopods associated with lateral displacement of highly ordered membrane domains: Zeitschr. Naturforschung, v. 31c, p. 190–194.

BÉ, A. W. H., 1960a, Ecology of recent planktonic foraminifera: Part 2, Bathymetric and seasonal distributions in the Sargasso Sea off Bermuda: Micropaleontology, v. 6, p. 373–392.

———, 1960b, Some observations on Arctic planktonic Foraminifera: Cushman Found. Foram. Research Contr., v. 11, p. 2, p. 64–68.

———, 1965, The influence of depth on shell growth in *Globigerinoides sacculifer* (Brady): Micropaleontology, v. 11, p. 81–97.

BÉ, A. W. H., and ANDERSON, O. R., 1976, Gametogenesis in planktonic Foraminifera: Science, v. 192, p. 890–892.

Bé, A. W. H., and Ericson, D. B., 1963, Aspects of calcification in planktonic Foraminifera (Sarcodina): Annals New York Acad. Sci. 109, article 1, p. 65–81.

Bé, A. W. H., and Hemleben, C., 1970, Calcification in a living planktonic foraminifer, *Globigerinoides sacculifer* (Brady): Neues Jahrb. Geologie u. Paläontologie Abh., v. 134, p. 221–234.

Bé, A. W. H., Jongebloed, W. L., and McIntyre, A., 1969, X-ray microscopy of Recent planktonic foraminifera: Jour. Paleontology, v. 43, p. 1384–1396.

Berlinrood, M., McGee-Russell, S. M., and Allen, R. D., 1972, Patterns of particle movement in nerve fibres in vitro—an analysis by photokymography and microscopy: Jour. Cell Science Jour., v. 11, p. 875–886.

Berrend, R. E., 1964, Filopodial movement in *Cyphoderia ampulla* (Ehr.), *in* Allen, R. D., and Kamiya, N., eds., Primitive motile systems in cell biology: New York, Academic Press, p. 433–443.

Bovee, E. C., 1964, Morphological differences among pseudopodia of various small amebae and their functional significance, *in* Allen, R. D. and Kamiya, N., eds., Primitive motile systems in cell biology: New York, Academic Press, p. 189–219.

Bradshaw, J. S., 1955, Preliminary laboratory experiments on ecology of foraminiferal populations: Micropaleontology, v. 1, p. 351–358.

Buchanan, J. B., and Hedley, R. H., 1960, A contribution to the biology of *Astrorhiza limicola* (Foraminifera): Marine Biol. Assoc. United Kingdom Jour., v. 39, p. 549–560.

Cachon, J., and Cachon, M., 1971, Le système axopodial des radiolaires nassellaires. Origine, organisation et rapports avec les autres organites cellulaires. Considérations générales sur l'organisation macromoléculaire du stéréoplasme des Actinopodes: Archiv. Protistenk., v. 113, p. 80–97.

———, 1972a, Les modalités du dépôt de la silice chez les Radiolaires: Archiv. Protistenk., v. 114, p. 1–13.

———, 1972b, Le système axopodial des Radiolaires Sphaeroidés. I. Les Centroaxoplastidiés: Archiv. Protistenk., v. 114, p. 51–64.

———, 1972c, Le système axopodial des Radiolaires Sphaeroidés. II. Les Périaxoplastidiés. III. Les Cryptoaxoplastidiés (Anaxoplastidiés). IV. Les fusules et le système rheoplasmique: Archiv. Protistenk., v. 114, p. 291–307.

———, 1975, Rôle des microtubules dans les courants cytoplasmiques des axopodes: C. R. Acad. Sci. Paris Compte Rendu, v. 280, p. 2341–2343.

Cachon, J., Cachon, M., Febvre-Chevalier, C., and Febvre, J., 1973, Determinisme de l'édification des systèmes microtubulaires stereoplasmiques d'Actinopodes: Archiv. Protistenk., v. 115, p. 137–153.

Cheissin, E. M., and Poljansky, G. I., 1963, On the taxonomic system of the Protozoa: Acta Protozoologica (Warzawa) v. 1, fasc. 31, p. 327–352.

Christiansen, B. O., 1958, The foraminifer fauna in the Dröbak Sound in the Oslo Fjord (Norway). NYTT Magasin for Zoologi, v. 6, p. 5–91.

———, 1965, A bottom form of the planktonic foraminifer *Globigerinoides rubra* (D'Orbigny, 1839): Publ. Staz. Zool., Napoli, v. 34, p. 197–202.

Davidson, L., 1973, Contractile axopodia of the centrohelidan heliozoan *Heterophrys marina*: Jour. Cell Biology, v. 59, p. 71a.

Doflein, F., 1916, Studien zur Naturgeschlichte der Protozoen. VII. Untersuchungen über das Protoplasma und die Pseudopodien der Rhizopodien: Zool. Jahrbuch, Abt. Anat. Ontog. Tiere, v. 39, p. 335–384.

Edds, K. T., 1975a, Motility in *Echinosphaerium*. I. An analysis of particle motions in the axopodia and a direct test of the involvement of the axoneme: Jour. Cell Biology, v. 66, p. 145–155.

———, 1975b, Motility in *Echinosphaerium nucleofilum*. II. Cytoplasmic contractility and its molecular basis: Jour. Cell Biology, v. 66, p. 156–164.

Febvre, J. 1971, Le myonème d'Acanthaire essai d'interprétation ultrastructurale et cinétique: Protistologica, v. 7, p. 379–391.

Febvre-Chevalier, C., 1971, Constitution ultrastructurale de *Globigerina bulloides* d'Orbigny, 1826 (Rhizopoda-Foraminifera): Protistologica, v. 7, p. 311–324.

Goreau, T., 1961, Problems of growth and calcium deposition in reef corals: Endeavour, v. 20, p. 32–39.

Green, K. E., 1960, Ecology of some Arctic Foraminifera: Micropaleontology, v. 6, p. 57–78.

Grell, K. G., 1973, Protozoology: New York, Springer-Verlag, p. 554.

Hecht, A. D., Bé, A. W. H., and Lott, L., 1976, Ecologic and paleoclimatic implications of morphologic variation of *Orbulina universa* in the Indian Ocean: Science, v. 194, p. 422–424.

Hedley, R. H., and Bertaud, W. S., 1962, Electron microscopic observations of *Gromia oviformis* (Sarcodina): Jour. Protozoology, v. 9, p. 79–87.

Hedley, R. H., Parry, D. M., and Wakefield, J. St. J., 1967, Fine structure of *Shepheardella taeniformis* (Foraminifera: Protozoa): Royal Micros. Soc. Jour., v. 87, p. 445–456.

Hemleben, C. 1967, Ultramicroscopic shell and spine structure of some spinose planktonic foraminifera: Internat. Conf. Planktonic Microfossils, 1st, Geneva, Proc. v. 2, p. 254–256.

———, 1969, Zur Morphogenese planktonischer Foraminiferen: Zitteliana, v. 1, p. 91–133.

Hofker, J., Sr., 1967, Have the genera *Porticulasphaera, Orbulina* (*Candorbulina*) and *Biorbulina* a biologic meaning?: Internat. Conf. Planktonic Microfossils, 1st, Geneva, Proc., v. 2, p. 279–286.

Hollande, A., Cachon, J., and Cachon, M., 1965, L'infrastructure des axopodes chez les Radiolaires Sphaerellaires *Périaxoplastidiés*: Acad. Sci. Comptes Rondus, v. 261, p. 1388–1391.

———, 1970, La signification de la membrane capsulaire des Radiolaires et ses rapports avec le plasmalemme et les membranes du réticulum endoplasmique. Affinités entre Radiolaires, Héliozaires et Péridiniens: Protistologica, v. 6, p. 311–318.

Hottinger, L., and Dreher, D., 1974, Differentiation of protoplasm in Nummulitidae (Foraminifera) from Elat, Red Sea: Marine Biology, v. 25, p. 41–61.

Jahn, T. L., and Bovee, E. C., 1965, Mechanisms of movement in taxonomy of Sarcodina. I. As a basis for a new major dichotomy into two classes, Autotractea and Hydraulea: Am. Midland Naturalist, v. 73, p. 30–40.

Jepps, M. W., 1942, Studies on *Polystomella* Lamarck (Foraminifera): Marine Biol. Assoc., United Kingdom Jour., v. 25, p. 607–666.

Kitching, J. A., 1964, The axopods of the sun animalcule *Actinophrys sol* (Heliozoa), *in* Allen, R. D., and Kamiya, N., eds., Primitive motile systems in cell biology: New York, Academic Press, p. 445–456.

Le Calvez, J., 1936, Modifications du test des foraminifères pélagiques en rapport avec la réproduction: *Orbulina universa* d'Orb., et *Tretomphalus bulloides* d'Orb.: Ann. Protistol., Paris, v. 5, p. 125–133.

Lee, J. J., Freudenthal, H. D., Kossoy, V., and Bé, A. W. H., 1965, Cytological observations on two planktonic foraminifera, [two planktonic foraminifera,] *Globigerina bulloides* d'Orbigny, 1826 and *Globigerinoides ruber* (d'Orbigny, 1839) Cushman, 1927: Jour. Protozoology, v. 12, p. 531–542.

Leidy, J., 1879, Fresh-water rhizopods of North Americana: U.S. Geol. Geog. Survey Terr. Rept., v. 12, p. 1–324.

Lipps, J., 1966, Wall structure, systematics and phylogeny studies of Cenozoic planktonic Foraminifera: Jour. Paleontology, v. 40, p. 1257–1274.

Mackinnon, D. L., and Hawes, R. S. J., 1961, An introduction to the study of Protozoa: Oxford, Clarendon Press.

Mannherz, H. G., and Goody, R. S., 1976, Proteins of contractile systems: Biochemistry Ann. Rev., v. 45, p. 427–465.

Marszalek, D. S., 1969, Observations on *Iridia diaphana*, a marine foraminifer: Jour. Protozoology, v. 16, no. 4, p. 599–611.

McGee-Russell, S. M., and Allen, R. D., 1971, Reversible stabilization of labile microtubules in the reticulopodial network of *Allogromia*: Advances Cell Molec. Biology, v. 1, p. 153–184.

Murray, J., 1897, On the distribution of the pelagic Foraminifera at the surface and on the floor of the ocean: Natural Science, v. 11, p. 17–27.

Murray, J. W., 1973, Distribution and ecology of living benthic foraminiferids: New York, Crane, Russak and Co., Inc., p. 1–274.

Myers, E. H., 1936, The life cycle of *Spirillina vivipara* Ehrenberg with notes on morphogenesis, systematics, and distribution in the Foraminifera: Royal Micros. Soc. Jour., v. 56, p. 120–146.

———, 1937, Culture methods for marine foraminfera of the littoral zone, *in* Galtsoff, P. S., ed., Culture methods for invertebrate animals: Ithaca, Comstock Pub. Co., p. 93–96.

———, 1943, Biology, ecology, and morphogenesis of a pelagic foraminifer: Stanford Univ. Pubs., Univ. Ser., Biol. Sciences, v. 9, p. 1–30.

Ochs, S., 1972, Fast transport of materials in mammalian nerve fibers: Science, v. 176, p. 252–260.

Ockleford, C. D., and Tucker, J. B., 1973, Growth, breakdown, repair, and rapid contraction of microtubular axopodia in the heliozoan *Actinophrys sol*: Ultrastructure Research Jour., v. 44, p. 369–387.

Owen, S. R. I., 1868, On the surface-fauna of mid-ocean. No. 2.—Foraminifera: Linnean Soc. London Jour., Zoology, v. 9, p. 147–157.

Parker, F. L., 1962, Planktonic foraminiferal species in Pacific sediments: Micropaleontology, v. 8, p. 219–254.

Pearse, V. B., and Muscatine, L., 1971, Role of symbiotic algae (zooxanthellae) in coral calcification: Biol. Bull., v. 141, p. 350–363.

Phleger, F. B., 1954, Foraminifera and deep-sea research: Deep-Sea Research, v. 2, p. 1–23.

———, 1960, Ecology and distribution of Recent Foraminifera: Baltimore, Johns Hopkins Press, p. 1–297.

Pollard, T. D., and Weihing, R. R., 1974, Actin and myosin and cell movement: CRC Critical Review of Biochemistry, v. 2, p. 1–65.

Rebhun, L. I., 1972, Polarized intracellular particle transport: saltatory movements and cytoplasmic streaming: Internat. Rev. Cytology, v. 32.

Roth, L. E., Pihlaja, D. J., and Shigenaka, Y., 1970, Microtubules in the heliozoan axopodium. I. The gradion hypothesis of allosterism in structural proteins: Ultrastructural Research Jour., v. 30, p. 7–37.

Roth, L. E., Vollett, J. J., and Davidson, M., 1975, Microtubules in the heliozoan axopodium. IV. Cell-surface relation by using hyaluronate: Cytobiologie, v. 12, p. 79–92.

Rhumbler, L., 1911, Die Foraminiferen (Thalamophoren) der Plankton Expedition: Ergebnisse Plankton-Exped. Humboldt Stift., v. 3, L.c., p. 1–331.

Sabatini, D. D., Bensch, K., and Barnett, R. J., 1963, Cytochemistry and electron microscopy. The preservation of cellular structure and enzymatic activity by aldehyde fixation. Cell Biology Jour., v. 17, p. 19–58.

Sandon, H., 1934, Pseudopodial movements in the Foraminifera: Nature, v. 133, p. 761–762.

———, 1963, Some observations on reticulose pseudopodia, *in* Progress in Protozoology: Internat. Cong. Protozoology, 1st, Prague, 1961, Proc. p. 166–169.

Shigenaka, Y., Roth, L. E., and Pihlaja, D. J., 1971, Microtubules in the heliozoan axopodium. III. Degradation and reformation after dilute urea treatment: Cell Science Jour., v. 8, p. 127–151.

Shigenaka, Y., Watanabe, K., and Kaneda, M., 1974, Degrading and stabilizing effects of Mg^{2+} ions on microtubule-containing axopodia: Exptl. Cell Research, v. 85, p. 391–398.

Sliter, W. V., 1965, Laboratory experiments on the life cycle and ecologic controls of *Rosalina globularis* d'Orbigny. Jour. Protozoology, v. 12, p. 210–215.

Tilney, L. G., 1971, Origin and continuity of microtubules, *in* Reinert, J., and Ursprung, H., eds., Results and problems in cell differentiation, v. 2, Origin and continuity of cell organelles, p. 222–260.

Tilney, L. G., and Porter, K. R., 1965, Studies on microtubules in Heliozoa. I. The fine structure of *Actinosphaerium nucleofilum* (Barrett) with particular reference to the axial rod structure: Protoplasma, v. 60, p. 317–344.

Vasiliev, Ju. M., and Gelfand, I. M., 1973, Interactions of normal and neoplastic fibroblasts with the substratum, *in* Locomotion of tissue cells, Ciba Foundation Symposium, vol. 14 (new series): New York, Elsevier, p. 311–331.

Vollet, J. J., and Roth, L. E., 1972, Culture, fusion, and cold treatment of *Echinosphaerium*: Jour. Protozoology, v. 19 (Suppl.), p. 26.

———, 1974, Cell fusion by nascent-membrane induction and divalent-cation treatment: Cytobiologie, v. 9, p. 249–262.

Vollet, J. J., Roth, L. E., and Davidson, M., 1972, Cell surface activity associated with fusion and retraction in protozoan cells: Jour. Cell Biology, v. 55, p. 269a.

Walton, W. R., 1952, Techniques for recognition of living Foraminifera: Cushman Found. Foram. Research Contr., v. 3, p. 56–60.

Watters, C., 1968, Studies on the motility of the Heliozoa. I. The locomotion of *Actinosphaerium eichorni* and *Actinophrys* sp.: Jour. Cell Science, v. 3, p. 231–244.

Wetzel, B., and Wollman, S. H., 1972, Scanning electron microscopy of pseudopod formation in rat thyroids: Jour. Cell Biology, v. 55, p. 279a.

Williams, D. C., and Roth, L. E., 1973, Natural and experimentally induced heliozoan fusion and its relation to mammalian cell fusion studies: Jour. Protozoology, v. 20, p. 507–508.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 127–133, 1980

FORAMINIFERAL CORRELATION OF QUATERNARY SEDIMENTS IN THE SANTA BARBARA CHANNEL, CALIFORNIA[1]

JAY G. MARKS,[2] ANDREW W. MARIANOS,[3] FILIPINAS R. GONZAGA,[3] AND CHARLES E. PFLUM[4]

ABSTRACT

Following the discovery of significant petroleum reserves in a part of the Santa Barbara Channel presently designated the Santa Ynez Unit, it became necessary to find a suitable location for an offshore platform from which development and production of these reserves could proceed. To obtain accurate and meaningful engineering data concerning the substrata at the proposed platform location, the uppermost 100 m of marine sediments were zoned by using changes in the coiling direction of the planktonic foraminifer *Neogloboquadrina pachyderma* (Ehrenberg). Biostratigraphic zones based on these coiling direction changes were traced throughout the area. When coupled with water depths interpreted from benthic foraminifera, depositional histories for each of the zones were obtained.

INTRODUCTION

In 1969 significant reserves of petroleum were discovered in the Santa Barbara Channel of Southern California. In order to develop and produce these reserves, it became necessary to obtain new geological and engineering data for the design and installation of production facilities for waters deeper than 270 m. The area studied for this purpose is now included in the Santa Ynez Unit (Fig. 1). The term "unit," as used in industry, refers to a group of leases unified for the purpose of exploration, development and production without regard to individual lease obligations.

One facet of the project was to determine the lithology, firmness, strength and other physical properties of the sea-floor sediments on which the production platform would rest. For this purpose a series of core-holes were drilled which penetrated as much as 107 m into the sea floor. To best utilize the physical data, it was necessary to establish some framework or scheme of reference that would permit comparison of the physical aspects of the sediments encountered in one corehole with another. To establish this framework, the use of conventional biostratigraphic methods employing range tops of foraminifers was not feasible because most of the species of fossils are extant. Consequently, an alternative approach based on O. L. Bandy's (1959 and 1960) studies of the coiling characteristics of the planktonic foraminifera *Neogloboquadrina pachyderma* (Ehrenberg) was utilized in constructing a scheme of reference.

GENERAL GEOLOGY

The sediments penetrated by the coreholes are late Pleistocene and Holocene. They consist of relatively unconsolidated but subtly stratified layers ranging from watery mud at the top to firm sediment at depth. Lithologic units cannot be distinguished by visual examination of the cored material. Seismic horizons are well defined in the eastern half of the Santa Ynez Unit, where argillaceous muds predominate, but are difficult to trace within the coarser sediments of the western half. They can be related to clearly defined biostratigraphic units based on coiling reversals of *Neogloboquadrina pachyderma*.

---

[1] Appreciation is extended to Exxon Production Research Company for funding this paper.
[2] Denver, Colorado.
[3] Exxon Company, U.S.A., Houston, Texas.
[4] Exxon Production Research Company, Houston, Texas.

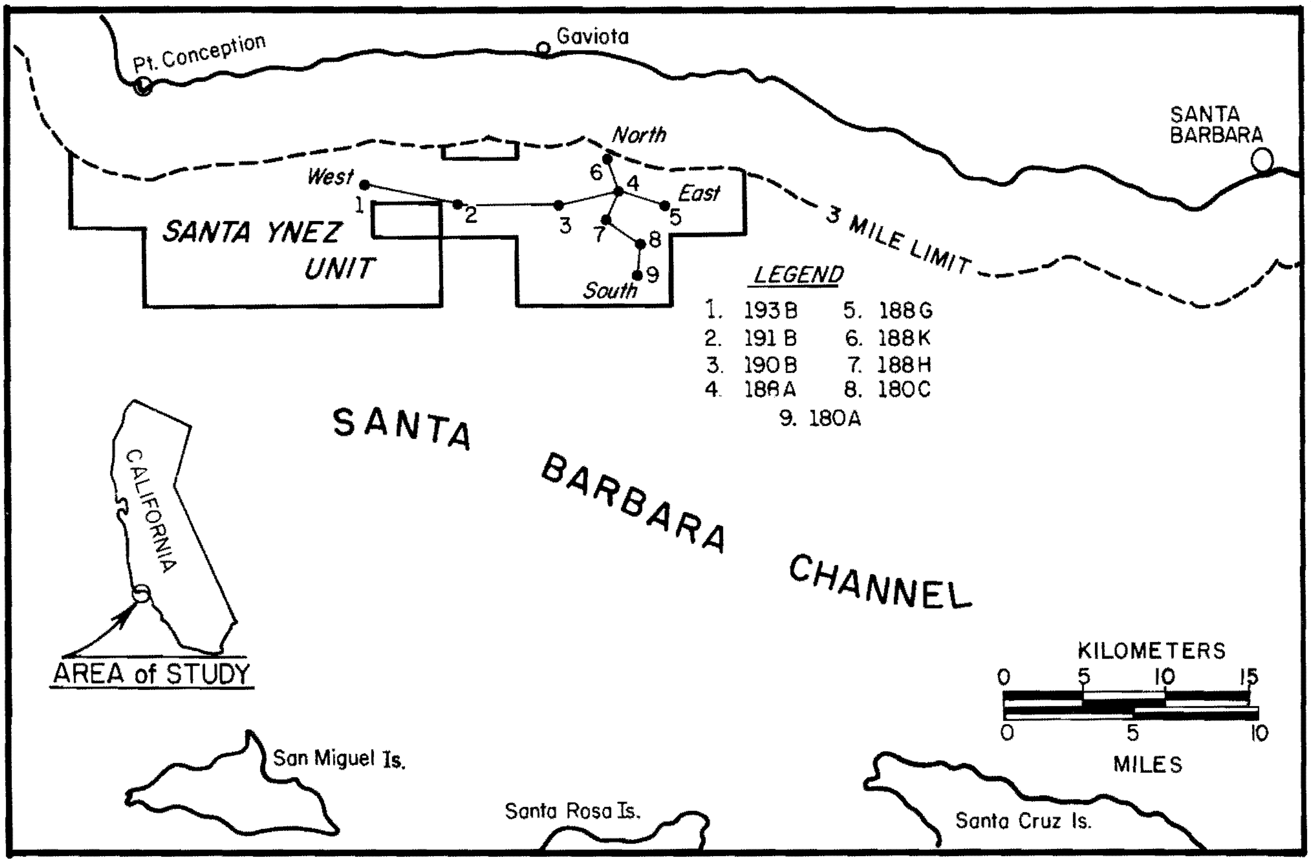


FIGURE 1

Location of the Santa Ynez Unit. The unit extends from 4.8 km to about 16 km offshore. Positions of the coreholes utilized in this report are shown on the W–E and N–S lines of the cross section. Water depths increase from about 120 m at the 3-mile limit to 490 m in the southeastern corner of the unit.

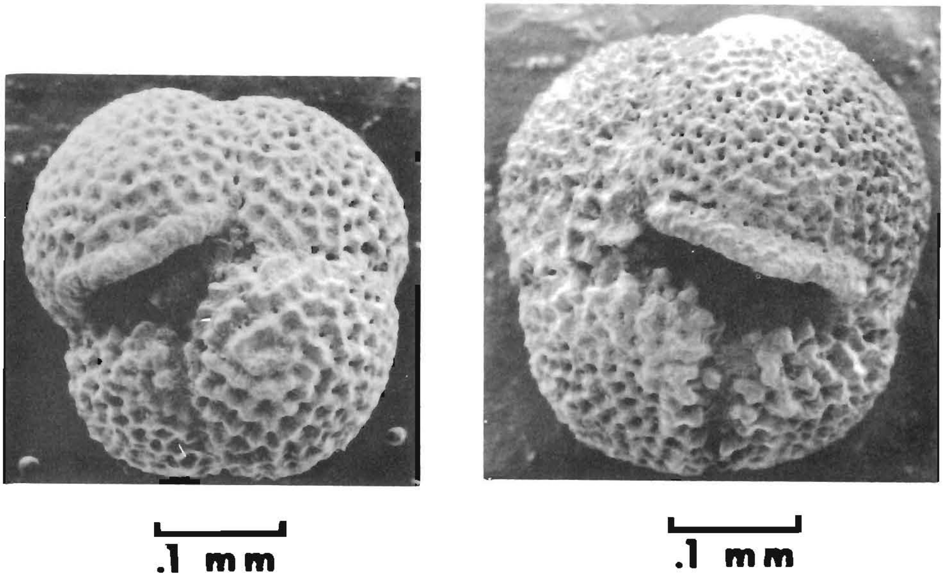
ESTABLISHMENT OF BIOSTRATIGRAPHIC UNITS

In separate publications, Bandy (1959) and Ericson (1959) described the method of using reversals in the coiling direction of *N. pachyderma* to distinguish sediments deposited in cold waters from those deposited in relatively warm waters. Bandy (1960) demonstrated that dextral forms have persisted in waters offshore from California for about the last 11,000 years, and that these forms were preceded by dominantly sinistral populations in the late Pleistocene. This change in coiling direction marks the Pleistocene-Holocene boundary. Bandy's method has proven useful in subdividing and mapping the thick upper Tertiary and Quaternary sediments of the Ventura Basin.

Detailed examination of Bandy's (1960) coiling pattern scheme shows that minor reversals occur within the principal trends of dominant coiling direction. These minor reversals are relatively limited in geographic extent, but can be used locally to further subdivide the sequence. Reasons for reversals and their varying geographic extent are described below.

In Arctic and Antarctic waters, 95 to 100 percent of living specimens of *N. pachyderma* are sinistrally coiled. In warmer seas, individuals of this species are about 80 to 100 percent dextrally coiled (Fig. 2). The critical temperature for separation of water masses bearing sinistral or dextral populations is about 7.2°C (Ericson, 1959). In areas of convergence, where warm and cold waters mix, the ratios of sinistral to dextral coiling are variable. In cold and temperate seas, sediments accumulating beneath 100 m or more of water receive a fairly steady rain of *N. pachyderma* tests.

In the Santa Barbara Channel, the Pleistocene and Holocene muds accumulated at the rate of about 40 cm every 1,000 years. Foraminiferal recovery from these sediments is excellent, and the microfossil sam-



Neogloboquadrina pachyderma
Dextral

Neogloboquadrina pachyderma
Sinistral

FIGURE 2
Scanning electron micrographs of dextrally- and sinistrally-coiled forms of *N. pachyderma* (Ehrenberg) from the Santa Barbara Channel. (Photographs by R. D. Hockett, Exxon Production Research Company, Houston.)

ples usually contain hundreds of specimens. Most samples contain an overwhelming majority of either sinstrally- or dextrally-coiled specimens. The intervals of sediment in which a single coiling direction predominates are sufficiently thick to constitute mappable units. These biostratigraphic units indicate that water masses of fairly uniform temperature remained in the area for thousands of years before being displaced by waters of different temperature. Boundaries between units seem to be nearly synchronous. The coast of Southern California and its offshore basins are ideally suited to record oscillations in water masses from coiling direction changes in *N. pachyderma*. The composite log of *N. pachyderma* coiling ratio curves developed for this study (Fig. 3) illustrates the biostratigraphic units described above. The coiling-ratio curves are based on counts of *N. pachyderma* specimens made at intervals of about 30 centimeters, one meter, or three meters.

BATHYMETRY

The sediments containing *N. pachyderma* also bear numerous benthic foraminifera, and in some samples the benthics outnumber the planktonics. The benthic assemblages, when related to the biostratigraphic units established from coiling direction curves, are used to interpret the depth of water in which those units were deposited. Water depth control was provided by samples of modern sediments collected at the surface of the sea floor before the drilling of each corehole and by two lines of punch cores collected in water ranging in depth from 124 to 513 m. Additional water depth control data were obtained from a foraminiferal study by O. L. Bandy (unpublished, 1972) conducted in an area adjacent to Purisima Point, California and from other pertinent published data on offshore Southern California by Bandy (1953, 1961) and Bandy and others (1957). This information was organized in computer-sensible form so that the environment could be interpreted rapidly for each sample. The list given below, applicable only to this study, indicates the upper depth limit of taxa except where marked with an asterisk (*), which indicates the uppermost depth occurrence of moderate numbers of each species (more than nine individuals per sample). The species are listed in approximate order of occurrence from shallow to deep.

LOWER NERITIC (92–183 M)

Uvigerina tenuistriata Reuss
Epistominella exigua (Brady)

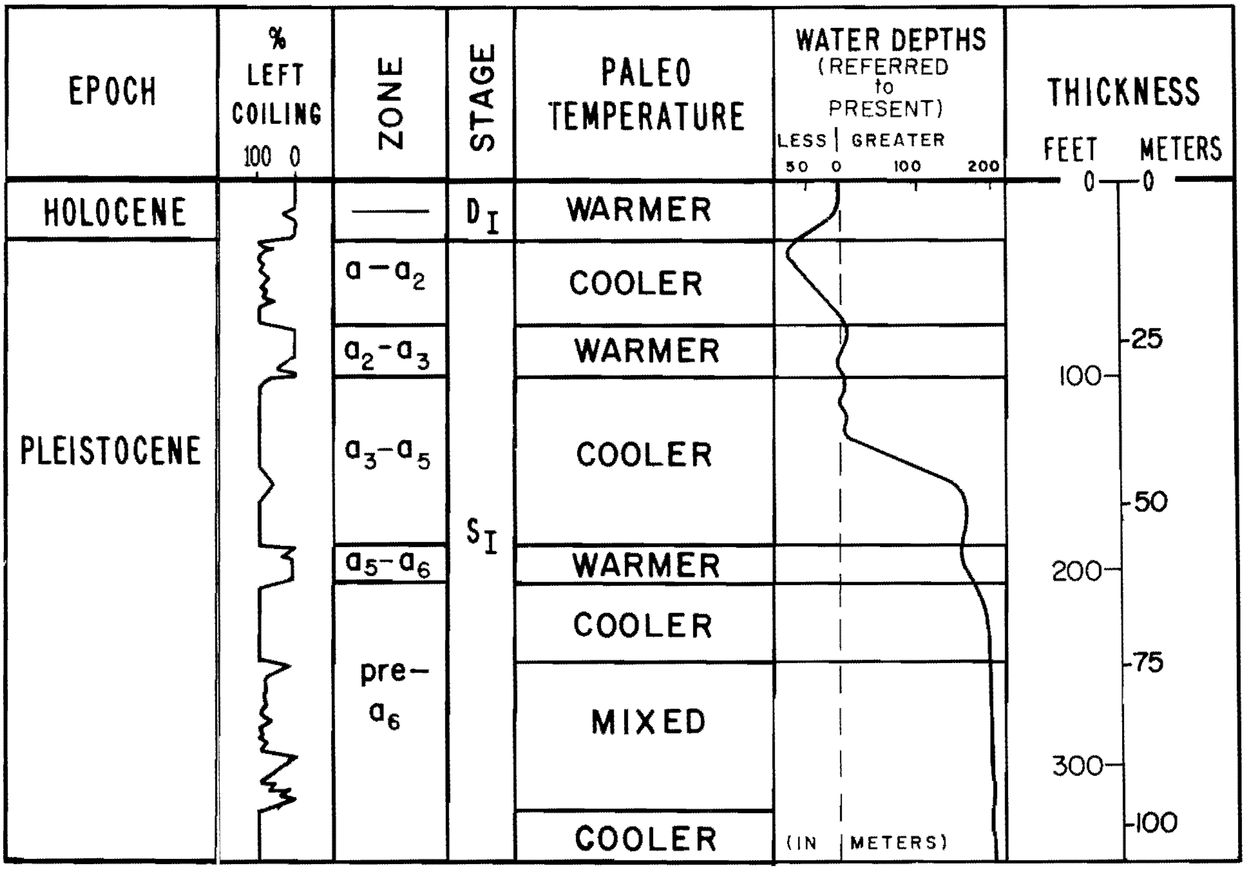


FIGURE 3
Composite log of *N. pachyderma* coiling-ratio curves.

Islandiella californica (Cushman and Hughes)
Angulogerina carinata Cushman
Buliminella curta Cushman var. *basispinata* R. E. Stewart and K. C. Stewart
Epistominella pacifica (Cushman)
Valvulineria araucana (d'Orbigny)
*_Bolivina interjuncta_ Cushman
Cibicides mckannai Galloway and Wissler var. *suppressus* Martin
Cancris auricula (Fichtel and Moll)

Upper Upper Bathyal (183–325 m)

Bolivina peirsonae Uchio
Karreriella grammostomata (Galloway and Wissler)
*_Bolivina argentea_ Cushman
*_B. pacifica_ Cushman and McCulloch
Fursenkoina bramletti (Galloway and Morrey)
Cancris panamensis Natland
Epistominella vitrea Parker

Lower Upper Bathyal (325–457 m)

*_Uvigerina peregrina_ Cushman
Bolivina pseudobeyrichi (Cushman)
Oridorsalis tenera (Brady) (over 0.6 mm diameter)
Cassidulinoides cornuta (Cushman)
Cassidulina laevigata d'Orbigny var. *carinata* Silvestri
*_Suggrunda eckisi_ Natland
Epistominella smithi (R. E. Stewart and K. C. Stewart)
Cassidulina delicata Cushman
C. translucens Cushman and Hughes
*_Uvigerina mediterranea_ Hofker
*_Globobulimina affinis_ (d'Orbigny)
Buliminella tenuata Cushman

Middle Bathyal (457–915 m)

Gyroidina subtenera (Galloway and Wissler)
*_Bolivina spissa_ Cushman

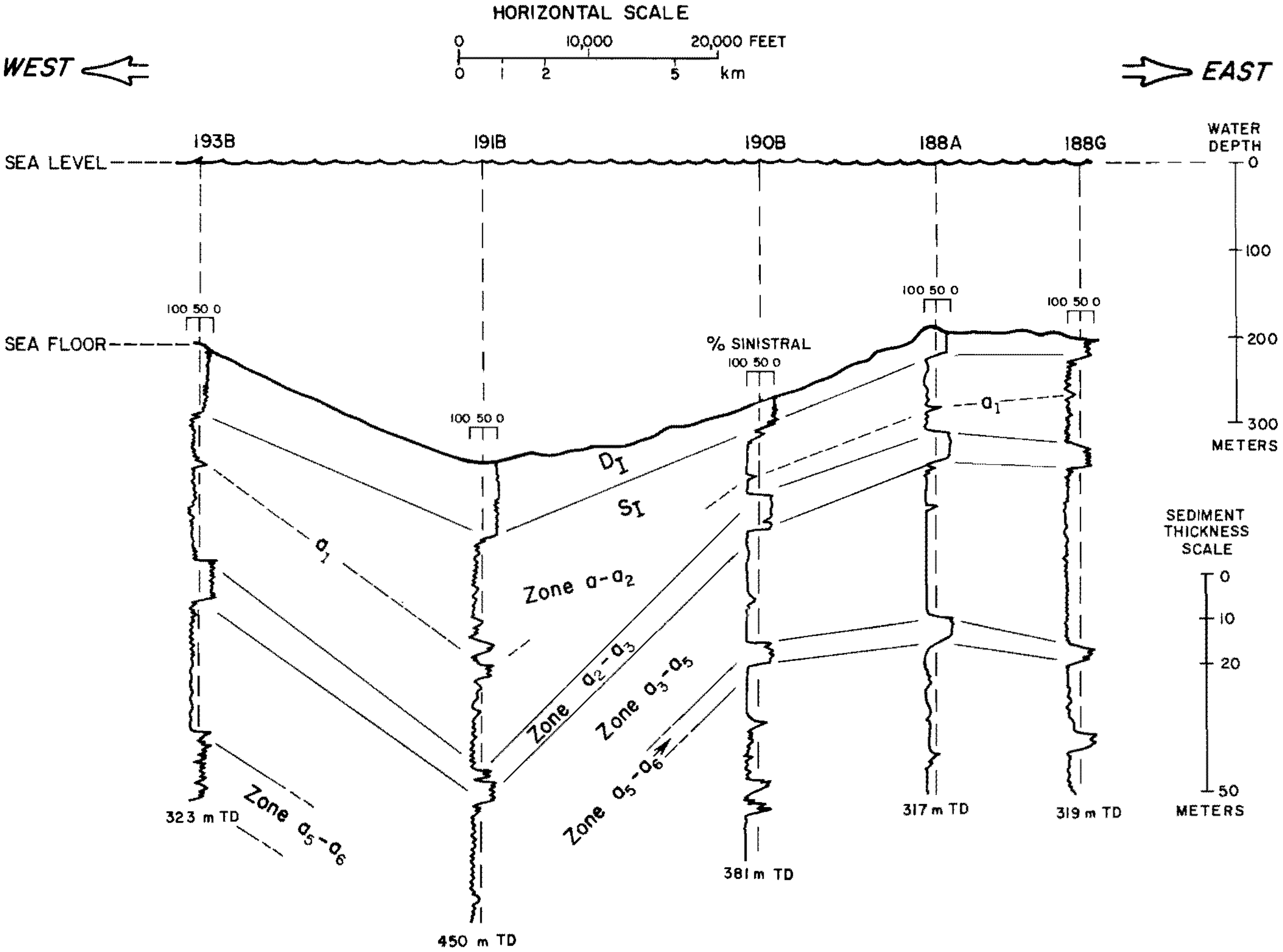


FIGURE 4
West-east cross section through the Santa Ynez Unit showing *N. pachyderma* coiling ratio curves.

B. seminuda Cushman
Cassidulinoides waltoni Uchio
Gyroidina soldanii d'Orbigny *altiformis* R. E. Stewart and K. C. Stewart
Bolivina plicata d'Orbigny
Bulimina subacuminata Cushman and R. E. Stewart
Bolivina sinuata Galloway and Wissler
Hoeglundina elegans (d'Orbigny)
Uvigerina hispidocostata Cushman and Todd
Gyroidina soldanii d'Orbigny

DESCRIPTION OF THE BIOSTRATIGRAPHIC UNITS

The units established on the basis of *N. pachyderma* coiling curves are shown in Figures 3 to 5. The uppermost unit, D_I, is Holocene and corresponds to Bandy's (1960) upper dextral coiling unit which was established through radiocarbon dating to be 0–11,000 years B.P. The average rate of sediment accumulation was about 80 centimeters per 1,000 years. Sediments in the upper part of the D_I unit contain the same assemblages of benthic foraminifera as now exist at the same locations in the Santa Barbara Channel, but the assemblages in the lower part were deposited in somewhat shallower water. Deposition of the lower D_I unit faunas occurred during the final episode of shoaling that prevailed in latest Pleistocene (Zone a-a_2) time.

Sediments of the S_I unit (Pleistocene) lie beneath the Holocene muds and sands throughout the entire area. In general, deposition occurred in cooler water than that of the D_I unit since *N. pachyderma* is pre-

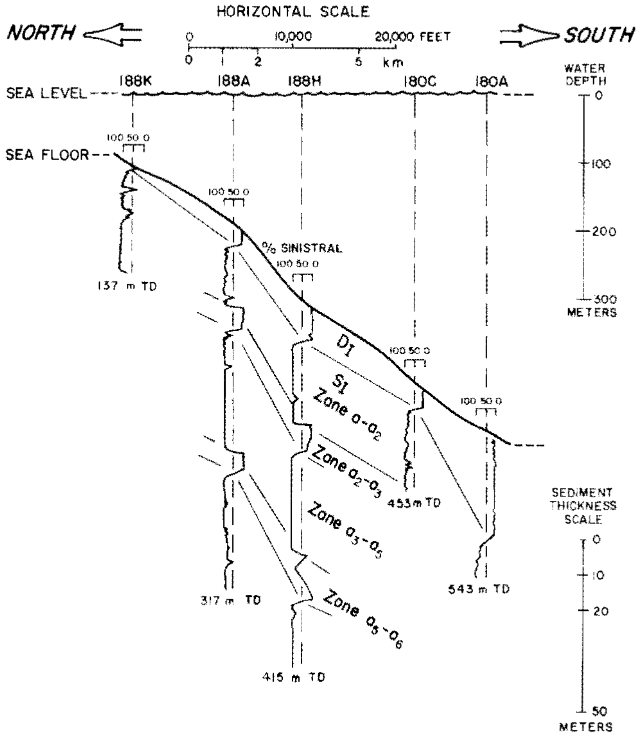


FIGURE 5

North-south cross section through the Santa Ynez Unit showing *N. pachyderma* coiling ratio curves.

dominantly sinistrally coiled, except in some thin intervals. None of the coreholes penetrates the entire Pleistocene section. Studies of coccoliths suggest that the oldest sampled Pleistocene sediments are no older than about 0.5 million years. Determinations of magnetic polarity indicate that the entire section is in the Brunhes normal interval and is younger than about 0.69 million years.

Zone a-a$_2$ contains predominantly sinistrally-coiled *N. pachyderma* although locally some samples contain a large percentage of dextrally-coiled forms. A short interval (a$_1$) of dominantly dextrally coiled *N. pachyderma* occurs near the middle of the zone and presumably represents a short-term incursion of warm water. Water depths at the inception of a-a$_2$ were similar to or greater than those of today. During a-a$_2$ time sea level lowered, reaching its minimum at about the end of the period. Sea level was then 60 to 90 m lower than it is now, except in the western half of the area where tectonism and rapid deposition masked the eustatic effects. Sediments of Zone a-a$_2$ are coarser and contain fewer foraminifers per volume of material than those of the D$_I$ unit. Large amounts of mica, lignite and tar are evident. The species *Florilus labradoricus,* which is not reported presently in California waters, is persistent in the foraminiferal assemblages representative of Zone a-a$_2$. Radiocarbon dates from mollusk shells in the upper part of the zone are 15,000 to 18,000 years B.P.

Zone a$_2$-a$_3$ is a remarkably uniform blanket of argillaceous sediment distinguished by its dextrally-coiled population of *N. pachyderma.* In the eastern part of the area the indicated water depths are about the same as those of today. In the western part they are a few hundred meters greater. The almost totally dextrally coiled assemblages of *N. pachyderma* are accompanied by other planktonic foraminifers indicating warmer water, substantiating the conclusion that water temperatures were as warm or warmer than those of today in the same area. The argillaceous nature of the sediment and high yields of foraminiferal tests per volume of sediment indicate that the rate of sediment accumulation was slower. A sample composed entirely of foraminifer tests was submitted for radiocarbon dating, but yielded only a determination of "greater than 35,000 years." Coccolith studies also indicate about the same age for this zone.

Zone a$_3$-a$_5$ is a relatively thick sequence of silty sediments. Water depths at its inception were about 160 m greater than they are today. During middle a$_3$-a$_5$ time a sudden shallowing took place, bringing water depths to about their present level.

Zone a$_5$-a$_6$ faunas indicate dominantly warm-water temperatures with erratic influxes of colder currents. The sediments are dominantly argillaceous throughout, and the rate of deposition was apparently rather slow. Water depths were generally 160 to 250 m greater than those of today. Sediments deposited prior to Zone a$_5$-a$_6$ represent generally cooler water temperatures with short periods of warmer waters. The water depths indicated for these strata, about 160 to 250 m greater than at present, are similar to those of Zone a$_5$-a$_6$.

SUMMARY

The biostratigraphic units defined by the direction of coiling of the planktonic foraminifer *N. pachyderma* extend throughout the Santa Ynez Unit. Definition and correlation of these biostratigraphic units have provided a framework that permits comparison of engineering data throughout the area of the Unit. The primary purpose of these studies is to aid in the positioning of drilling platforms in deep water with confidence. In addition, studies of the bottom-dwelling foraminifera have helped us understand some of the conditions of deposition of the subtly layered shallow sediments. The paleobathymetric picture is complicated by local tectonic effects, and some water-depth fluctuations which appear to be eustatic changes of sea level are probably due instead to local uplift or subsidence. We believe that additional studies of foraminifers in this area will lead to a more exact accounting of the physical factors that have affected the Santa Ynez Unit during Quaternary time.

REFERENCES

BANDY, O. L., 1953, Ecology and paleoecology of some California foraminifera, Pt. 1, The frequency distribution of Recent Foraminifera off California: Jour. of Paleontology, v. 27, p. 161–182.

———, 1959, Geologic significance of coiling ratios in the foraminifer *Globigerina pachyderma* (Ehrenberg): Geol. Soc. America (abstracts), v. 70, p. 1708.

———, 1960, The geologic significance of coiling ratios in the foraminifer *Globigerina pachyderma* (Ehrenberg): Jour. of Paleontology, v. 34, no. 4, p. 671–681, 7 figs.

———, 1961, Distribution of foraminifera, radiolaria, and diatoms in sediments of the Gulf of California: Micropaleontology, v. 7, p. 1–26.

———, 1967, Foraminiferal definition of the boundaries of the Pleistocene in southern California, U.S.A.: Progress in Oceanography (Pergamon Press), v. 4, p. 27–49.

———, 1972, Origin and development of *Globorotalia* (*Turborotalia*) *pachyderma* (Ehrenberg): Micropaleontology, v. 18, p. 294–318.

BANDY, O. L., and ARNAL, R. E., 1957, Distribution of Recent foraminifera off west coast of Central America: Am. Assoc. Petroleum Geologists Bull., v. 41, p. 2037–2053.

BANDY, O. L., BUTLER, E. A., and WRIGHT, R. C., 1969, Alaskan upper Miocene marine glacial deposits and the *Turborotalia pachyderma* datum plane: Science, v. 166, p. 607–609.

BRADY, H. B., 1881, On some Arctic foraminifera from soundings obtained on the Austro-Hungarian North-Polar Expedition of 1872–1874: Ann. Mag. Hist., ser. 5, v. 8, no. 48, p. 393–418.

COLLEN, J. D., and VELLA, P., 1973, Pliocene planktonic foraminifera, southern North Island, New Zealand: Jour. Foram. Research, v. 3, p. 13–29.

ERICSON, D. B., 1959, Coiling direction of *Globigerina pachyderma* as a climatic index: Science, v. 130, p. 219–220.

OLSSON, R. K., 1974, Pleistocene paleoceanography and *Globigerina pachyderma* (Ehrenberg) in Site 36, DSDP, northeastern Pacific: Jour. Foram. Research, v. 4, p. 47–60.

SRINIVASAN, M. S., and KENNETT, J. P., 1976, Evolution and phenotypic variation in the late Cenozoic *Neogloboquadrina dutertrei* plexus: Progress in Micropaleontology (Micropaleontology Press), the American Museum of Natural History, p. 329–355.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 134–162, pls. 1–8, 1980

SURFACE ULTRASTRUCTURAL VARIATION IN *NEOGLOBOQUADRINA PACHYDERMA* (EHRENBERG): PHENOTYPIC VARIATION AND PHYLOGENY IN THE LATE CENOZOIC

J. P. KENNETT AND M. S. SRINIVASAN[1]
Graduate School of Oceanography, University of Rhode Island, Kingston, R. I. 02881

ABSTRACT

The scanning electron microscope was used to examine over 1,000 specimens of *Neogloboquadrina pachyderma* (Ehrenberg) and related forms from different water masses throughout the late Cenozoic to study the ancestry, evolution, and environmental relations within this species and phylogenetic relations with several other forms. Two principal surface types are distinguished: reticulate microcrystalline ultrastructure which predominates in Arctic and subantarctic populations, and crystalline ultrastructure which dominates in populations from other areas. In subtropical populations, crystalline forms are distinguished from those of high latitudes by thinner walls, higher pore concentration, and a lack of rosette-patterned crusts.

These ultrastructural differences reflect the degree of secondary calcification with reticulate microcrystalline ultrastructure representing an earlier stage. Difference in dominance of the ultrastructural types presumably reflects environmental differences associated with the various water masses. Overall similarity in ultrastructure within *N. pachyderma* links subtropical populations with temperate populations from the late Miocene to the Recent as one phylogenetic species that evolved from "*Globorotalia*" *continuosa* in the late middle Miocene and early late Miocene.

Neogloboquadrina acostaensis is considered to be a tropical to warm subtropical phenotypic variant of a late Miocene to early Pliocene cline with the temperate to polar variant represented by *N. pachyderma*. Identical surface ultrastructure and morphological intergradation between *N. pachyderma* and *N. dutertrei dutertrei* populations in subtropical sequences suggest that the two forms are genetically linked as a cline.

INTRODUCTION

The late Miocene to Recent planktonic foraminifer "*Globigerina*" *pachyderma* (Ehrenberg) has been studied intensively over the past decade mainly because of its value as a paleoclimatic-paleoceanographic tool resulting from its importance in the cooler water masses in both hemispheres and its distinct coiling direction patterns. This species, which is the only planktonic foraminiferal species occurring in true polar waters, occurs as far north as about 25°S in the Southern Hemisphere and as far south as about 25°N in the Northern Hemisphere. Occasional specimens from lower latitudes such as at the equator (Parker, 1962) and in the Arabian Sea (Zobel, 1973) appear to be young individuals of *Neogloboquadrina dutertrei*.

The value of "*G.*" *pachyderma* as a paleoceanographic tool was first recognized by Ericson (1959) and Bandy (1959, 1960). These workers demonstrated that coiling direction change in "*G.*" *pachyderma* is relat-

---

[1] Permanent address: Department of Geology, Banaras Hindu University, India.

ed to changing surface-water temperatures. Studies on the distribution of Recent "*G.*" *pachyderma* (Bé, 1960, 1969; Bé and Tolderlund, 1971; Bé, Vilks, and Lott, 1971; Boltovskoy, 1969; Bandy and Theyer, 1971; Bandy, 1972; Kennett, 1968, 1969; Herb, 1968; Stehman, 1972) show that sinistral forms dominate in polar and subpolar waters while dextral forms dominate in temperate and warm subtropical water masses. Paleoceanographic interpretations on late Cenozoic sediments using this method have since been made by a number of workers including Bandy (1967, 1968, 1969, 1971, 1972), Bandy and others (1969, 1971), Jenkins (1967), Kennett (1967), Ingle (1967), and Ujiie and Ichikura (1973).

Many other planktonic foraminiferal species exhibit morphological variation in response to changing water-mass conditions (Bandy, 1960, 1972; Bé, 1969; Kennett, 1968, 1969; Zobel, 1968). Kennett (1968, 1969) and Herb (1968) recognized three morphological groups of "*G.*" *pachyderma* corresponding to different water masses in surface sediments of the southwest Pacific Ocean. Similar oceanographically related variation in "*G.*" *pachyderma* has been observed by Stehman (1972) in the Baffin Bay area. It is possible that no other planktonic foraminiferal species exhibits as much morphological variation in response to changing conditions as "*G.*" *pachyderma*. This variation has made the taxonomy of this species somewhat controversial. Many authors have considered some of the differences to have been caused by speciation or subspeciation and have applied different specific names for "*G.*" *pachyderma* in different regions. Cifelli (1961), for example, proposed *Globigerina incompta* for dextral "*G.*" *pachyderma* from the Recent north Atlantic (Fig. 1) and considered this form to be closely related to *Neogloboquadrina dutertrei* (d'Orbigny). Parker (1962) believed "*G.*" *incompta* to be a synonym, but possibly a subspecies of "*G.*" *pachyderma*. Berger (1969, 1970) and Parker and Berger (1971) have even suggested that dextral forms of "*G.*" *pachyderma* and *N. dutertrei* may be identical.

The highly variable nature and position of the aperture in "*G.*" *pachyderma* have sometimes created confusion with *Globigerina bulloides*. For instance, "*G.*" *pachyderma* has been considered to be intergradational with *G. bulloides* and *Globigerina quinqueloba* by Cifelli and Smith (1969, 1970).

As pointed out by Bandy (1972) serious doubts and confusion in recent years as to the identity of "*G.*" *pachyderma* has been to a large extent due to misidentification. The application of scanning electron microscope (SEM) ultrastructural studies to planktonic foraminifera enables greater precision in taxonomy because it assists in differentiating between phylogenetic and phenotypic variations. The value of ultrastructural variation of planktonic foraminifera in studying phenotypic variation and phylogeny was demonstrated by Srinivasan and Kennett (1974, 1976) and Keller (in press). These authors showed that relationships exist between the surface ultrastructure of forms within the *Neogloboquadrina dutertrei* plexus and changing water masses. Kennett (1970), Olsson (1971), Bandy and Theyer (1971) and Bandy (1972) conducted the first SEM examinations of "*G.*" *pachyderma*, these mostly being confined to gross morphological features rather than surface ultrastructure. Recently, Cifelli (1973) concluded from an SEM examination of whole and sectioned specimens of "*G.*" *pachyderma* and "*G.*" *incompta* from the north Atlantic that these two forms are separate species. Olsson (1976) has differentiated "*G.*" *pachyderma* and "*Globorotalia*" *pseudopachyderma* based on an ultrastructural study of specimens from the DSDP Sites 36 and 207. He has retained "*Globigerina*" *pachyderma* for Pleistocene and Holocene sinistral forms, but considers all sinistral and dextral forms older than the Pleistocene to be "*Globorotalia*" *pseudopachyderma* (Fig. 1).

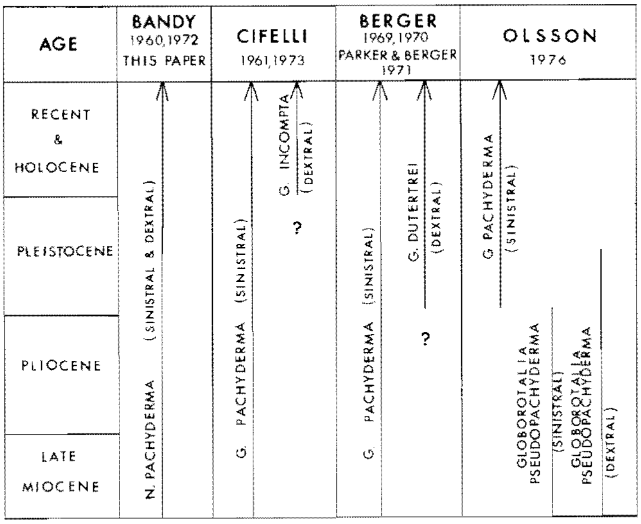


FIGURE 1

Taxonomy of *Neogloboquadrina pachyderma* proposed by various workers. Coiling-direction differences have been used as a major criterion for taxonomic subdivision of this group. G = *Globigerina*; N = *Neogloboquadrina*.

In this contribution we have utilized the scanning electron microscope to examine the range of variation

TABLE 1

Location of cores and outcrop samples examined.

I. Deep-sea core materials			
Core location	Latitude	Longitude	Water depth
A. Southwest Pacific Ocean			
Leg 21 (DSDP), Site 206	32°00.75"S	165°27'15"E	3,196 m
Leg 21 (DSDP), Site 207	36°57'75"S	165°26'06"E	1,389 m
Leg 21 (DSDP), Site 207A			
Leg 21 (DSDP), Site 208	26°06'61"S	161°13'27"E	1,545 m
Leg 21 (DSDP), Site 209	15°56'19"S	152°11'27"E	1,428 m
Eltanin 1243	60°03'	140°53'W	3,614 m
E. 1230	62°57'	159°55'W	2,708 m
E. 1197	56°12'	160°27'W	4,060 m
E. 1189	54°01'	159°59'W	4,191 m
N.Z.O.I. E. 120	43°00'	175°30'W	872 m
B. South Pacific and South Indian Ocean			
Leg 28 (DSDP), Site 264	34°58.13'S	112°02.68'E	2,873 m
Leg 28 (DSDP), Site 264A	34°58.13'S	112°02.68'E	2,873 m
Leg 28 (DSDP), Site 265	53°32.45'S	109°56.74'E	3,582 m
Leg 29 (DSDP), Site 284	40°30.48'S	167°40.81'E	1,068 m
Leg 29 (DSDP), Site 284A	40°30.48'S	167°40.81'E	1,068 m
Eltanin 48-13	28°30'95"S	93°30'30"E	3,346 m
Eltanin 48-36	30°55'81"S	87°46'35"E	1,344.6 m
Eltanin 39-75	36°28'3"S	161°12'8"E	3,834 m
Eltanin 49-52	39°00'28"S	99°56'90"E	4,131 m
Eltanin 49-50	40°36'66"S	99°54'82"E	3,996 m
Eltanin 34-11	45°13'S	147°47'E	3,395 m
Eltanin 36-21	49°21'S	149°09'E	3,320 m
C. Subantarctic			
Eltanin 36-14	58°05'S	150°14'E	2,637 m
Eltanin 15-16	56°03'S	119°55'W	3,039 m
Eltanin 47-4	64°07.1'S	80°23.9'E	3,598 m
D. Ross Sea, Antarctica			
Eltanin 32-8	73°58.0'S	176°07.0E	580 m
Eltanin 27-22	64°58'S	160°37'E	2,920 m
E. North Pacific			
Leg 29 (DSDP), Site 188	53°45.21'N	178°39.56'E	2,949 m
Tanner Basin (S. California)	32°47'N	119°30'W	1,350 m
F. Central Pacific			
Leg 7 (DSDP), Site 62	1°52.2'N	141°56.3'E	2,602 m
G. Arctic			
No. 98	87°12'N	64°06'W	1,340 m
298A	84°22'N	169°48'E	3,175 m
22	76°11'N	141°56'W	3,700 m
73C	74°28'N	141°58'W	3,650 m
66-18UC	77°05'N	109°12'W	457 m
H. North Atlantic			
Leg 12 (DSDP), Site 111A	50°25.57'N	46°22.05'W	1,797 m
I. Northeast Azores			
TR-121-14	39°53.0'N	17°53.1'W	3,980 m
TR-121-8	38°58.0'N	22°44.0'W	3,650 m
TR-121-24	38°01.0'N	23°19.0'W	3,800 m
J. South Atlantic			
Leg 3 (DSDP), Site 15	30°53.38'S	17°58.99'W	3,927 m
K. Gulf of Mexico			
KANE 138-120	23°17.9'	96°10.8'	2,537 m
TR-126-26	20°55.4'N	95°04.6'	3,075 m

TABLE 1

Continued.

2. Outcrop samples

A. JAPAN: (Collected by J. Ingle, Jr.)
One sample from the Nobori Formation, Zone N 21 (late Pliocene).

B. ITALY: (Collected by J. P. Kennett)
Samples collected from the summit of the crest south-west of Sadigliano at a large outcrop of blue-grey clayey marls, upper part of type locality of Tortonian Stage.

C. ANDAMAN-NICOBAR: (Collected by M. S. Srinivasan)
Mf/526 to Mf/531; Mudstone Member, Neil Island, Bay of Bengal, zone N 18 (late Miocene).
Mf/66 and Mf/55; Sawai Bay Mudstone Member, Car Nicobar Island, Bay of Bengal. Zone N 19 (Early Pliocene).

D. JAMAICA: (Collected by J. P. Kennett)
J1: Buff Bay, No. 41, Zone N 18 (late Miocene).
J2: Buff Bay, No. 43, Zone N 19 (Pliocene).
J3: Navy Island Member, Manchioneal Formation, ER/692, Zone N 22 (Pleistocene).
J4: Navy Island Member, Manchioneal Formation, ER/693, Zone N 22 (Pleistocene).
J5: Navy Island Member, Folly Point, ER/537, Zone N 22 (Pleistocene).

in surface ultrastructure in "*Globigerina*" *pachyderma* from different water masses and from different intervals of time during the late Cenozoic; to study the ancestry, evolution, and environmental relations of the species; and to study phylogenetic relationships in the *N. dutertrei* plexus and *N. acostaensis* during the late Cenozoic.

It is fitting that our contribution dealing with the ultrastructure of "*G.*" *pachyderma* be included in this volume dedicated to the memory of Dr. Orville L. Bandy, as he was foremost in recognizing and utilizing this species as a late Cenozoic paleoceanographic index.

We have examined more than 1,000 specimens of "*G.*" *pachyderma* and related forms including "*G.*" *incompta* Cifelli, "*Globorotalia*" *pseudopachyderma* Cita, Premoli-Silva, and Rossi, *Globigerina atlantica* Berggren, and "*Globorotalia*" *continuosa* Blow, using the SEM (Cambridge S 4). In addition we have examined several hundred specimens of *N. dutertrei* s.l. Materials examined in this study are from the following locations:

1. Deep Sea Drilling Project (DSDP) cores collected by means of "GLOMAR CHALLENGER" during Legs 3, 7, 12, 19, 21, 28 and 29 (Table 1); from the north and south Atlantic, north and south Pacific, and south Indian Ocean.
2. Cores collected from Antarctic, subantarctic, and temperate regions in the south Pacific and south Indian Ocean during operations of USNS "ELTANIN."
3. Dredge and bottom trawls from the Arctic Sea floor collected from ice islands (Arliss II; Fletcher's Ice Island, T-3).
4. A core (CHAIN 61-171) collected in the north Atlantic during operations of the Woods Hole Oceanographic vessel RV "CHAIN."
5. Cores from the Tanner Basin, off Southern California, collected from RV "VELERO."
6. Three cores (TR-121-8; TR-121-14; TR-121-24) collected from northeast of the Azores during operations of RV "TRIDENT" and two cores (KANE 138-120; and TR-126-26) collected in the Gulf of Mexico during cruises of the USNS "KANE" and RV "TRIDENT."
7. Outcrop samples from the marine Late Cenozoic of Italy, Japan, Jamaica, and Andaman-Nicobar Islands, Bay of Bengal.

GENERIC ASSIGNMENT

Although considerable data have been gathered on the origin, distribution, morphology, coiling ratios, and relationships between depth habitat and wall thickness of Recent "*Globigerina*" *pachyderma* (Ericson, 1959; Bandy, 1959, 1960, 1972; Bé, 1960; Jenkins, 1967; Kennett, 1967, 1968, 1969, 1970; Cifelli, 1973; Vella, 1974; Boltovskoy, 1969, 1971a, b; and Olsson, 1976), this species has remained somewhat enigmatic and controversial and different opinions still persist on its generic assignment, variations, value as a paleoclimatic tool, and ancestry.

The problem of generic assignment of this species was discussed by Bandy (1972) who pleaded for its placement in the genus *Globorotalia* (*Turborotalia*). Collen and Vella (1973) placed *pachyderma* in *Neo-*

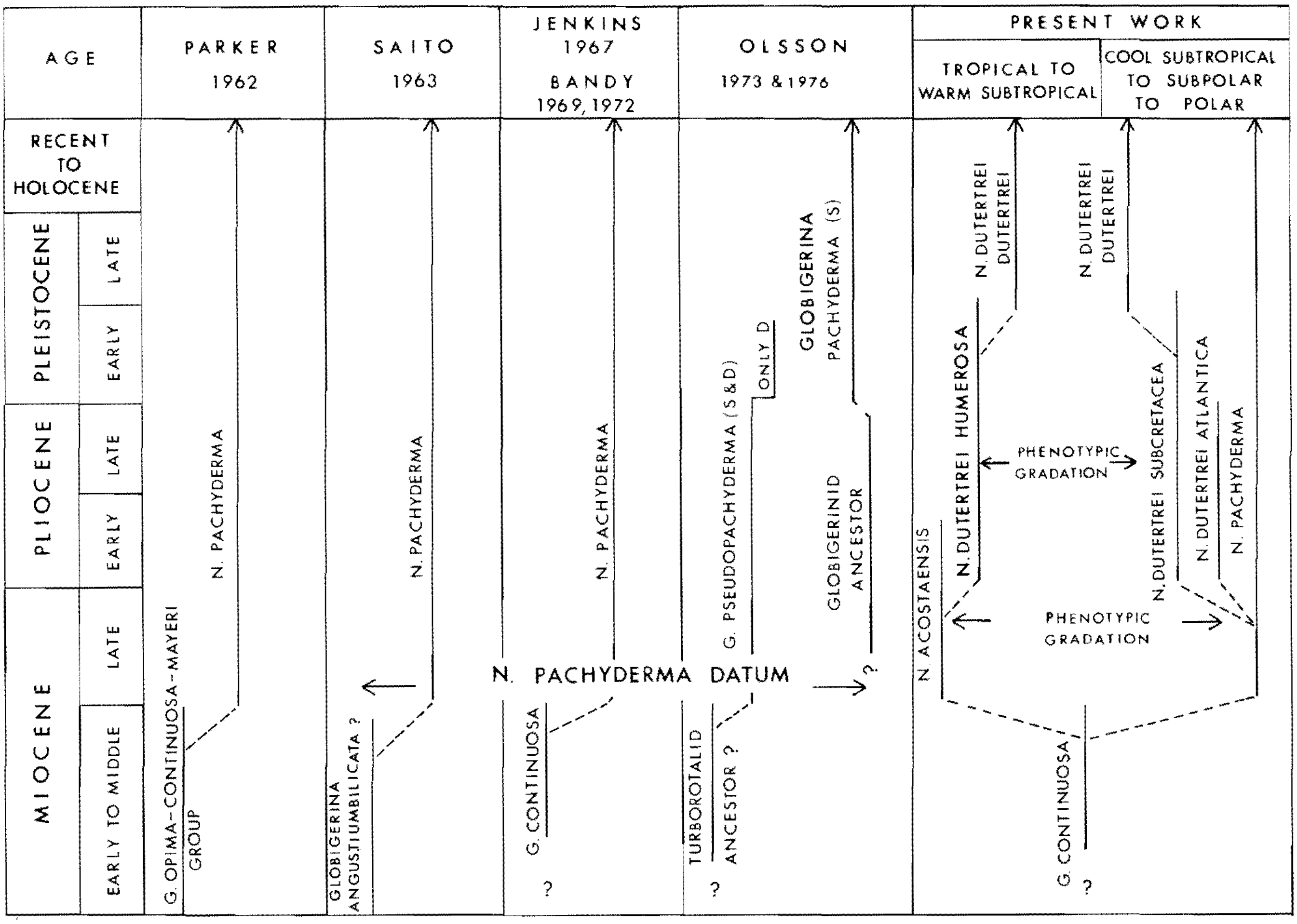


FIGURE 2

Evolutionary relationships proposed by various workers for *Neogloboquadrina pachyderma* and related forms in the Late Cenozoic. S = sinistral coiling; D = dextral coiling. G = *Globorotalia*; N = *Neogloboquadrina*.

globoquadrina on the grounds that intergradation of *pachyderma* and *dutertrei* in New Zealand marine sequences indicates close relationships. Bé and Tolderlund (1971) suggested that *pachyderma* be placed in yet another genus, *Globoquadrina*. Srinivasan and Kennett (1976) discussed this problem at length on evidence of surface ultrastructures in the "*G.*" *pachyderma* and *N. dutertrei* plexus from cool subtropical regions. Srinivasan and Kennett (1976) found that, besides the intergradation of *pachyderma* and *dutertrei*, as already noted by Bé and Tolderlund (1971) and Collen and Vella (1973), the surface ultrastructures are also identical, including the crystal twinning habit and surface textures of the rhombohedrons. Therefore, *pachyderma* is treated as a member of *Neogloboquadrina* (Fig. 2).

PRINCIPAL SURFACE ULTRASTRUCTURAL TYPES

Our investigations have shown that two primary types of external surface ultrastructures occur in populations of *Neogloboquadrina pachyderma* throughout the late Cenozoic. These are defined as follows:

1. *Reticulate Wall Structure*. Test characterized by smooth surface with distinct pore pits. The pores are circular in shape located in the center of a flat to gently sloping base of the pore pit. The interpore area is a smooth, microcrystalline surface without any discernible rhombohedral crystals even at ×5,000 magnification. The pore pits are surrounded by polygonal ridges of varying heights. Normally, individual pore pits enclose a single pore, but occasionally more than one

pore may occur (Pl. 1, Fig. 5; Pl. 3, Figs. 5, 6, 8, 12; Pl. 4, Fig. 10).

2. *Crystalline Wall Structure*. Test covered by distinct euhedral calcite rhombs which cluster around the pores on the final chamber. The crystals increase in size on successively earlier chambers and as a result, pores are obscured. The crystals on the antepenultimate chamber produce penetration twins which form a stellate or star-shaped-patterned crust. In high-latitude forms, each stellate structure coalesces with adjacent similar structures producing a rosette-patterned crust. The pores on earlier chambers are almost obliterated in high-latitude forms, while in subtropical forms the stellate structures do not completely fuse with the adjacent one, and the pores are still visible on the earlier chambers. The crystal faces are normally marked by growth facets. (Pl. 1, Figs. 7–9; Pl. 4, Fig. 7; Pl. 6, Fig. 6).

Individuals that have the reticulate surface on the final chamber and the crystalline crust on earlier chambers link the two types of ultrastructures. This supports the conclusion that reticulate surface structure precedes calcite encrustation.

SURFACE ULTRASTRUCTURES IN RECENT *NEOGLOBOQUADRINA PACHYDERMA*

ANTARCTIC REGION

In the Antarctic region, *N. pachyderma* is dominated by four chambered forms (umbilical view) with highly thickened, compact tests. The wide range of variation in Antarctic forms was discussed and illustrated by Kennett (1968, 1970), Herb (1968), Bandy and Theyer (1971), and Bandy (1972). Two forms of *N. pachyderma* from the Antarctic water mass are identified from their ultrastructural characteristics, one group with crystalline wall structure, and one with reticulate wall structure.

Reticulate wall structure. This form, which is relatively uncommon, is distinguished by a pitted, reticulate, microcrystalline wall surface (Pl. 1, Figs. 5, 6, 10). About 99 percent of the tests are sinistrally coiled and almost all have a ropelike apertural rim. A few specimens have the apertural rim expanded as an apertural flange. The number of chambers in the final whorl is usually four or sometimes four and a half. Thin-walled individuals are high spired with lobulate chambers and show the distinct reticulate-patterned surface. Specimens with extreme calcification assume a more or less spherical shape (Pl. 1, Fig. 1) and the aperture is smaller and restricted to the umbilicus (Pl. 1, Fig. 12). In this group the reticulate wall is normally made of distinct pore pits surrounded by polygonal, steep-sided, blunt ridges or discrete tubercles (Pl. 1, Figs, 4–6). The pits are usually shallow and angular on the final chamber of normalform specimens. In kummerform specimens, the surface of the final chamber is covered by very shallow depressions with pores near the center, rather than a distinct reticulate pattern. The interpore area is covered with microcrystals smaller than 0.2 μm in length. In some kummerform specimens, the pores on the last chamber are almost obscured by the microcrystalline surface. Sometimes two or even three pores may occur in one pore pit (Pl. 1, Fig. 5; Pl. 3, Figs. 5, 8). Pore pits are generally equidimensional but become elongated when they enclose more than one pore. These represent incomplete stages of calcification leading to the structural separation of pores. The floor of pore pits are normally flat (Pl. 3, Figs. 5, 6, 8) but may be sloping making them funnel shaped (Pl. 1, Figs. 4, 5; Pl. 3, Fig. 12). The interpore area may be almost smooth (Pl. 1, Fig. 5) or have a sugary surface texture formed by microcrystals smaller than 0.2 μm (Pl. 1, Fig. 4). In contrast to Olsson's (1976) observation, we found that dextral forms (though rare) have identical surface ultrastructures to sinistral forms.

Pore pits deepen on successively earlier chambers due to the development of secondary calcification consisting of irregular microcrystals surrounding the pores (Pl. 3, Fig. 10). Irregular microcrystalline tubercles coalesce to form continuous ridges surrounding the pores. In most specimens, the reticulate surface is covered along the umbilical shoulders of earlier chambers by the irregular growth of tubercles (Pl. 3, Fig. 9).

On the internal wall, the pores are circular to oval in shape and smaller in diameter than the exterior surface (1 to 0.5 μm). The interpore area on the internal surface is almost flat and is covered with irregular microcrystals which are hardly discernible at ×5,000 magnification. The smaller diameter of pores on the internal wall may result from secondary surficial calcite encrustation that partly seals the pores.

Crystalline wall structure. Individuals with this ultrastructure dominate Antarctic population. This is distinguished by a test wall which is covered almost entirely by distinct euhedral calcite crystals (Pl. 1, Figs. 2, 3). The test is almost globular in shape, and is extremely thickened. In some individuals, the surface of the final chamber retains the original reticulate structure with distinct pore pits, but this feature is covered on successively older chambers by the growth of euhedral rhombs. At first, small calcite crystals cluster around the pore pits. As they grow they interpenetrate producing penetration twins, with the edges of rhombohedrons projecting radially, forming a stellate pattern. The stellate pattern is best developed on the umbilical shoulders of early chambers and ranges in diameter from 10 to 15 μm (Pl. 1, Figs. 8, 9). With an increase in crystal size, each stellate structure interpenetrates the adjacent one, and almost obliterates the pores. The surface thus becomes almost covered with euhedral rhombs exhibiting penetration twins (Pl. 1, Fig. 8). The crystal faces are marked by growth lines which give a terraced or stepped appearance to the rhombohedron faces. This is in marked contrast with Olsson's (1976) observation that penetration twins with coarse facets on rhombohedral faces are a diagnostic feature of dextral populations which he prefers to call "*Globorotalia*" *pseudopachyderma*. With the coalition of several stellate structures and the general constriction of pores, individual interpenetration twins become less distinct and the crust produces a compact rosette patterned surface easily observed under low magnification (Pl. 1, Fig. 7). Normally, a single specimen exhibits the stellate-patterned surface on the penultimate and antepenultimate chambers and the rosette-patterned crust on earlier chambers, due to the coalition of stellate structures.

In some individuals, pores on the last chamber are small (1 to 1.2 μm) and almost circular in shape. In others, even the pores on the final chamber are constricted by the growth of crystals. Calcification starts with medium-sized calcite crystals which increase in size successively on earlier chambers (up to 14 μm). Most pores on earlier chambers are totally obscured with those remaining much reduced in diameter. On the internal wall the pores are subcircular to irregular in shape, and in contrast to the forms with the reticulate wall the internal surface is a highly thickened, rough, secondary crust formed by irregular calcite plates.

ARCTIC REGION

Arctic populations of *Neogloboquadrina pachyderma* (Pl. 2) are readily distinguished from Antarctic populations (Pl. 1) by their distinctly lobulate, less heavily encrusted test with a highly arched and more open aperture (Kennett, 1970; Cifelli, 1973). The Arctic populations are dominated by forms with 4.5 to 5 chambers (umbilical view) in contrast to the four-chambered compact rounded form characteristic of the Antarctic region. Besides the differences in morphology, Arctic populations are dominated by individuals with reticulate ultrastructure, while the Antarctic populations are dominated by forms with cyrstalline ultrastructure. Three ultrastructural forms can be distinguished: reticulate, crystalline, and tuberculate.

Reticulate wall structure. About 80 percent of individuals possess a similar reticulate wall surface to *N. pachyderma* from the Antarctic water mass, except for a less encrusted surface. As demonstrated by Cifelli (1973) in sectioned specimens (Pl. 2, Fig. 10), the

→

PLATE 1

Antarctic Forms

1–3, 11 *Neogloboquadrina pachyderma* (Ehrenberg). Crystalline form. 1. Hypotype, ventral view; Eltanin 32-8, 521–523 cm. ×180. 2. Hypotype, ventral view; Eltanin 36-14; 1–3 cm. ×194. 3. Hypotype, ventral view; same location as 2. ×200. 11. Hypotype, ventral view; Eltanin 47-4; 1–3 cm. ×150.

4 Enlarged view of the final chamber of Figure 1. Note that the pores on the last chamber are almost obscured by the microcrystalline surface. ×1,188.

5 Surface of final chamber of sinistral, reticulate form, with circular central pores, microcrystalline wall and funnel shaped pore pits. Also note some with flat pore base. ×1,312.

6 Surface of final chamber of Figure 10 (reticulate form), showing distinct pore pits surrounded by polygonal, blunt ridges. Note that the pores are almost covered by microcrystalline surface. ×1,125.

7 Surface of the earliest chamber in last whorl of sinistral crystalline form. Note the rosette-patterned arrangement of calcite crystals. ×625.

8 Surface of antepenultimate chamber of Figure 2. Note stellate-patterned (starlike) surface produced as a result of interpenetrating rhombohedrons sharing a common vertical axis. Also note the interpenetrating stellate-pattern structure with the adjacent one and almost obliterating pores. ×2,375.

9 Large penetration twin on the antepenultimate chamber of Figure 2. Note the coarse crystal facets or growth lines of the rhombohedrons resembling the crystal habit characteristic of dextral *N. pachyderma* from cool subtropical water mass. ×3,438.

10 *Neogloboquadrina pachyderma* (Ehrenberg). Reticulate form. Hypotype, ventral view; Eltanin 32-8, 521–523 cm. ×125.

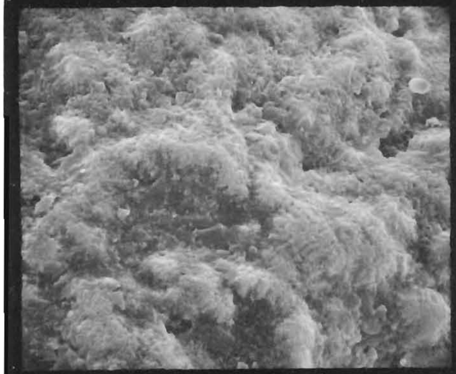
12 Enlarged view of the umbilical area of Figure 1. Note the small umbilical aperture and the distinct apertural rim. ×594.

1

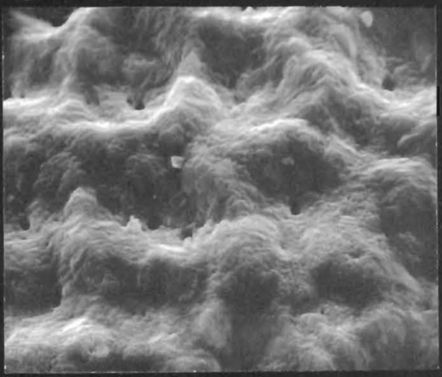
2

3

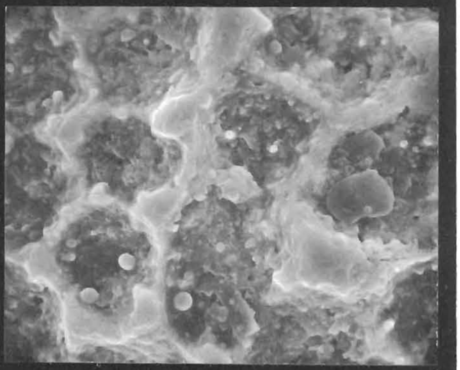
4



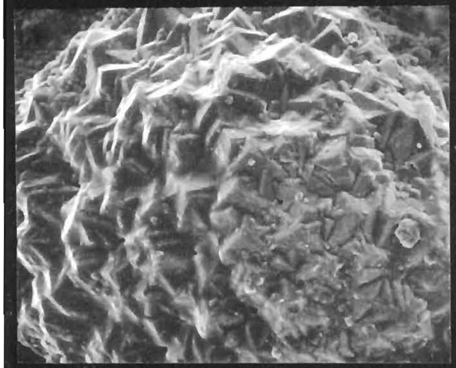
5



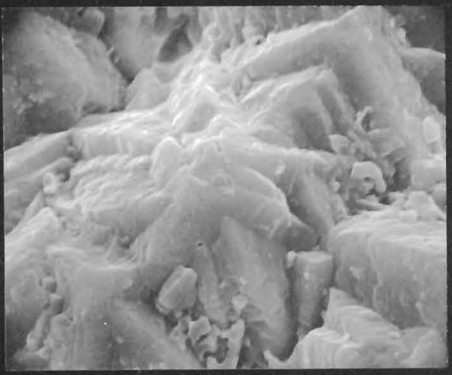
6



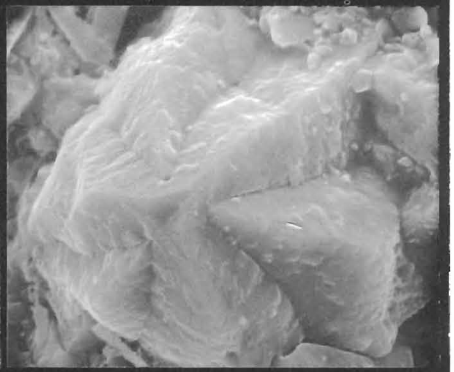
7



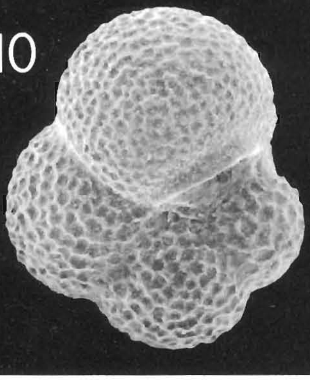
8



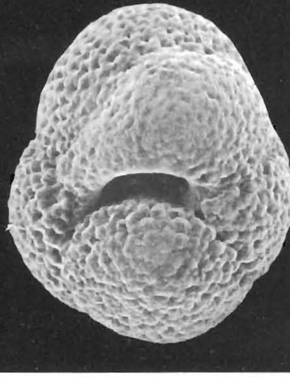
9



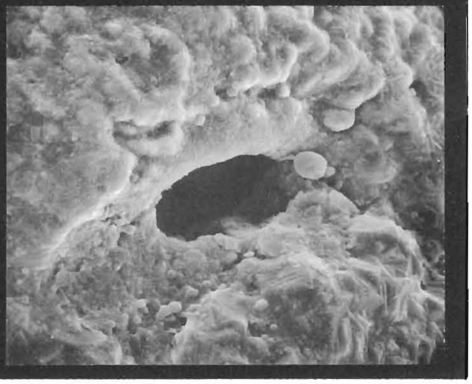
10

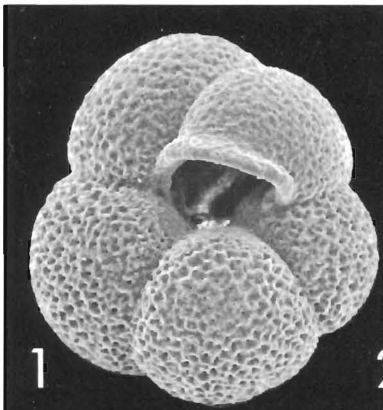


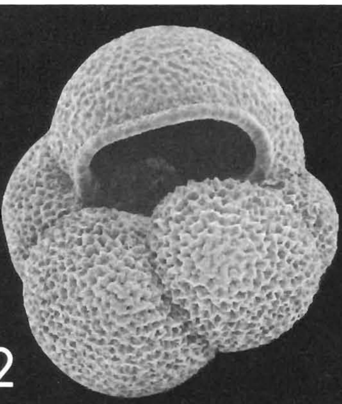
11

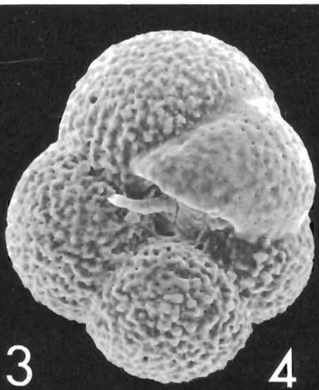


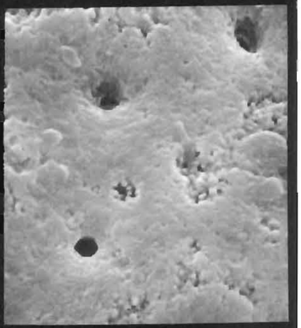
12

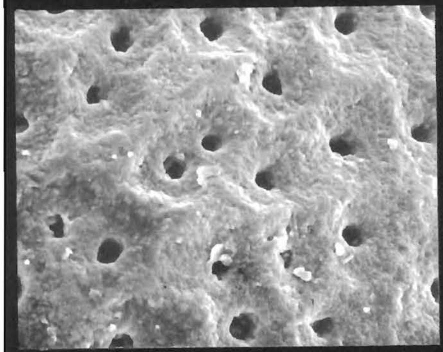


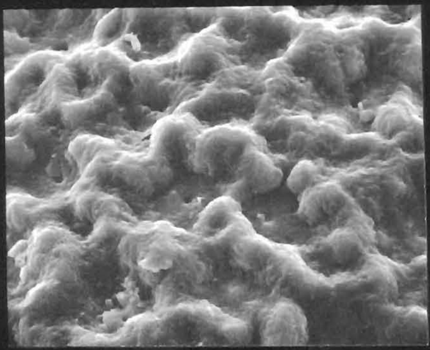

1

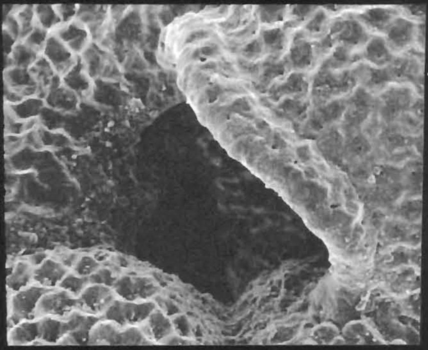

2

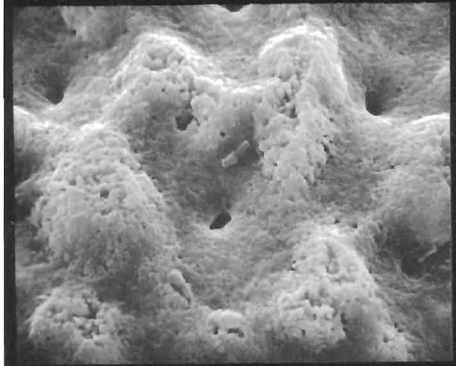

3

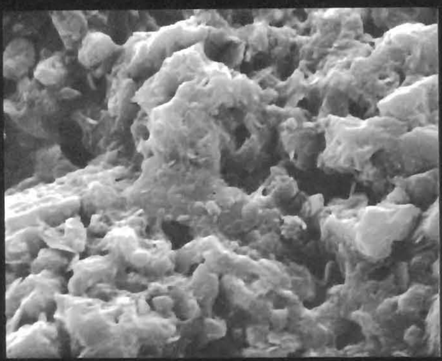

4

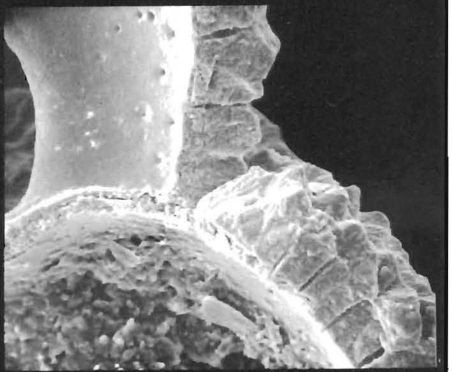

5


6

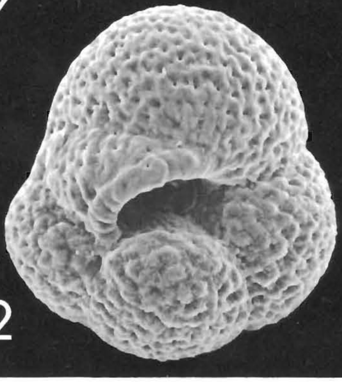

7


8


9


10


11


12


13

septa are thin compared with the outer wall indicating a secondary stage of calcification. The pores extend throughout the thickness of the test and are clearly visible on the surface. Occasionally, the wall appears to be multilayered, but the laminations are not continuous throughout, and as a result, laminations may not be visible on the inner wall.

Crystalline wall structure. The test wall is covered almost entirely by distinct euhedral calcite rhombs, and corresponds to the crystalline form of Antarctic waters. The specimens illustrated by Hunkins and others (1971, Pl. 1, Figs. 3–5) and Olsson (1976, Pl. 3, Figs. 4–8) are this form. Individuals may have a combination of both structures with reticulate wall on the final chamber and stellate pattern on earlier chambers (Pl. 2, Fig. 11). A polygonal pattern of ridges surrounding pores precedes the formation of the calcite crust (Hunkins and others, 1971).

Olsson (1976) considers that the surface ultrastructure of the calcite crust of sinistral *N. pachyderma* (Olsson, 1976, Pl. 3, Figs. 4–8) is fundamentally different from that of dextral *N. pachyderma* (Olsson, 1976, Pl. 5, Figs. 6–8) which he prefers to call "*Globorotalia*" *pseudopachyderma* Cita, Premoli-Silva, and Rossi. Olsson (1976) believes sinistral *N. pachyderma* lacks the stellate-patterned crust and coarse facets (growth lines or rings) on the rhombohedral faces. Our study demonstrates that the development of stellate-patterned surface precedes the formation of rosette-patterned crystalline crust and is found both in sinistral and dextral *N. pachyderma* (Pl. 1, Figs. 7–9; Pl. 4, Fig. 7). Our observation is supported by figures published by Hunkins and others (1971, Pl. 1, Figs. 3, 5), which show Arctic sinistral *N. pachyderma* with stellate-patterned surface identical to figures of dextral forms referred by Olsson (1976) to "*G.*" *pseudopachyderma*. A figures of Hunkins and others (1971, Pl. 1, Fig. 5) also clearly shows the coarse facets on the rhombohedral faces which according to Olsson (1976) distinguishes dextral "*G.*" *pseudopachyderma* from the sinistral form *N. pachyderma*. We believe, on the other hand, that there is no fundamental difference between the ultrastructures of sinistral and dextral forms and therefore, Olsson's (1973, 1976) splitting of *N. pachyderma* into "*Globigerina*" *pachyderma pseudopachyderma* is unwarranted.

Tuberculate surface structure. The third ultrastructural type observed in *N. pachyderma* populations from the Arctic region is characterized by irregular discrete tubercles distributed around the pores without forming continuous polygonal ridges of equal heights (Pl. 2, Figs. 3, 8). The surface is thus covered with tubercles of different heights with deep pore pits. As the wall progressively thickens, the sutures become less depressed and finally become flush (Pl. 2, Fig. 13), and the surface is smoothed off with irregular plates of calcite causing the pores to disappear leaving a crisp sugary surface (Pl. 2, Fig. 9). Even at higher magnifications it is difficult to distinguish a definite pattern

---

←

PLATE 2

Arctic Forms

1, 2 *Neogloboquadrina pachyderma* (Ehrenberg). Reticulate form. Hypotypes, ventral view; sample No. 22. ×141.

3, 13 *Neogloboquadrina pachyderma* (Ehrenberg). Tuberculate form. 3. Hypotype, ventral view; sample No. 66-18 UC. ×188. 13. Hypotype, ventral view; sample No. 98. ×169.

4 Surface of final (kummerform) chamber of Figure 3. Note the absence of tubercles or ridges on this chamber. The pores are located on almost flat microcrystalline surface. ×2,969.

5 Surface of final chamber of Figure 1, with circular pores and microcrystalline wall. Note the pore pits which are funnel shaped, also a few with flat pore base. ×1,250.

6 Surface of final chamber of Figure 2. Note the flat pore bases and the steeply rising polygonal ridges. Occasionally more than one pore is enclosed in a single pore pit. ×1,250.

7 Enlarged view of umbilical region. Note the deep umbilicus, symmetrical umbilical aperture with ropelike apertural rim. ×375.

8 Surface of the penultimate chamber of Figure 3 (tuberculate form). Note that the surface is characterized by irregular discrete tubercles distributed around the pores without forming continuous polygonal ridges of equal heights. ×2,969.

9 Surface of the final chamber of Figure 13. The surface is covered with irregular but uniform plates of calcite leaving a crisp sugary surface. The pores are almost covered, and it is difficult to distinguish any definite pattern of crystal arrangement. ×3,250.

10 Section of junction between thickened outer wall and thin septum of sinistral *N. pachyderma*. Section shows multilaminate septum. ×625.

11, 12 *Neogloboquadrina pachyderma* (Ehrenberg). Specimens showing intermediate surface structure between reticulate form and crystalline form (i.e., reticulate surface on final and penultimate chambers which is replaced by crystalline surface on earlier chambers). 11. Hypotype, ventral view; same location as Figure 13. ×175. 12. Hypotype, ventral view; same location as Figure 3. ×194.

of crystal arrangement. This ultrastructure appears to be more closely related to the reticulate form, because a faint reticulate pattern occurs on the final chamber of a few individuals. Individuals with this ultrastructure were first illustrated by Bandy and Theyer (1971, Figs. 2, 12, 13), and Bandy (1972, Pl. 6, Figs. 6, 7) from Fletcher's Ice Island, T-3, (86°06'N, 95°20'W). Recently Cifelli (1973, Pl. 2, Figs. 13, 14) recorded this form as "*Globigerina*" aff. *pachyderma* in the surface waters of the North Atlantic. No individuals have been recorded so far from the southern ocean. The uniform size of crystals on all chambers of the test (Pl. 2, Fig. 13) suggests post-depositional crystal growth but such a process is difficult to invoke in Recent forms from surface sediments.

Kennett (1970) suggested that the morphological differences between the Antarctic and the Arctic populations of *N. pachyderma* might be due to subspeciation resulting from geographic isolation or an expression of phenotypic variation. The distinct ultrastructures in populations from the two regions may be related to environmental differences because the respective ultrastructures are found in varying proportions in different oceanic regions.

SUBANTARCTIC REGION

The subantarctic populations of *N. pachyderma* examined are from the region between the Subtropical Convergence and the Antarctic Convergence. They are dominantly 4.5- to 5-chambered sinistral forms (Kennett, 1968; Herb, 1968), with relatively less thickened apertural rims. As in Antarctic waters, the two ultrastructural types are readily distinguished. More than 60 percent of the individuals of *N. pachyderma* populations from the subantarctic have the reticulate-patterned wall. These are very similar to such forms in the Antarctic water mass, except that the subantarctic form is less encrusted (Pl. 3, Figs. 1–3, 13) and has greater pore diameter on the final chamber usually from 2.0 to 3.0 μm (Pl. 3, Figs. 5, 6, 8).

The crystalline-walled form is likewise similar to such forms occurring in the Antarctic, except specimens are less thickened and the stellate pattern is more pronounced, whereas the rosette-patterned crust which is highly developed on earlier chambers in Antarctic forms is less pronounced in the subantarctic. This results from less encrustation in subantarctic forms. Both dextral and sinistral populations have a crystalline crust.

COOL-SUBTROPICAL (TEMPERATE) REGIONS

South Pacific and South Indian Ocean. The cool-subtropical populations of *N. pachyderma* examined from the south and southwest Pacific and south Indian Ocean are from temperate areas north of the subtropical convergence. As observed by Kennett (1968) these populations are dominantly 4 chambered and dextrally coiled as are those in other temperate areas of the world oceans.

Individuals of *N. pachyderma* with reticulate microcrystalline ultrastructure are fairly infrequent in the cool subtropical water mass. Both dextral and sinistral

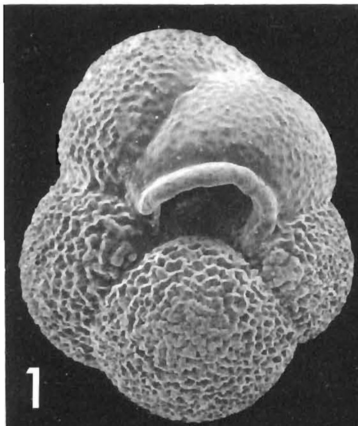
→

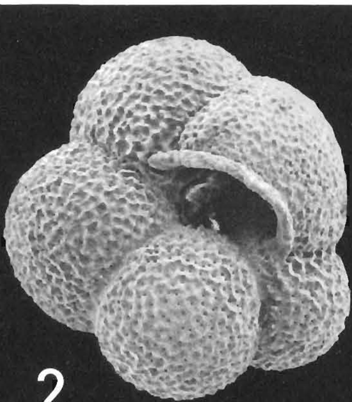
PLATE 3

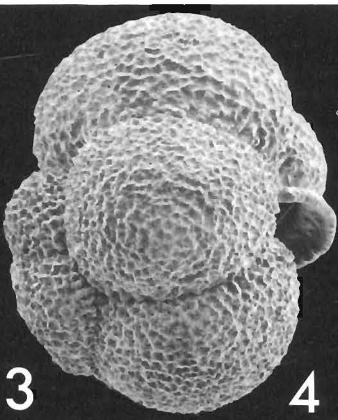
Subantarctic Forms

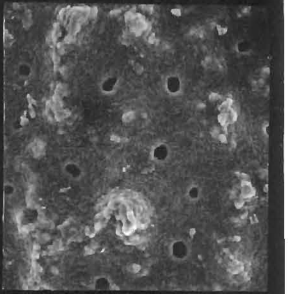
1–10, 12, 13 *Neogloboquadrina pachyderma* (Ehrenberg). Reticulate form. 1. Hypotype, ventral view; Eltanin 1197. ×180. 2. Hypotype, ventral view, Eltanin 15–16. ×175. 3. Hypotype, side view, same location as Figure 2. ×178. 13. Hypotype, ventral view, same location as Figure 2. ×131. 4. Surface of final chamber of sinistral form. Note the discrete tubercles with only slight coalescence around the pores. This resembles the surface of the surface-water form illustrated by Cifelli (1973, Pl. 4, Fig. 5). ×1,250. 5, 6. Surface of final chambers of sinistral form. Note that the topography consists of a pore opening surrounded by an almost flat outer wall bordered by steeply rising polygonal ridges which imparts the diagnostic reticulate appearance to the surface. ×1,313. 7. Surface of the earliest chamber in the last whorl of sinistral form. Compared with the corresponding portion of the final chamber (Figs. 5, 6), the topography of the earliest chamber is much coarser and more rugged due to irregular growth of tubercles on the interpore region. ×1,375. 8. Surface of the final chamber of the dextral form, showing pores lying at the center of flat surfaced pits. The shape of the pore pit varies from equidimensional (Fig. 6) to elongate depending on the number of pores present in the pit. ×1,313. 9. Umbilical area with irregular growth of tubercles or "pseudospines." ×1,225. 10. Surface of the earliest chamber in the last whorl of the dextral form. ×3,125. 12. Surface of final chamber of sinistral form. Note that pores are located in funnel-shaped pore pits and the interpore area is covered with microcrystalline surface. ×3,438.

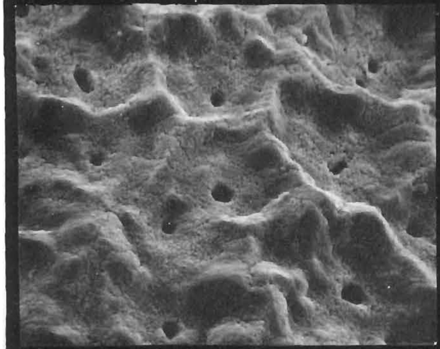
11 *Neogloboquadrina pachyderma* (Ehrenberg). Crystalline form. Hypotype, oblique ventral view; same location as Figure 2. ×213.

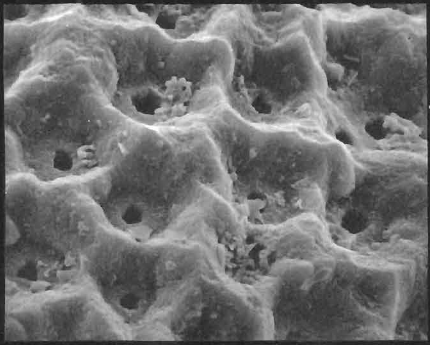

1

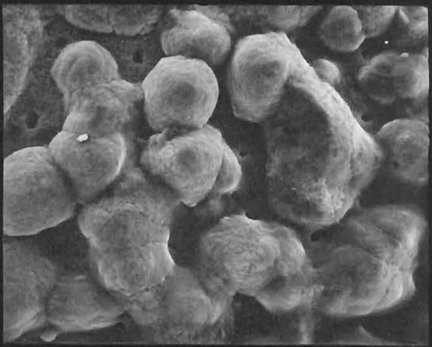

2

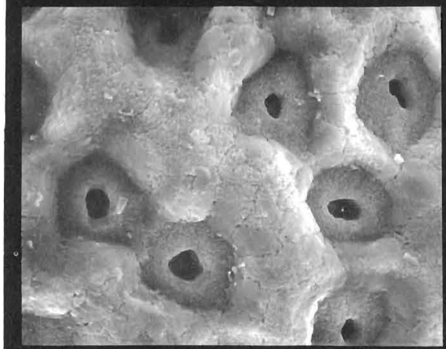

3

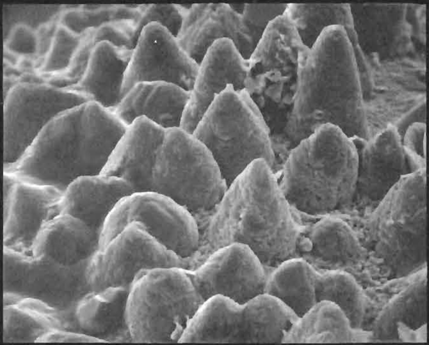

4

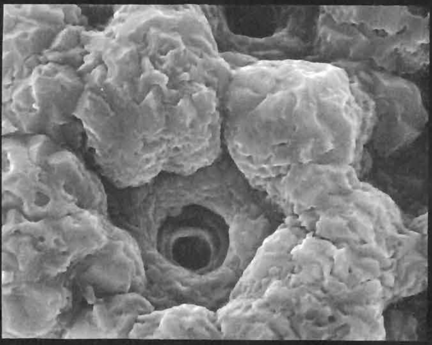

5

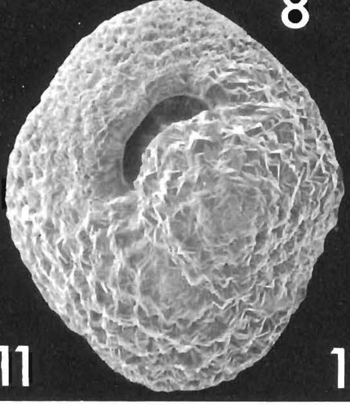

6

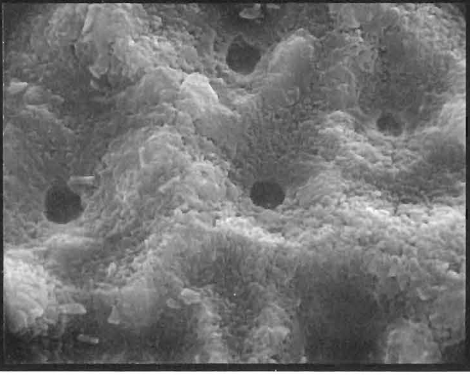

7

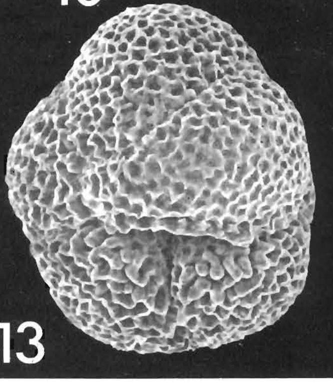

8

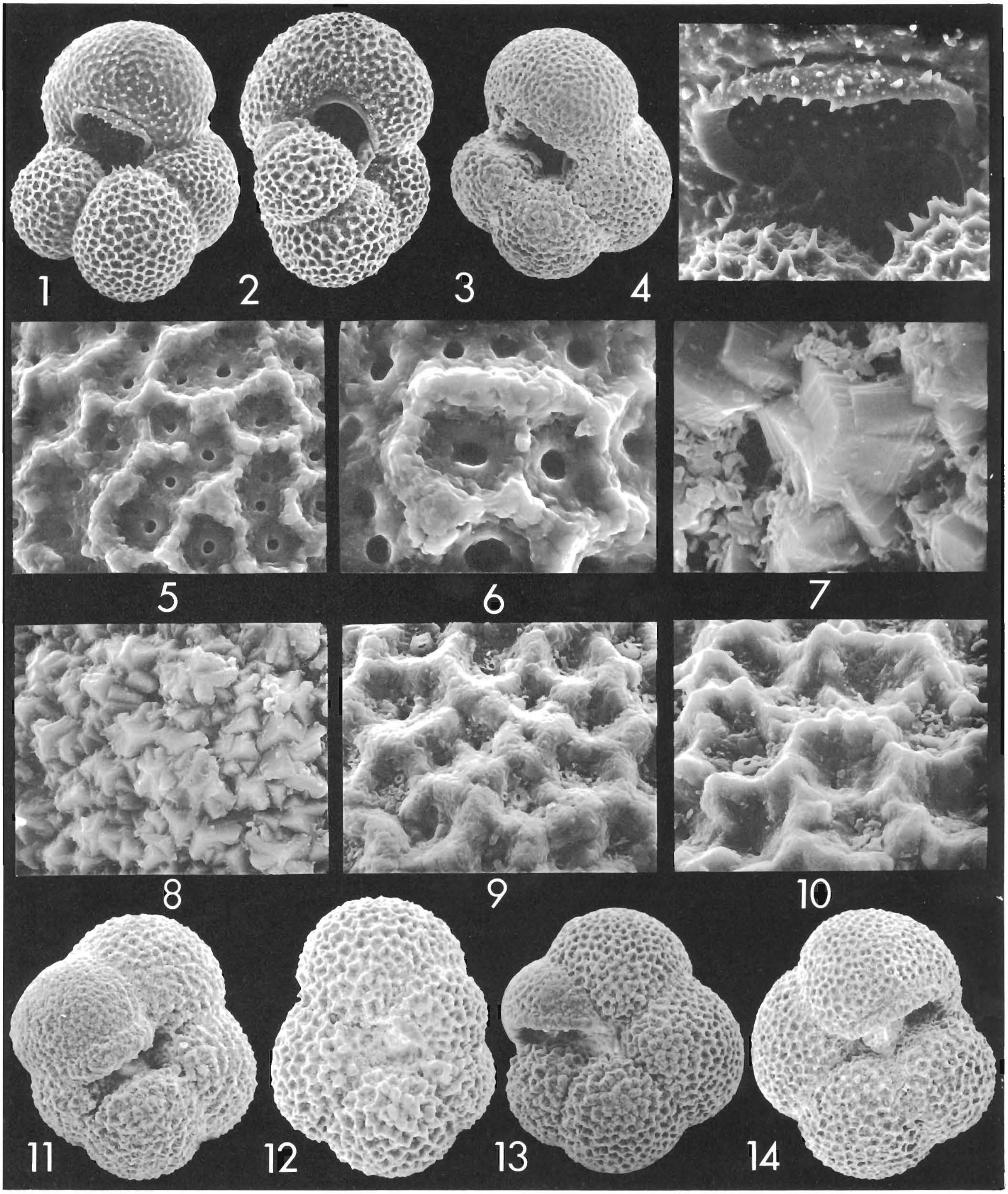

9


10


11


12


13


1
2
3
4
5
6
7
8
9
10
11
12
13
14

forms have similar ultrastructural characteristics. The crust is normally very thin. Most specimens examined (approximately 95%) have a crystalline crust producing the characteristic stellate pattern with coarse facets on crystal faces (Pl. 4, Fig. 7). They differ from crystalline individuals from Antarctic and subantarctic areas by having distinct pores that are not sealed off by crystal growth, a thinner wall, and more distinct pore pits (Pl. 4, Figs. 3, 7). A few individuals have the rosette-patterned crust on earlier chambers, but these are distinguished from high latitude forms by their relatively thin wall, lobulate chambers and distinctly depressed sutures.

The final chamber normally has a microcrystalline (less than 0.2 μm) reticulate wall. On the penultimate chamber the test becomes more encrusted with small medium-sized (about 2 to 3 μm) crystalline aggregates surrounding the pores. The crystals increase further in size up to 8 to 10 μm on the antepenultimate and earlier chambers and develop interpenetration twins producing the characteristic stellate-patterned crust (Pl. 4, Fig. 7).

Olsson (1976) considered stellate-patterned ultrastructure in dextral forms to be fundamentally different from the ultrastructure in sinistral forms and therefore referred the dextral form to "*Globorotalia*" *pseudopachyderma* which was described by Cita and others (1965) from the Tortonian (late Miocene) of Italy. The penetration twins producing the stellate-patterned surface, however, are found both in sinistral (Pl. 1, Figs. 8, 9) and dextral populations (Pl. 4, Fig. 7). The thin-walled form with stellate pattern and coarse crystal facets merely happen to be diagnostic of cool subtropical areas where dextral forms predominate and on which Olsson (1976) based most of his observations.

Therefore, the differences noted by Olsson (1973, 1976) between high latitude sinistral populations of *N. pachyderma* and the dextral forms from cool subtropical regions which he designates as "*G.*" *pseudopachyderma* result from environmental differences between the two regions rather than any specific difference.

Within individual populations, some forms have a microcrystalline reticulate wall while others have a well-developed crystalline wall. The presence of individuals with both types of surface ultrastructures in both sinistral and dextral forms in individual populations indicates that the differences in dominance of the ultrastructural types is not specifically or genetically controlled but is related to environmentally induced calcification differences. According to Stapleton (1973) environmental factors including oxygen concentration, pressure, or pH may control the extent to

←

PLATE 4

Subtropical and Plio-Pleistocene Forms

1, 2, 4–6 *Neogloboquadrina pachyderma* (Ehrenberg). Reticulate form (=*Globigerina incompta* Cifelli). 1. Hypotype, ventral view; AII-32-9; (plankton tow, 0-100 m). ×188. 2. Hypotype, side view; same location as Figure 1. ×178. 4. Enlarged view of the umbilical area of Figure 1. Note the "pseudospines" on the umbilical shoulder. Also note the wide flangelike apertural rim. ×625. 5. Surface of final chamber of Figure 2. Note the distinct reticulate structure with distinct pore pits. Also note that two or three pores often occur in a single pore pit. ×1,188. 6. Surface of the earliest chamber of Figure 2. The pores lie on almost flat based pore pits and resemble the subantarctic dextral form (Pl. 3, Fig. 10) in ultrastructure. ×1,781.

3 *Neogloboquadrina pachyderma* (Ehrenberg). Specimen showing reticulate structure on final chamber and crystalline structure on early chambers. Hypotype, ventral view; E. 120. ×150.

7 Enlarged view of the second chamber from the earliest in the last whorl of a dextral form. Location same as Figure 3. Note the penetration twins of the rhombohedrons impart a stellate appearance. The coarse growth facets of the rhombohedrons are distinct, and also note the irregular-shaped pores between the stellate structures. ×3,281.

8 Surface of final chamber of Figure 11. Note that even on final chamber the pores are almost obliterated by calcite rhombohedrons. ×1,563.

9 Surface of penultimate chamber of Figure 13. The pore pits become funnel shaped due to the secondary encrustation on the flat-bottomed interpore area. ×1,250.

10 Surface of final chamber of Figure 12. Note the distinct funnel shaped pore pits and steeply rising polygonal ridges. ×1,563.

11–14 *Neogloboquadrina pachyderma* (Ehrenberg). DSDP, Leg 29, Site 284 (west of New Zealand). 11. Crystalline form; Hypotype, ventral view; ×197 (early Pleistocene—Hautawan Stage). 12. Reticulate form. Hypotype, ventral view; ×231 (late Pliocene—Waipipian Stage). 13. Specimen showing reticulate structure on final and penultimate chamber which is replaced on successively earlier chambers by crystalline structure (early Pleistocene—Hautawan Stage) ×181. 14. Typical reticulate form. Hypotype, ventral view (late Pliocene—Waipipian Stage) ×181.

which calcite crust develops in different species. From a study of the ultrastructure of some Recent benthic hyaline foraminifera, Stapleton (1973) demonstrated that the secondary calcite crust becomes thicker with increasing depth, whereas lowering of oxygen concentration inhibits the development of the crust. Further, we have demonstrated that the microcrystalline reticulate wall precedes extensive crystal development, with the reticulate and crystalline ultrastructural forms merely reflecting the extent of calcification of the crust.

North Pacific. Specimens examined from the North Pacific are from the Tanner Basin, southern California. Almost all the specimens encountered are dextrally coiled having 4 chambers in the final whorl. Like populations from other cool subtropical areas, individuals with crystalline surface ultrastructure predominate. Normalform individuals have a mature surface ultrastructure even on the final chamber, while in kummerform individuals, the ultimate chamber usually is smooth with circular to subcircular pores.

According to Olsson (1976), pores in dextral forms lie at the base of funnel-shaped depressions whereas in sinistral forms they occur on the flat base of the pore pit. Furthermore, Olsson (1976) believes that in dextral forms each pore pit, except in rare cases, is occupied by only one pore. These features have been considered by Olsson to be of fundamental taxonomic importance and, as a result, he differentiated sinistral forms as "*Globigerina*" *pachyderma* and the dextral as "*Globorotalia*" *pseudopachyderma*. The ultrastructure of the immature final chamber of dextral forms shows a reticulate wall structure identical to those of the sinistral forms from high latitudes. More than two pores may occupy a single pore pit. These factors indicate that there is no fundamental difference in surface ultrastructure between dextral and sinistral populations of *N. pachyderma*. On the other hand, there is a difference in the proportions of individuals with reticulate and crystralline ultrastructure in different regions. As both these two types of surface ultrastructures are independent of coiling mode, as the reticulate form seems to be an incipient stage leading to the crystalline stage, and as individuals exist that represent the intermediate stages, it appears that the difference in these ultrastructural proportions result from environmentally controlled differences rather than any apparent taxonomic difference.

North Atlantic. Populations examined are from the northeast of the Azores and are predominantly 4 chambered, dextrally coiled with both reticulate and crystalline surface ultrastructure. Most specimens examined (approximately 90%) have a crystalline crust producing the stellate pattern with growth facets on crystal faces. Individuals representing intermediate stages between these two surface ultrastructures are also frequent. For dextral populations with crystalline walls, individuals differ in the nature of crystal formation. In some individuals, perfect euhedral calcite rhombs are developed on the penultimate chamber,

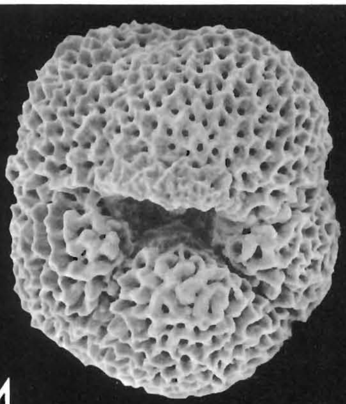
→

PLATE 5

Pleistocene and Late Pliocene Forms

1–12 *Neogloboquadrina pachyderma* (Ehrenberg). 1. Reticulate form. Hypotype, ventral view; DSDP, Leg 19, Site 188, 7 CC (early Pleistocene) ×213. 2. Reticulate form. Hypotype, ventral view; DSDP, Leg 19, Site 188, 1-1-106-108 cm. (late Pleistocene) ×181. 3. Reticulate form. Hypotype, ventral view; Same location as Figure 1 (early Pleistocene) ×213. 4. Surface of final chamber of Figure 1. Note the large pores and the microcrystalline interpore area. Also note the traces of flat-bottomed pore pits. ×1,188. 5, Surface of the earliest chamber on last whorl of Figure 1. Compared with corresponding portion of the final chamber (Fig. 4), the surface texture of the earliest chamber is much more rugged due to the irregular development of ridges. This topography is identical to *N. dutertrei dutertrei* Group A (tropical form) ×1,250. 6. Surface of the earliest chamber on the last whorl of Figure 7. Note the development of interpenetrating rhombohedrons producing stellate-patterned crust. Coarse facets of rhombohedron faces are clearly seen. ×1,219. 7. Crystalline form, Hypotype, ventral view; same location as Figure 1 (early Pleistocene) ×219. 8. Surface of the second chamber from the earliest in the last whorl of Figure 12. The crust consists of coarse interpenetrating rhombohedrons with coarse facets. This crystal habit is also observed in both dextral and sinistral Recent *N. pachyderma* (Pl. 1, Fig. 8; Pl. 4, Fig. 7) ×1,313. 9. Surface of final chamber of Figure 11, showing typical reticulate crust. ×1,313. 10. Crystalline form. Hypotype, ventral view; Nobori Formation, N 21 (late Pliocene). Note the distinct stellate-patterned surface structure. ×169. 11. Reticulate form. Hypotype, dorsal view; Nobori Formation; N 21 (late Pliocene) ×153. 12. Specimen representing an intermediate stage between *N. acostaensis* and *N. pachyderma*. Note the nature of aperture, the diminishing apertural plate and the position of last chamber, which are characteristic of *N. acostaensis* yet the form has surface ultrastructure (Fig. 8) diagnostic of *N. pachyderma*. ×144.

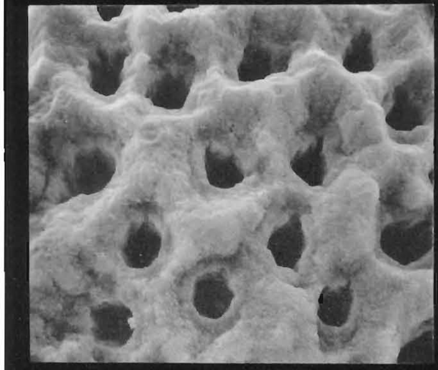
1



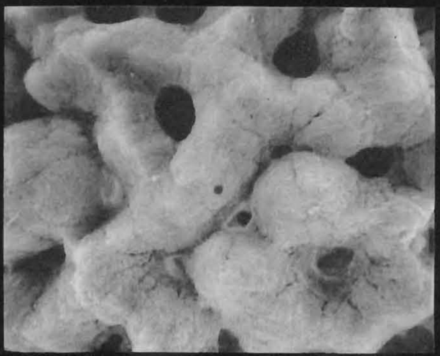
2

3

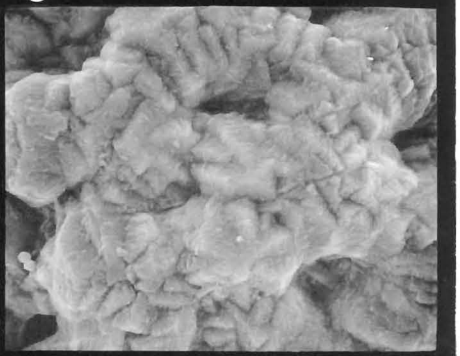
4



5



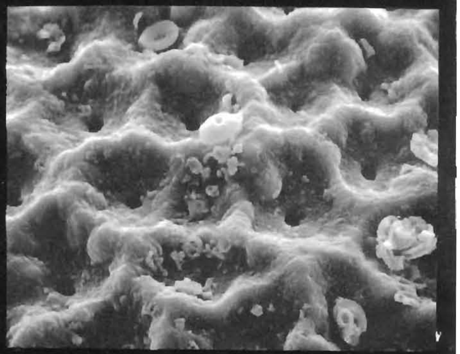
6



7

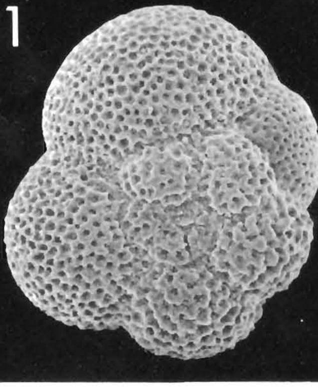
8

9

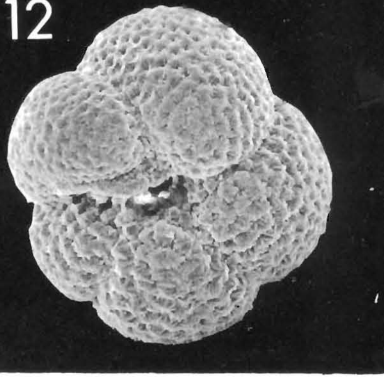


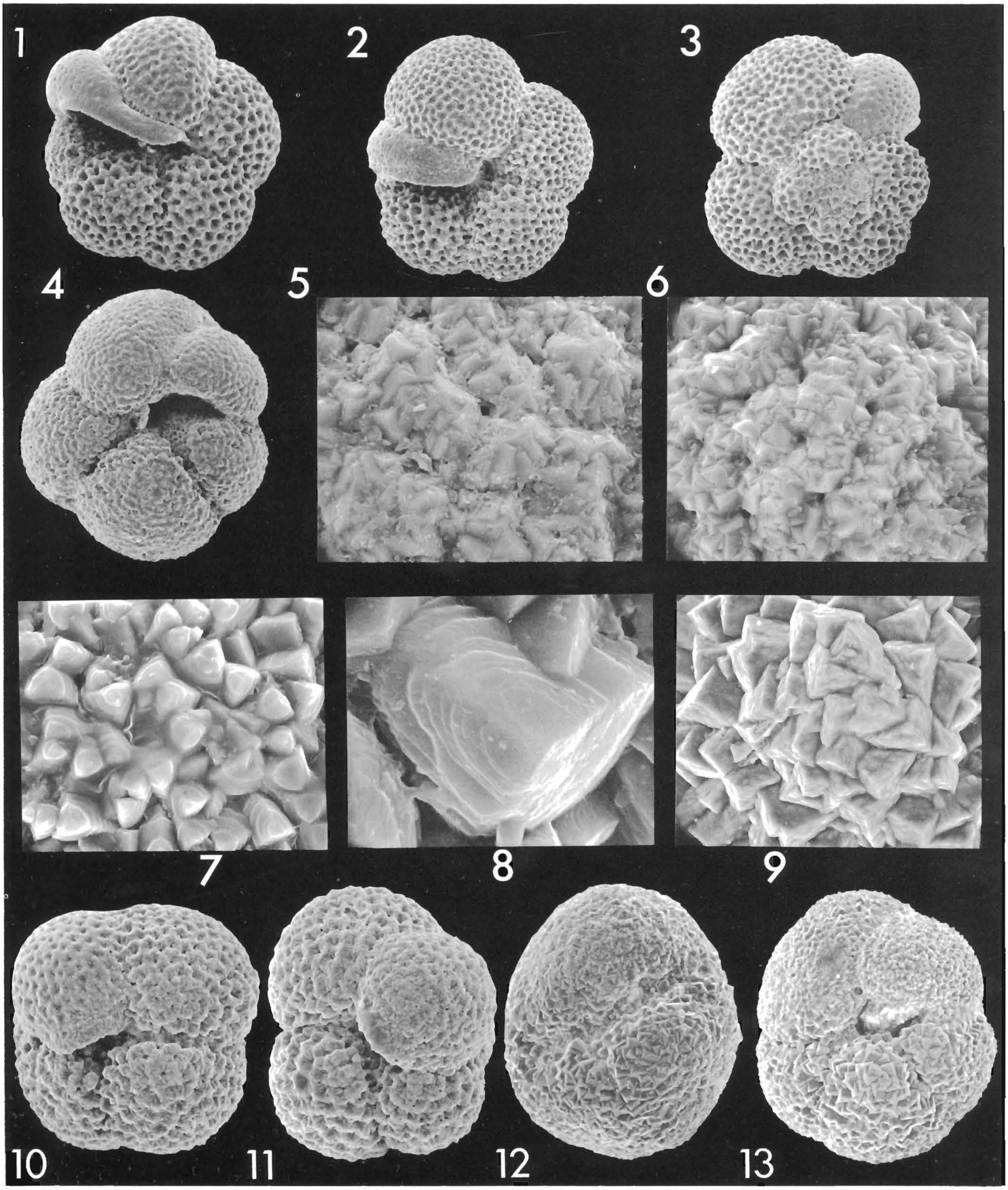
10

11



12




1
2
3
4
5
6
7
8
9
10
11
12
13

while in others, the crystals have not yet assumed perfect euhedral shape on that chamber indicating different rates of encrustation.

SURFACE ULTRASTRUCTURE OF "*GLOBIGERINA*" *INCOMPTA* CIFELLI

Recently Cifelli (1973) described in North Atlantic plankton tows and surface sediment samples the surface structure of the sinistral form of *N. pachyderma* and the dextral form which he refers to "*Globigerina*" *incompta*. He considered these to be separate species, mainly because sinistral populations tend to be thicker walled than dextral forms.

Examination of "*G.*" *incompta* from surface plankton tows kindly provided by Dr. Cifelli from the North Atlantic shows the following characteristics:

"*Globigerina*" *incompta* has a thin, delicate wall and usually four chambers in the final whorl (Pl. 4, Figs. 1, 2, 4). The surface of the final chamber consists of pore openings surrounded by discrete tubercles. With progressive thickening the tubercles coalesce forming steep-sided, blunt ridges separating each pore area, thus forming a reticulate surface. Because encrustation is incomplete in "*G.*" *incompta*, structural separations around each pore area on the final chamber are mostly incomplete. Thus, two or three pores often occur in a single pore area (Pl. 4, Figs. 5). The pores are located on almost flat surfaces which abut against steeply rising, blunt-topped ridges. Pores are circular to subcircular and are uniformly distributed. Pore diameters on final chamber range from 1 to 2 μm. The interpore area and the ridges surrounding the pore pit are microcrystalline. Thus, "*G.*" *incompta* has the typical reticulate wall surface. In contrast to Cifelli (1973), we have found thin-walled sinistral forms in bottom sediments, with surface ultrastructures identical to "*G.*" *incompta* (Pl. 3, Fig. 4). The illustrations of Cifelli (1973, Pl. 4, Figs. 3, 5) show that in surface waters the dextral form ("*G.*" *incompta*) is more heavily encrusted with a more clearly developed reticulate pattern than in sinistral forms.

Furthermore, Cifelli illustrated (1973, Pl. 4, Fig. 4) the surface ultrastructure of sinistral *N. pachyderma* having crystalline surface structure and compared it with "*G.*" *incompta* having reticulate wall structure, and on this evidence he believed sinistral forms to be thicker walled than those with dextral coiling. Cifelli (1973) however did not realize that these two types of surface ultrastructure exist in varying proportions within populations of *N. pachyderma*. Our studies indicate that there is no fundamental difference in sur-

←

PLATE 6

Pliocene Forms

1–3 *Neogloboquadrina acostaensis* (Blow). 1,2. Hypotypes, ventral view, DSDP Leg 21, Site 206; 13 CC (late Pliocene). Note the abnormal final chamber resembling a kummerform chamber of *N. pachyderma* Figure 1. ×156. Figure 2. × 213. 3. Hypotype, dorsal view: DSDP Leg 21, Site 208, 9-3-50–52 cm (middle Pliocene). Note the typical reticulate topography of the chambers identical to *N. pachyderma*. ×163.

4, 5 *Neogloboquadrina dutertrei altantica* (Berggren). 4. Hypotype, ventral view, DSDP Leg 12, Site 111A, 6-3-31-32 cm (late Pliocene). ×94. 5. Enlarged view of final chamber of Figure 4. Note the arrangement of small calcite rhombohedrons of the interpore region. The pores are circular and are generally bounded by the bases of 5 or 6 crystals which often constrict the pores. This topography is identical to the final chamber of crystalline form of *N. pachyderma* (Fig. 6). ×1,250.

6–9 *Neogloboquadrina pachyderma* (Ehrenberg). 6. Enlarged view of final chamber of *N. pachyderma*, Figure 11. Note the distinct euhedral calcite rhombs clustering around each pore giving a funnel-shaped appearance to the pore pits. ×1,188). 7. Enlarged view of final chamber of *N. pachyderma*, Figure 13. Note that the crystals are arranged with the points of intersection of three faces normal to the test surface. The projecting ends of the crystal faces give a prickly appearance to the test. This arrangement of rhombohedrons is slightly different than in Figure 6. × 1,188. 8. Enlarged view of the antepenultimate chamber of Figure 13, showing large rhombohedron with coarse growth lines or crystal facets. Penetration twin the diagnostic feature of the crystal habit is also seen. ×3,063. 9. Surface of the second chamber from the earliest in the last whorl of *N. pachyderma*—Figure 13. Note the euhedral calcite rhombs arranged radially to produce a rosette-patterned surface. The coarse rhombic crystals almost constrict the pores. ×563.

10–13 *Neogloboquadrina pachyderma* (Ehrenberg). Crystalline form. 10. Hypotype, ventral view; DSDP Leg 12, Site 111A; 6-3-31-32 cm, early Pliocene. ×200. 11. Hypotype, ventral view; Same location as Figure 10, early Pliocene. ×213. 12. Hypotype, ventral view; DSDP, Leg 12, Site 111A: 6-2-40-41 cm, late Pliocene. Note the extremely thickened and globular shape of the test with almost flush sutures resembling typically Antarctic crystalline form (Pl. 1, Figs. 1–3). ×169. 13. Hypotype, ventral view; same location as Figure 12, late Pliocene. ×156.

face structure between "*G.*" *incompta* and *N. pachyderma* and hence "*G.*" *incompta* is considered to be a synonym of *N. pachyderma* as already stated by Bandy (1972).

SURFACE ULTRASTRUCTURES IN THE PLEISTOCENE

SOUTH PACIFIC AND SOUTH INDIAN OCEAN

Pleistocene populations of *N. pachyderma* examined from DSDP Leg 21, 28, 29, and "ELTANIN" cores show both the reticulate and crystalline surface ultrastructures observed in Recent populations.

The surface structure of late Pleistocene populations of *N. pachyderma* examined from Leg 28, Site 264 (south Indian Ocean) , are similar to those illustrated by Bandy (1972, Pl. 4) from the continental borderland of southern California in having a distinct coarsely reticulate wall, and pores which are mostly obscured by secondary thickening. In contrast, early Pleistocene dextral populations from this site are dominated by forms with a more thickened crystalline wall.

Olsson (1976, Pl. 5) illustrated the dextral form of *N. pachyderma* (as "*G.*" *pseudopachyderma*) with crystalline stellate-patterned surface crust, from the Pleistocene of the temperate DSDP Site 207, and considered it to be different from the sinistral populations. We observed that even within dextral populations some individuals have the microcrystalline reticulate wall, while others have a crystalline, stellate-patterned wall. Dextral individuals have identical surface characteristics to the sinistral individuals from the subantarctic and Arctic water mass (see Hunkins and others, 1971, Pl. 1, Figs. 3–5). Olsson (1971, Pl. 1, Figs. a–d) also illustrated sinistral individuals with crystalline walls. One of his illustrations (Pl. 1, Fig. a) shows a stellate-patterned surface on the antepenultimate chamber and rosette-patterned crust on the earlier chambers.

Our work indicates that there is no fundamental taxonomically based difference in the surface structure between dextral individuals with crystalline ultrastructure and sinistral individuals with reticulate wall surface throughout the late Cenozoic.

NORTH PACIFIC

Pleistocene populations examined from the North Pacific (DSDP Leg 19, Site 188, Bering Sea) are very distinct in having a highly perforated test (Pl. 5, Figs. 1–3, 7). Individuals with sinistral coiling and reticulate walls are dominant. The test wall is highly thickened with large circular open pores giving a netlike appearance to the surface (Pl. 5, Figs. 4, 5). The pores extend through the test except locally near the aperture on the ventral side (Pl. 5, Fig. 6). The diameter of pores on the final chamber vary from 4 to 6 μm. Sutures are

→

PLATE 7

Late Miocene Forms

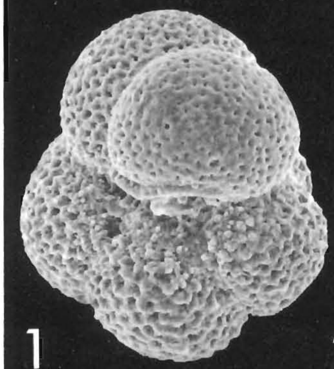
1–7 *Neogloboquadrina pachyderma* (Ehrenberg), (=*Globorotalia pseudopachyderma* Cita, Premoli-Silva and Rossi). Type Tortonian (late Miocene), Italy. 1. Reticulate form. Hypotype, ventral view. ×175. 2. Specimen showing reticulate surface on final chamber which on successively earlier chambers is replaced by crystalline crust. Also note the distinct apertural plate showing morphological resemblance to *N. acostaensis*. ×191. 3. Crystalline form. Hypotype, ventral view. ×188. 4. Reticulate form. Hypotype, dorsal view. × 184. 5. Surface of penultimate chamber of Figure 4. Note the deep pore pits and microcrystalline surface. ×1,188. 6. Surface of the antepenultimate chamber of Figure 3. Note the penetration twin of the rhombohedrons producing stellate-patterned surface, identical to Recent crystalline form of *N. pachyderma*. ×1,313. 7. Surface of final chamber of Figure 3. Crystals on final chamber are much smaller than on earlier chambers (Figure 6), and they cluster around the pores. The pore pits are deep and funnel shaped. ×1,313.

8, 9 *Neogloboquadrina pachyderma* (Ehrenberg). 8. Reticulate form, ventral view; DSDP, Leg 29, Site 284, 22-6-40 (latest Miocene—Tongaporutuan Stage). ×194. 9, Crystalline form, ventral view; DSDP, Leg 29, Site 284, 16-6-40 (late Miocene—Kapitean Stage). ×194.

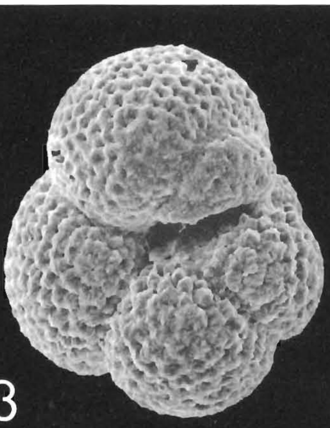
10 *Neogloboquadrina acostaensis* (Blow). Hypotype, ventral view; DSDP, Leg 21, Site 208, 12 CC late Miocene. Note the microcrystalline reticulate surface on final and penultimate chamber and crystalline stellate-patterned crust on earlier chambers characteristic of *N. pachyderma* (compare fig. 3, 9) and yet the form has distinct apertural plate typical of *N. acostaensis*. ×144.

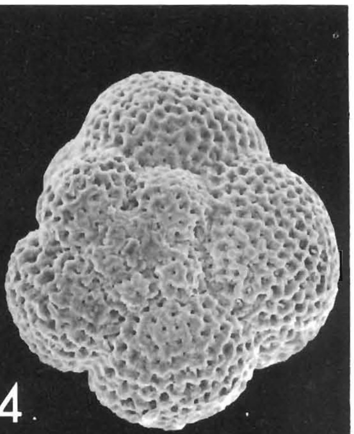
11, 12 Specimen ex interc *N. acostaensis–N. pachyderma*, specimens from DSDP, Leg 29, Site 284, 22-6-40 (late Miocene Tongaporutuan Stage). The nature of aperture, the extended apertural plate, is typical of *N. acostaensis* while the surface ultrastructure (reticulate and crystalline) is identical to *N. pachyderma*. 11. Reticulate form, ventral view. ×169. 12. Crystalline form, ventral view. ×175.

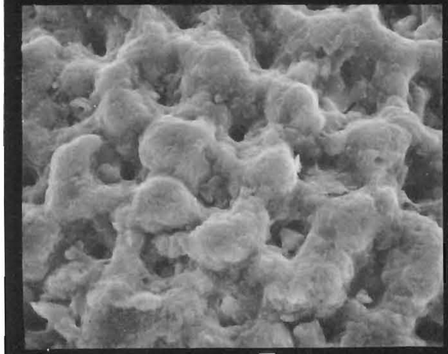
13 Surface of penultimate chamber of sinistral *N. pachyderma*. Location same as Figure 8. Note the distinct reticulate surface with pores located on the flat even area surrounded by steeply rising blunt ridges. ×1,313.

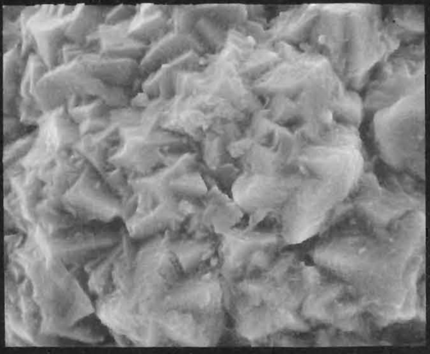

1

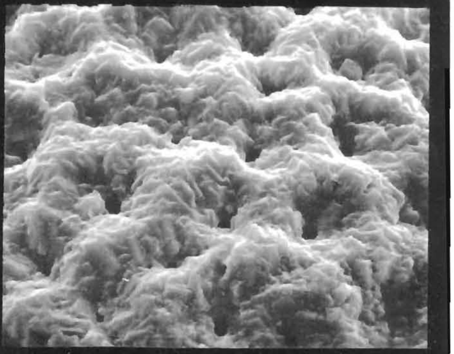

2


3


4

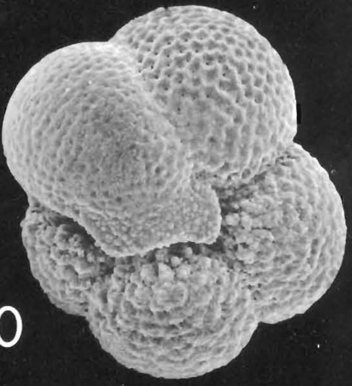

5

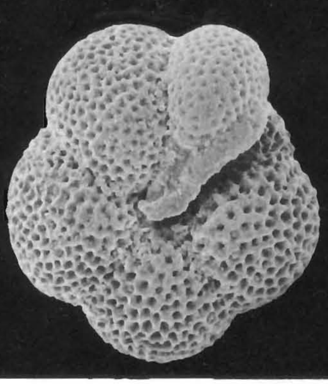

6


7

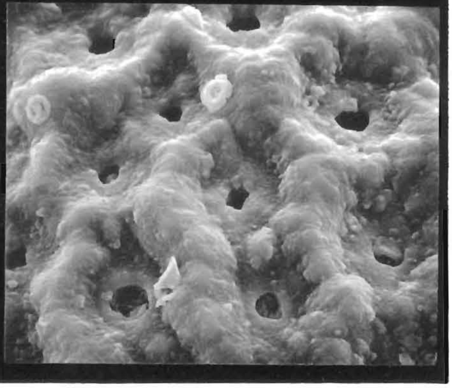

8

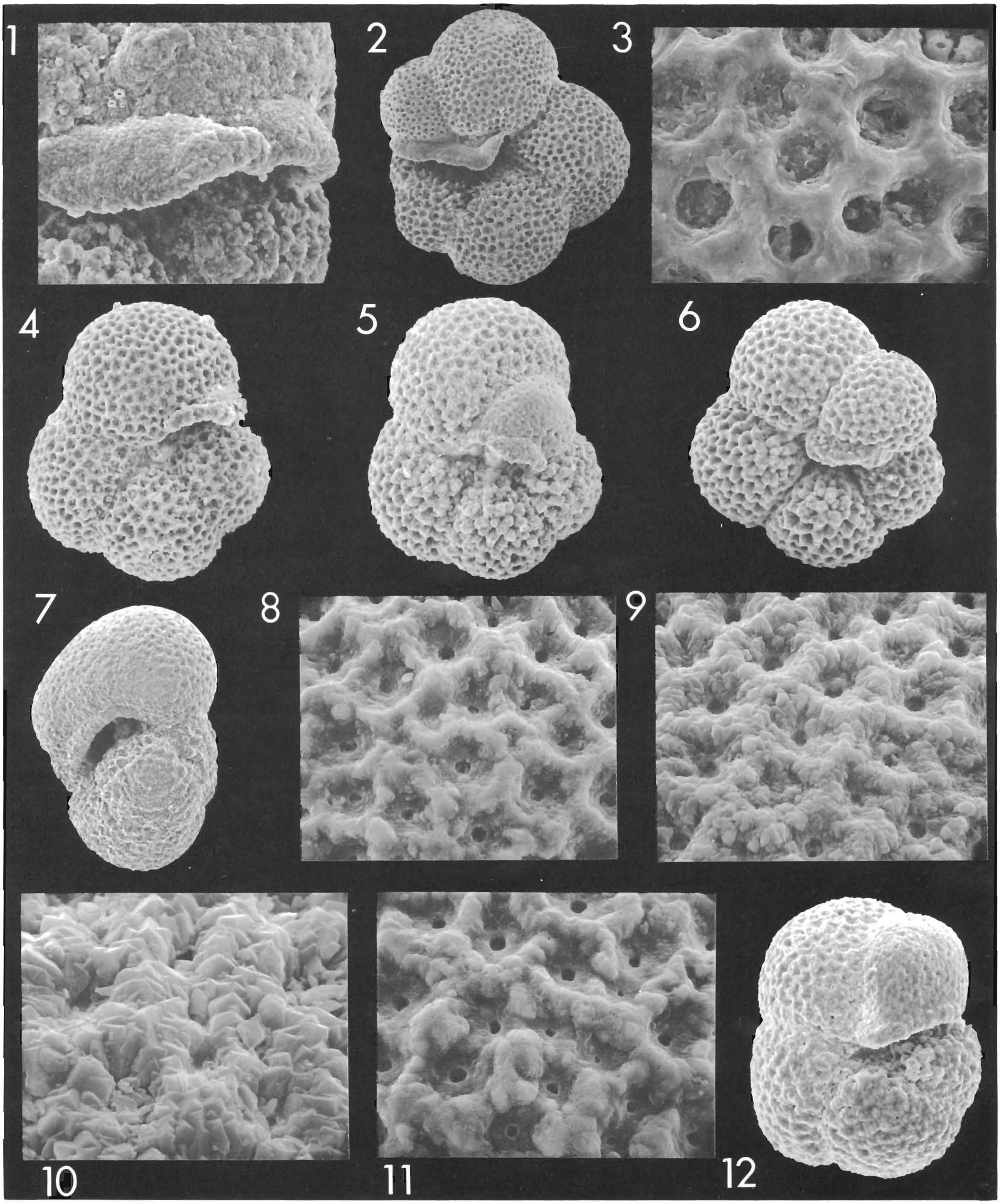

9


10


11


12


13


1
2
3
4
5
6
7
8
9
10
11
12

almost obscured by the high perforation of the test and thick ropelike ridges (Pl. 5, Fig. 3). Like the earlier chambers, the final chamber has mature surface topography. Dextral forms have more heavily encrusted test compared with sinistral forms (Pl. 5, Figs. 6, 7). A single pore is usually located in one pore pit (Pl. 5, Fig. 4). The pores are surrounded by steep-sided irregular ridges of varying heights, giving a spinose surface appearance to the test at low magnifications (Pl. 5, Figs. 1, 2). This feature of the surface led Olsson (1976) to suggest a close relation between the surface structure of *Globigerina bulloides* and *N. pachyderma*. However, no indication of the presence of spines or spine bases characteristic of the surface structure of *G. bulloides* were observed by us in any of the specimens of *N. pachyderma*. Consequently, we believe surface ultrastructures indicate that *N. pachyderma* is unrelated to *Globigerina*.

SURFACE ULTRASTRUCTURES IN THE PLIOCENE

SOUTH PACIFIC

Pliocene populations of *N. pachyderma* from the temperate area of the South Pacific (DSDP Leg 29, Site 284) are dominated by forms with 4.5 chambers in the final whorl and reticulate surface ultrastructure (Pl. 4, Fig. 14). The pores are open even on the earliest chamber, surrounded by secondary spikelike tubercles (Pl. 4, Fig. 12), that superficially resemble spine bases on the surface of *Globigerina*. The apertural rim shows a variation in the Pliocene population examined from typical ropelike apertural rim typical of high latitude *N. pachyderma*, to an apertural plate typical of *N. acostaensis* from tropical to warm subtropical areas. Individuals having 5 chambers in the final whorl with distinct apertural plate and extra umbilical aperture closely resemble *N. acostaensis* (Pl. 5, Fig. 12; Pl. 6, Figs. 1, 2).

In contrast to Site 284, early Pliocene forms in the temperate southern Indian Ocean Site DSDP 264 are almost entirely sinistral and dominated by crystalline wall surface. Coiling changes from sinistral to dextral in the early middle Pliocene to mainly dextral in the Pleistocene. Corresponding to the change in coiling, surface ultrastructure changes from predominantly crystalline in the early Pliocene to predominantly reticulate in the middle and late Pliocene. A similar trend in the surface ultrastructure corresponding to the change in coiling mode is observed in the Pliocene populations at Leg 21, Site 208 (warm subtropical. South Pacific).

←

PLATE 8

Middle and Late Miocene Forms

1 Enlarged view of the apertural plate of a specimen of *N. acostaensis* illustrated on Plate 7, Figure 12. Note that the apertural plate extends onto the penultimate chamber. ×613.

2, 3 *Neogloboquadrina acostaensis* (Blow). 2. Hypotype, ventral view; Neil Island, Bay of Bengal, N 18 (late Miocene). ×138. 3. Enlarged view of the surface of final chamber of Figure 2. Note the high pore density and the microcrystalline reticulate wall diagnostic of tropical form. ×1,388.

4, 7, 10–11 *Globorotalia continuosa* (Blow). 4. Hypotype, ventral view; reticulate form, DSDP, Leg 21, Site 207A; 8-3-75-77 cm, early late Miocene. ×225. 7. Hypotype, side view; crystalline form, DSDP, Leg 21, Site 206, 27 CC, middle Miocene. ×169. 10. Surface of final chamber of *G. continuosa* (Crystalline form). DSDP Leg 21, Site 206, 23 CC, early late Miocene. Note the euhedral calcite rhombs clustering aroung the pores. Note its similarity in the surface structure with *N. pachyderma* (Pl. 6, Fig. 6; Pl. 7, Fig. 7). ×2,000. 11. Surface of final chamber of *G. continuosa* (reticulate form). Location same as Figure 4. Note the similarity in the surface structure with Figure 8. Even the pore diameters are same. ×1,250.

5, 6, 12 Specimens intermediate between *G. continuosa–N. pachyderma*. 5. Ventral view, showing development of abortive or abnormal final chamber positioned over the umbilicus. Also note the similarity in size with *G. continuosa* (Fig. 4). DSDP Leg 21, Site 207A, 8-3-75-77 cm, early late Miocene. ×225. 6. Ventral view showing deep umbilicus and umbilical aperture. DSDP Leg 21, Site 207A; 7-3-75-77 cm, early late Miocene. ×219. 12. Ventral view showing abortive final chamber and yet retaining the aperture characteristic of *G. continuosa*. DSDP Leg 21, Site 206, 27 CC, late middle Miocene. ×213.

8 Surface of final chamber of very early *N. pachyderma* (reticulate form). Location same as Figure 4. Note the similarity in the surface structure with Figure 11. × 1,250.

9 Surface of final chamber of specimen intermediate between *G. continuosa–N. pachyderma* Figure 5. Note the development of secondary calcite crust on the interpore area replacing the original reticulate microcrystalline surface. ×1,313.

NORTH PACIFIC

Late Pliocene populations of *N. pachyderma* from the Nobori Formation, Japan, are dominantly dextrally coiled. Approximately 60 percent of the dextral individuals show crystalline ultrastructure, the rest having a reticulate surface (Pl. 5, Figs. 10–12). The Nobori samples also contain individuals of *N. pachyderma* closely resembling *N. acostaensis* (Pl. 5, Fig. 12). Besides this morphological intergradation, a similarity in the surface ultrastructure between *N. pachyderma* and *N. acostaensis* suggests that these two are related and appear to be linked as a geographical cline in the Pliocene and late Miocene (Srinivasan and Kennett, 1974, 1976).

NORTH ATLANTIC

Early Pliocene populations from the Labrador Sea DSDP Leg 12, Sites 111 and 111A, are slightly dominated by dextral forms, while late Pliocene populations are almost all sinistral. Most individuals examined have a thickly calcified crystalline crust.

Both dextral and sinistral forms from the early Pliocene have a crystalline wall with stellate pattern on earlier chambers (Pl. 6, Figs. 10, 11). In comparison, late Pliocene populations have more highly encrusted walls with flushed sutures. The test is spherical to subspherical (Pl. 6, Figs. 12, 13). The development of crystalline crust on the final chamber is variable. In individuals with crystalline ultrastructure on the final chamber, several small calcite rhombs usually cluster around each pore giving a funnel-shaped appearance to the pore pit (Pl. 6, Fig. 6). In some individuals, on the other hand, the crystals on the final chamber are much longer (6 to 10 μm) and are arranged with the points of intersection of three faces normal to the test surface (Pl. 6, Figs. 7, 8). The projecting ends of the crystal faces give a prickly appearance to the test. Crystal faces have the characteristic coarse facets or growth lines (Pl. 6, Fig. 8). Crystals almost obscure the pores on the final chamber (Pl. 6, Fig. 7), and the rosette-patterned crust is well developed on earlier chambers (Pl. 6, Fig. 9).

STATUS OF "*GLOBIGERINA*" *ATLANTICA* BERGGREN

Berggren (1972) described "*G.*" *atlantica* from the North Atlantic Pliocene sediments cored during DSDP Leg 12, and noted its morphological resemblance to the *N. pachyderma, N. humerosa,* and *N. dutertrei* group. At that time he preferred not to speculate on phylogenetic relations of this form. Surface ultrastructural studies on topotypes of "*Globigerina*" *atlantica,* kindly provided by Drs. W. A. Berggren and R. Z. Poore, indicate that both the reticulate ultrastructure and crystalline ultrastructure diagnostic of *N. pachyderma* are found in "*G.*" *atlantica,* suggesting a close relationship (Pl. 6, Fig. 5). "*Globigerina*" *atlantica* differs from *N. pachyderma,* however, in being consistently larger, having a more open umbilical region and generally lacking an apertural lip (Pl. 6, Fig. 4).

Because of identical surface ultrastructures in *N. pachyderma, N. dutertrei,* and "*G.*" *atlantica* and because of morphological intergradation between these three forms, "*G.*" *atlantica* is here treated as a member of *Neogloboquadrina.*

Neogloboquadrina atlantica is morphologically closest to *N. dutertrei subcretacea* or *N. dutertrei humerosa.* Srinivasan and Kennett (1976) suggested that *N. dutertrei subcretacea* is a cool subtropical phenotypic variant within a Pliocene cline with the tropical to warm subtropical variant represented by *N. dutertrei humerosa.* Srinivasan and Kennett (1976) also consider that *N. dutertrei subcretacea* is an intermediate member of an evolutionary bioseries derived from *N. pachyderma* and ancestral to *N. dutertrei dutertrei* group B (cool subtropical form), while *N. dutertrei humerosa* is an intermediate member of the evolutionary sequence derived from *N. acostaensis* and ancestral to *N. dutertrei dutertrei* group A (tropical form) (Fig. 2).

Surface ultrastructural studies of *N. atlantica, N. dutertrei subcretacea,* and *N. dutertrei humerosa* show that morphologically and ultrastructurally these three taxa intergrade with each other suggesting that they are genetically linked as a cline. However, the North Atlantic Pliocene populations are distinguished from the other members of the cline by the tightly coiled test, with 4.5 to 5 chambers, and large apertural variability. Because of obvious close relations to these forms, *N. atlantica* is considered to be a subspecies of *N. dutertrei,* and to be a North Atlantic representative of a cline that also includes *N. dutertrei subcretacea* as the cool subtropical representative.

Neogloboquadrina dutertrei atlantica is also an intermediate member of the evolutionary bioseries from *N. pachyderma* to *N. dutertrei dutertrei.*

SURFACE ULTRASTRUCTURES IN THE LATE MIOCENE

Specimens of *N. pachyderma* have been examined from the late Miocene of South Pacific DSDP Sites 284 and 207A at intervals that are correlated with the Tongaporutuan and Kapitean Stages of New Zealand.

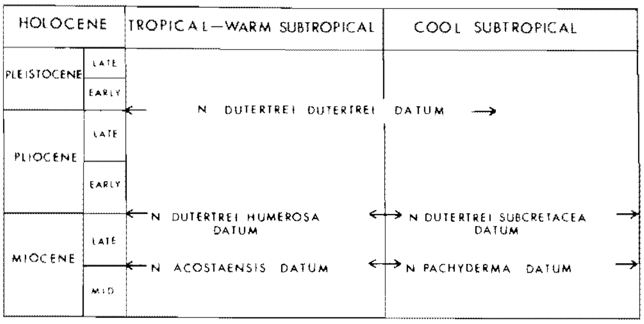


FIGURE 3

Datum planes provided by the evolution of the *Neogloboquadrina* plexus from tropical to cool-subtropical (temperate) regions.

About 95 percent of the specimens in Site 284 are sinistrally coiled and more than 80 percent are kummerforms. Kummerforms range from those with small to those with large abortive chambers (Pl. 7, Figs. 8, 9). In the Kapitean individuals with crystalline crust are dominant, (Pl. 7, Fig. 9) while in the Tongaporutuan individuals with reticulate wall surface predominate (Pl. 7, Fig. 8). The reticulate wall in these earliest representatives of *N. pachyderma* have pore pits surrounded by a flat even area and steeply rising ridges (Pl. 7, Fig. 13), like those with reticulate ultrastructure in high latitude areas. Thus, no surface ultrastructural difference exists between the earliest representatives with reticulate walls and Recent forms from the polar regions. The nature of apertural rim is highly variable, ranging from the characteristic ropelike rim of *N. pachyderma* to the characteristic apertural plate of *N. acostaensis* (Pl. 7, Figs. 8–12), further suggesting that these two are closely related (Srinivasan and Kennett, 1976).

In the late Miocene of DSDP Sites 207A and 206, about 80 percent of the specimens examined have reticulate microcrystalline walls, with the rest being intermediate between reticulate and crystalline. Sinistral forms dominate in the populations. Further to the north within the warm subtropical region DSDP Site 208, late Miocene populations have higher proportions of dextrally coiled forms. Both sinistral and dextral populations have microcrystalline surfaces on final chambers, while on successively earlier chambers they develop a crystalline crust.

STATUS OF *GLOBOROTALIA PSEUDOPACHYDERMA* CITA, PREMOLI-SILVA, AND ROSSI

Cita and others (1965) described *Globorotalia pseudopachyderma* from the Tortonian Stage (late Miocene) of Italy and considered it to be ancestral to *N. pachyderma*. These authors also considered that specimens from the Nobori Formation of Japan and the Mohole Core of southern California to be "*G.*" *pseudopachyderma*. Bandy (1972) included "*G.*" *pseudopachyderma* in synonymy with *N. pachyderma* stating that the Tortonian form falls within the variation of late Miocene to Recent *N. pachyderma*.

Olsson (1973, 1976) suggested that both sinistral and dextral Pliocene forms and dextral forms in the Pleistocene be placed in "*G.*" *pseudopachyderma* and that *N. pachyderma* be restricted to Pleistocene sinistral forms (Fig. 1).

Populations of "*G.*" *pseudopachyderma* examined from the type Tortonian Stage of Italy are almost exclusively sinistral with 80 percent kummerform individuals (Pl. 7, Figs. 1–4). About 95 percent of the specimens have from 4 to 4.5 chambers in the final whorl. The apertural rim in these forms also shows a wide range of variation from the apertural rope typical in *N. pachyderma* to the apertural plate typical of *N. acostaensis*, observed in late Miocene populations of *N. pachyderma* in other areas (Pl. 7, Fig. 2).

Topotypes of "*G.*" *pseudopachyderma* have both the reticulate and crystalline ultrastructure, although crystalline forms dominate (Pl. 7, Figs. 5–7). Therefore, on the basis of ultrastructures and other morphological characters, we conclude that *Globorotalia pseudopachyderma* is a synomym of *N. pachyderma* as Bandy (1972) suggested.

ORIGIN AND DEVELOPMENT OF *NEOGLOBOQUADRINA PACHYDERMA*

Parker (1962) postulated that *N. pachyderma* may have evolved from the *Globorotalia opima-mayeri* group, and Saito (1963) suggested that it may have arisen from *Globigerina angustiumbilicata* Bolli. Jenkins (1967) pointed out the possibility that *N. pachyderma* may have evolved from "*Globorotalia*" *continuosa* Blow in the late Miocene. Bandy and others (1969) and Bandy (1972) also considered *N. pachyderma* to have evolved from "*G.*" *continuosa* Blow and the level of origin in the late Miocene was termed the "*Turborotalia*" *pachyderma* datum (Fig. 3). Olsson (1976) suggested that *N. pachyderma* probably evolved from a globigerinid species in water masses transitional between temperate and tropical areas and feels that it never had a dextral population.

We have observed an evolutionary gradation from "*G.*" *continuosa* to *N. pachyderma* in late middle Miocene to early late Miocene in South Pacific deep-sea drilled sites 207A and 206 ("*G.*" *continuosa* Zone of Kennett, 1973). "*Globorotalia*" *continuosa* changes upwards into *N. pachyderma* by a reduction in size, shape, and position of the final chamber from being larger than the penultimate to the formation of a reduced bulla-like chamber positioned over the umbilicus. The aperture correspondingly changes to a more umbilical position, with the development of a deep umbilicus (Pl. 8, Figs. 5, 6). In the early late Miocene, the test size in *N. pachyderma* is almost the same as in "*G.*" *continuosa*, but becomes successively larger in younger populations.

The surface ultrastructure of *N. pachyderma* and "*G.*" *continuosa* are identical (Pl. 8, Figs. 8–11). We, therefore, support the observations of Jenkins (1967) and Bandy (1972) that *N. pachyderma* evolved from "*G.*" *continuosa* in the early late Miocene (Figs. 2 and 3) and do not support the conclusion of Olsson (1976) who, from a study of the sequence at DSDP Site 36 (northeastern Pacific), considers that *N. pachyderma* first appeared in the early Pleistocene.

CHARACTERISTICS OF "*GLOBOROTALIA*" *CONTINUOSA*

The typical form of "*Globorotalia*" *continuosa* usually has four chambers in the final whorl with a distinct arched aperture and apertural rim (Pl. 8, Figs. 4, 7). The tropical forms are mostly dextral, while warm to cool subtropical forms are dominantly sinistral.

The tropical form of "*G.*" *continuosa* has a distinctly pitted microcrystalline wall and high pore concentration with a diameter of pores ranging from 5 to 7μm (Srinivasan and Kennett, 1976, Pl. 8, Fig. 13). This feature is similar to that of tropical *N. acostaensis* (Pl. 8, Figs. 2, 3). A phylogenetic relationship is indicated by the similarities of the surface ultrastructure of tropical "*G.*" *continuosa* and *N. acostaensis* and by the intergradation of the two forms (Fig. 2).

In warm to cool subtropical forms, the final chamber has a reticulate microcrystalline wall with reduced pore diameter (Pl. 8, Figs. 9–11). This is replaced on earlier chambers by a crystalline crust. Similarity in the surface ultrastructure of "*G.*" *continuosa* and *N. pachyderma* in subtropical regions supports a phylogenetic relationship between the two taxa.

RELATIONSHIP BETWEEN *NEOGLOBOQUADRINA PACHYDERMA* AND *N. ACOSTAENSIS*

Several authors, such as Blow (1959, 1969), Parker (1967), and Lamb and Beard (1972), working with tropical Neogene assemblanges considered "*Globorotalia*" *continuosa* to be ancestral to *N. acostaensis*. On the other hand, Jenkins (1967), Bandy and others (1969), and Bandy (1972) working with temperate assemblages considered "*G.*" *continuosa* to be ancestral to *N. pachyderma*. Recently, Srinivasan and Kennett (1974, 1976) on the basis of surface ultrastructural studies pointed out that *N. acostaensis* is a tropical to warm-subtropical phenotypic variant of a cline with the cool-subtropical to subpolar and polar variant represented by *N. pachyderma* and that both *N. acostaensis* and *N. pachyderma* evolved at the same time from "*G.*" *continuosa*.

The typical tropical form of *N. acostaensis* normally has five chambers in the final whorl arranged in a tight coil, a well-developed apertural plate and no distinct umbilicus. The abortive (kummerform) final chamber common to *N. pachyderma* is also common to *N. acostaensis*. Specimens of *N. acostaensis* from warm-subtropical regions have a less distinct apertural plate than in tropical forms, and the pore density is reduced because of the development of a crystalline crust (Pl. 7, Fig. 10). Some individuals of *N. acostaensis* from cool-subtropical (temerate) areas almost approach *N. pachyderma* with the reduction of the apertural plate to a blunt apertural rim (Pl. 7, Figs. 11, 12). Cita and others (1965) have also observed similar morphological resemblance between *N. acostaensis* and *N. pachyderma* in type Tortonian material. In cool-subtropical areas *N. acostaensis* not only resembles *N. pachyderma* but also has identical surface ultrastructure.

Thus, a continuous latitudinal gradation exists between *N. acostaensis* in tropical areas with high pore density (Pl. 8, Figs. 2, 3) and reticulate microcrystalline wall to *N. pachyderma* in cool-subtropical areas with reduced pore density and stellate-patterned crystalline surface (Pl. 7, Fig. 12). This indicates that these forms are linked as a geographical cline and that differences in the surface ultrastructures between the two "species" are environmentally related rather than reflecting genetic differences.

RELATIONSHIP BETWEEN *NEOGLOBOQUADRINA PACHYDERMA* AND *N. DUTERTREI DUTERTREI*

Strong morphologic similarity between *N. pachyderma* and *N. dutertrei* s.l. was noted by Cifelli (1961, 1965), Parker (1962), Smith (1963), Zobel (1968), and Collen and Vella (1973). Bé (1969) and Bé and Tolderlund (1971) suggested that a complete gradation exists from sinistral *N. pachyderma* in polar waters to dextral *N. pachyderma* in temperate waters to *N. dutertrei* in subtropical and tropical waters.

Srinivasan and Kennett (1976) demonstrated that the ultrastructures are identical in *N. pachyderma* and *N. dutertrei dutertrei* in subtropical stratigraphic sequences in the southwest Pacific. Other morphological characteristics also grade within samples of *N. pachyderma* and *N. dutertrei* (Srinivasan and Kennett, 1976, Pl. 5). Srinivasan and Kennett (1976) consider that *N. dutertrei dutertrei* Group A (tropical form) evolved from *N. acostaensis* (through *N. dutertrei humerosa*), whereas *N. dutertrei dutertrei* Group B (warm to cool subtropical form) developed from *N. pachyderma* (through *N. dutertrei subcretacea*), both ancestral forms being phenotypic variants within the same group and both having previously evolved from "*Globorotalia*" *continuosa* (Fig. 2).

PALEOCEANOGRAPHIC CONSIDERATIONS

Ericson (1959) and Bandy (1959, 1960) first recognized the value of *N. pachyderma* in paleoceanographic studies. Bandy (1967, 1968, 1969, 1971, and 1972) placed much emphasis on coiling-ratio changes for determining paleoclimatic oscillations during the late Cenozoic. From these studies Bandy suggested a paleoclimatic model of late Cenozoic polar contractions and expansions in the circum-Pacific region. Bandy and others (1971) believed that the expansion of polar planktonic faunas during the late Miocene and middle Pliocene were almost as great as the one that occurred during the glacial Pleistocene. Jenkins (1967), Kennett (1967, 1968, 1970), and others also recognized cool and warm cycles in the late Cenozoic sequences based on the evidence of the coiling ratios of *N. pachyderma*.

Our ultrastructural studies of *N. pachyderma* indicate two principal types of surface sculpture that are independent of coiling direction. Reticulate forms are dominant in subantarctic and Arctic populations, while crystalline forms dominate Antarctic and subarctic populations. In subtropical populations, crystalline forms also dominate but are distinguished from the high latitude forms by thinner walls, higher pore concentration, and a lack of rosette-patterned crusts. Differences in the proportions of the two ultrastructural types result from differences in the degree of secondary calcification presumably as a result of environmental differences between the water masses.

Secondary calcification is primarily an adult characteristic within numerous species of planktonic foraminifera, taking place below certain critical water depths. Bé and Ericson (1963) have given 300 to 500 m as the depth below which secondary thickening takes place in living specimens of *Globorotalia truncatulinoides* (d'Orbigny). Orr (1967) notes critical increases in secondary calcification at depths of 120 to 700 m for three other species of *Globorotalia* in the Gulf of Mexico. However, the differences in secondary calcification that we have observed in *N. pachyderma* are not related to changing depths but with differences in water masses. At this time almost nothing is known about the environmental controls on secondary calcification in planktonic foraminifera. What are the environmental factors that reduce secondary calcification in most adult specimens of *N. pachyderma* in both Arctic and subantarctic waters (dominance of reticulate ultrastructure) and yet enhance surface crystallinity in populations from other water masses especially that of the Antarctic region? According to Stapleton (1973), who studied calcification in Recent benthonic hyaline foraminifera, environmental factors including oxygen concentration, pressure, or pH may control the extent to which calcite crust develops in different species. It is important that information be gained on the environmental controls of secondary calcification in planktonic foraminifera. In the meantime, however, surface ultrastructural characteristics in populations from different water masses appear to be more consistent than other morphological features such as chamber number and therefore provide a more reliable criterion for determining paleoceanographic changes. It will be of interest in the future to compare paleoceanographic oscillations determined by ultrastructural variations in populations with interpretations based on coiling direction changes.

SUMMARY AND CONCLUSIONS

1. Stereoscan examination of the test surface of *N. pachyderma* from different water masses throughout the late Cenozoic show the occurrence of two main types of surface ultrastructure.

Reticulate microcrystalline surface structures predominate in Arctic and subantarctic populations, whereas forms with crystalline surfaces predominate in populations from other areas. In Antarctic and subarctic populations the crystalline surface is highly developed with the formation of rosette-patterned crust due to a concentric arrangement of euhedral calcite rhombs. In subtropical populations the crystalline surface is slightly less well developed and hence a stellate-patterned crust formed by penetration twins is most characteristic. Also subtropical forms have higher pore density and thinner walls than Antarctic and subantarctic populations. Intermediate forms with stellate-patterned crust on earlier chambers and microcrystalline reticulate wall on the final chamber link these two types in cool-subtropical areas. The study shows that the surface ultrastructure is independent of coiling mode and is sensitive to the respective water mass conditions because of the control these have on the degree of secondary calcification. However, it is yet uncertain as to what relationship, if any, surface ultrastructural variations in *N. pachyderma* have with coiling-ratio oscillations.

2. Similarity in ultrastructure links subtropical *N. pachyderma* populations to temperate populations of *N. pachyderma* from the late Miocene to Recent as one phylogenetic species. Therefore, the separation of the plexus by Olsson (1973, 1976) into two taxonomic groups as "*Globigerina*" *pachyderma* (Pleistocene polar and subpolar sinistral forms) and "*Globorotalia*" *pseudopachyderma* (dextral forms of the Pleistocene and sinistral and dextral populations of the pre-Pleistocene) is unacceptable.

3. The surface ultrastructure of "*Globigerina*" *incompta* shows the characteristic reticulate microcrystalline surface structure of *N. pachyderma*. No distinct differences occur in the surface ultrastructure of "*G.*" *incompta* and *N. pachyderma*, hence "*G.*" *incompta* Cifelli is considered as a synonym of *N. pachyderma*.

4. Because of similar and gradational surface ultrastructural and other characteristics between *N. pachyderma*, *N. dutertrei dutertrei*, and "*Globigerina*" *atlanctica*, "*G.*" *atlantica* is placed in *Neogloboquadrina*. Surface ultrastructural examinations of *N. atlantica*, *N. dutertrei subcretacea*, and *N. dutertrei humerosa* suggest that these forms intergrade with each other as a Pliocene cline. *Neogloboquadrina atlantica* is retained as a subspecies of *N. dutertrei*, characteristic of the Pliocene of the North Atlantic area.

5. Examination of late middle Miocene to early late Miocene deep-drilled sequences in the south Pacific has revealed morphologically intergrading populations between "*Globorotalia*" *continuosa* and *N. pachyderma* strongly suggesting that "*G.*" *continuosa* is the ancestral form of *N. pachyderma*.

6. A continuous gradation exists in late Miocene to early Pliocene sequences from *N. acostaensis* in tropical areas with high porosity and pitted microcrystalline wall to typical temperate *N. pachyderma* with reduced pore density and stellate-patterned surface. *Neogloboquadrina acostaensis* is considered to be a tropical to warm subtropical phenotypic variant of a cline with the temperate to polar variant represented by *N. pachyderma*. Both *N. acostaensis* and *N. pachyderma* evolved from "*G.*" *continuosa* in the early late Miocene. Co-existence of *N. acostaensis* and *N. pachyderma* in Neogene assemblages indicate a warmer temperate environment.

7. Surface ultrastructures are identical in *N. pachyderma* and *N. dutertrei dutertrei* populations from subtropical sequences in the South Pacific. This, in addition to morphological intergradation between *N. pachyderma* and *N. dutertrei*, strongly suggest that these two forms are genetically linked as a cline.

ACKNOWLEDGMENTS

Specimens of *N. pachyderma* and "*Globigerina*" *atlantica* from the North Atlantic cores were supplied by Drs. W. A. Berggren and R. Z. Poore; Dr. R. K. Cifelli provided specimens of "*G.*" *incompta* and Dr. Ronald Echols provided us with DSDP Leg 19 samples. Specimens of *N. pachyderma* from the Canadian Arctic were supplied by Dr. G. Vilks. Mr. Donald Scales assisted in the operation of the scanning electron microscope and Ms. Annette Doherty assisted in making the plates. Photographic work was carried out by Dennis S. Cassidy and secretarial work by Ms. Nancy Meader.

The scanning electron microscope facility at the University of Rhode Island was established with the assistance of a grant from the National Science Foundation (Oceanography Division; GA-28905). This research was supported by National Science Foundation Grant GA-35252.

REFERENCES

Bandy, O. L. 1959, The geologic significance of coiling ratios in the foraminifer *Globigerina pachyderma* (Ehrenberg): Geol. Soc. America Bull., v. 70, p. 1708 (abs.).

———, 1960, The geologic significance of coiling ratios in the foraminifer *Globigerina pachyderma* (Ehrenberg): Jour. Paleontology, v. 34, p. 671–681.

———, 1967, Foraminiferal definition of the boundaries of the Pleistocene in Southern California, U.S.A., *in* Sears, M., ed., Progress in Oceanography: New York, Pergamon Press, v. 4, p. 27–49.

———, 1968, Cycles in Neogene Palaeoceanography and eustatic changes: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 5, p. 63–75.

———, 1969, Relationships of Neogene planktonic foraminifera to paleoceanography and correlation: Internat. Conf. Planktonic Microfossils, 1st, Geneva (1967), Proc, v. 1, p. 46–57.

———, 1971, Definition of Upper Miocene Neogene Zone 18, Mohole, Guadalupe site: Nature, v. 233, p. 476–478.

———, 1972, Origin and development of *Globorotalia* (*Turborotalia*) *pachyderma* (Ehrenberg): Micropaleontology, v. 18, p. 294–318.

Bandy, O. L., Butler, E. A., and Wright, R. C., 1969, Alaskan Upper Miocene glacial deposits and the *Turborotalia pachyderma* datum plane: Science, v. 166, p. 607–609.

Bandy, O. L., Casey, R. E., and Wright, R. C., 1971, Late Neogene planktonic zonation, magnetic reversals, and radiometric dates, Antarctic to the tropics, *in* Reid, J. L., ed., Antarctic Oceanology I: Am. Geophys. Union, Antarctic Research Series, v. 15, p. 1–26.

Bandy, O. L., and Theyer, F., 1971, Growth variation in *Globorotalia pachyderma* (Ehrenberg): Antarctic Jour., v. 6, p. 172–174.

Bé, A. W. H., 1960, Some observations on Arctic planktonic Foraminifera: Jour. Foram. Research, v. 11, p. 64–68.

———, 1969, Planktonic Foraminifera: New York, Am. Geographic Soc., Antarctic Map Folio Series, Folio 11, p. 9–12.

Bé, A. W. H., and Ericson, D. B., 1963, Aspects of calcification in planktonic foraminifera (Sarcodina), *in* Comparative Biology of Calcified Tissues: New York Acad. Sci. Ann., v. 109, p. 65–81.

Bé, A. W. H., and Tolderlund, D. S., 1971, Distribution and ecology of living planktontic Foraminifera in surface waters of the Atlantic and Indian Oceans, *in* Funnell, B. M., and Reidel, W. R., eds., The Micropaleontology of the Oceans: Cambridge, Cambridge Univ. Press, p. 105–149.

Bé, A. W. H., Vilks, G., and Lott, L., 1971, Winter distribution of planktonic foraminifera between the Grand Banks and the Caribbean: Micropaleontology, v. 17, p. 31–42.

Berggren, W. A., 1972, Cenozoic biostratigraphy and paleobiogeography of the North Atlantic: Deep Sea Drilling Proj., v. 12, p. 965–1001.

Berger, W. H., 1969, Anaerobic basin sedimentation and differential preservation of planktonic foraminifera [abs.]: Am. Assoc. Petroleum Geologists Bull., v. 53, p. 468–469.

———, 1970, Planktonic Foraminifera: Differential productivity and expatriation off Baja California: Limnology and Oceanography, v. 15, p. 183–204.

Blow, W. H., 1959, Age, correlation and biostratigraphy of the Upper Tocuyo (San Lorenzo) and Pozon Formations, eastern Falcon, Venezuela: Bull. Am. Paleontology, v. 39, p. 67–251.

———, 1969, Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy: Internat. Conf. Planktonic Microfossils, 1st, Geneva (1967), Proc., v. 1, p. 199–422.

Boltovskoy, E., 1969, Living planktonic Foraminifera at the 90° E meridian from the equator to the Antarctic: Micropaleontology v. 15, p. 237–255.

———, 1971a, Ecology of the planktonic foraminifera living in the surface layer of Drake passage: Micropaleontology, v. 17, p. 53–68.

———, 1971b, Planktonic Foraminiferal assemblages of the Epipelagic Zone and their Thanatocoenoses, *in* Funnel, B. M., and Riedel, W. R., eds., The Micropaleontology of the Oceans: Cambridge, Cambridge Univ. Press, p. 277–288.

Cifelli, R., 1961, *Globigerina incompta*, a new species of pelagic foraminifera from the North Atlantic: Cushman Found. Foram. Research Contr., v. 12, pt. 3, p. 83–86.

———, 1965, Planktonic Foraminifera from the Western North Atlantic: Smithsonian Misc. Colln., v. 148, p. 1–36.

———, 1973, Observations on *Globigerina pachyderma* (Ehrenberg) and *Globigerina incompta* Cifelli from the North Atlantic: Jour. Foram. Research v. 3, p. 157–166.

Cifelli, R., and Smith, R. K., 1969, Problems in the distribution of Recent planktonic Foraminifera and their relationships with water-mass boundaries in the North Atlantic: Internat. Conf. Planktonic Microfossils, 1st, Geneva (1967), Proc., v. 2, p. 68–81.

———, 1970, Distribution of planktonic Foraminifera in the vicinity of the North Atlantic current: Smithsonian Inst., Contr. Paleobiology, p. 1–52.

Cita, Maria B., Premoli-Silva, Isabella, and Rossi, R., 1965, Foraminiferi planctonici del Tortoniano-tipo: Riv. Italiana Paleontologia Stratigrafia, v. 71, p. 217–309.

Collen, J. D., and Vella, P., 1973, Pliocene planktonic Foraminifera, southern North Island, New Zealand: Jour. Foram. Research v. 3, p. 13–29.

Ericson, D. B., 1959, Coiling direction of *Globigerina pachyderma* as a climatic index: Science, v. 130, p. 219–220.

Herb, R., 1968, Recent planktonic Foraminifera from sediments of the Drake Passage, Southern Ocean: Ecologae Geol. Helvetiae, v. 61, p. 467–480.

Hunkins, K., Bé, A. W. H., Opdyke, N. D., and Mathieu, G., 1971, The Late Cenozoic history of the Arctic Ocean, *in* Turekian, K. K., ed., The Late Cenozoic Glacial Ages: New Haven, Yale Univ. Press, p. 215–237.

Ingle, J. C., Jr., 1967, Foraminiferal biofacies variation and the Miocene-Pliocene boundary in Southern California: Bull. Am. Paleontology, v. 52, p. 217–394.

Jenkins, D. G., 1967, Recent distribution, origin and coiling ratio changes in *Globorotalia pachyderma* (Ehrenberg): Micropaleontology, v. 13, p. 195–203.

Kennett, J. P., 1967, Paleo-oceanographic aspects of the foraminiferal zonation in the Upper Miocene-Lower Pliocene of New Zealand, *in* Committee on Neogene, 4th International Congress, Bologna: Gior. Geologia, v. 35, no. 2, p. 143–156.

———, 1968, Latitudinal variation in *Globigerina pachyderma* (Ehrenberg) In surface sediments of the southwest Pacific Ocean: Micropaleontology, v. 14, p. 305–318.

———, 1969, Distribution of planktonic Foraminifera in surface sediments southeast of New Zealand: Internat. Conf. Planktonic Microfossils, 1st, Geneva (1967), Proc., v. 2, p. 307–322.

———, 1970, Comparison of *Globigerina pachyderma* (Ehrenberg) in Arctic and Antarctic areas: Cushman Found. Foram. Research Contr., v. 21, pt. 2, p. 47–49.

———, 1973, Middle and Late Cenozoic planktonic foraminiferal biostratigraphy of the southwest Pacific—DSDP Leg 21: Deep Sea Drilling Proj., v. 21, p. 575–639.

Keller, G., 1978, Morphologic Variation of *Neogloboquadrina pachyderma* (Ehrenberg) in sediments of the marginal and central northeast Pacific Ocean and paleoclimatic interpretation: Jour. Foram. Research, v. 8, p. 208–224.

Lamb, J. L., and Beard, J. H., 1972, Late Neogene planktonic foraminifers in the Caribbean, Gulf of Mexico and Italian Stratotypes: Kansas Univ. Paleontol. Contr. Art. 57 (Protozoa 8), p. 1–67.

Olsson, R. K., 1971, Pliocene-Pleistocene planktonic foraminiferal biostratigraphy of the Northeastern Pacific: Internat. Conf. Planktonic Microfossils, 2nd, Rome (1970), Proc., v. 1, p. 921–928.

———, 1973, Pleistocene history of *Globigerina pachyderma* (Ehrenberg) in Site 36, Deep Sea Drilling Proj., Northeastern Pacific [abs.]. Am. Assoc. Petroleum Geologists Bull., v. 57, p. 798.

———, 1976, Wall structure, topography, and crust of *Globigerina pachyderma* (Ehrenberg), *in* Takayanagi, Y., and Saito, T., eds., Progress in micropaleontology: Selected papers in honor of Prof. Kiyoshi Asano: New York, Micropaleontology Press, p. 244–257.

ORR, W. N. 1967, Secondary calcification in the foraminifera genus *Globorotalia*: Science, v. 157, p. 1554–1555.

PARKER, F. L., 1962, Planktonic foraminiferal species in Pacific sediments: Micropaleontology, v. 8, p. 219–254.

———, 1967, Late Tertiary biostratigraphy (Planktonic foraminifera) of tropical Indo-Pacific deep-sea cores: Bull. Am. Paleontology, v. 52, p. 115–208.

PARKER, F. L., and BERGER, W. H., 1971, Faunal and solution patterns of planktonic Foraminifera in surface sediments of the South Pacific: Deep-Sea Research, v. 18, p. 73–107.

SAITO, T., 1963, Miocene Planktonic foraminifera from Honshu, Japan: Tohoku Univ. Sci. Rept., Ser. 2 (Geol.), v. 35, p. 123–209.

SMITH, B. A., 1963, Distribution of living planktonic foraminifera in the Northeastern Pacific: Cushman Found. Foram. Research Contr., v. 14, p. 1–15.

SRINIVASAN, M. S., and KENNETT, J. P., 1974, SEM ultrastructural variation in planktonic Foraminifera: value in evolution and phenotypic studies: Am. Assoc. Petroleum Geologists Bull., Ann. Mtg. abstracts, v. 1, p. 86.

———, 1976, Evolution and phenotypic variation in the Late Cenozoic *Neogloboquadrina dutertrei* plexus, *in* Takayanagi, Y., and Saito, T., eds., Progress in micropaleontology: Selected papers in nonor of Prof. Kiyoshi Asano: New York, Micropaleontology Press, p. 329–355.

STAPLETON, R. P., 1973, Ultrastructure of tests of some Recent benthic Hyaline Foraminifera: Palaeontographica, Abt. A, Band 142, p. 16–49.

STEHMAN, C. F., 1972, Planktonic Foraminifera in Baffin Bay, Davis Strait and the Labrador Sea: Maritime Sediments, v. 8, p. 13–19.

UJIIE, H., and ICHIKURA, M., 1973, Holocene to uppermost Pleistocene Planktonic foraminifers in a Piston Core from off SAN'IN District, Sea of Japan: Palaeont. Soc. Japan Trans. Proc., N.S., No. 91, p. 137–150.

VELLA, P., 1974, Coiling ratios of *Neogloboquadrina pachyderma* (Ehrenberg); Variations in different size fractions: Geol. Soc. America Bull., v. 85, p. 1421–1424.

ZOBEL, B., 1968, Phanotypische Varianten von *Globigerina dutertrei* d'Orbigny (Foram.): ihre Bedeutung für die Stratigraphie in quärtaren Tiefsee-Sedimenten: Geol. Jahrb., v. 85, p. 97–122.

———, 1973, Biostratigraphische Untersuchungen an Sedimenten des Indisch-Pakistanischen Kontinentalrandes (Arabisches Meer): "Meteor" Forsch. Ergebnisse, Reihe C, No. 12, Seite 9–73, Berlin, Stuttgart.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 163–195, 1980

CENOZOIC PALEOBATHYMETRY AND DEPOSITIONAL HISTORY OF SELECTED SEQUENCES WITHIN THE SOUTHERN CALIFORNIA CONTINENTAL BORDERLAND

JAMES C. INGLE, JR.
Department of Geology, School of Earth Sciences, Stanford University, Stanford, California 94305

ABSTRACT

Analyses of foraminiferal biofacies and lithofacies within thick Cenozoic sequences exposed in the Santa Ynez Mountains, Ventura Basin, Santa Rosa and San Miguel Islands, Palos Verdes Hills, and the Santa Ana Mountains-San Joaquin Hills area of southern California clearly delineate major Paleogene and Neogene depositional cycles characterizing the tectonically complex portion of the Pacific rim assigned to the Southern California Continental Borderland. Emphasis is placed on estimated upper depth limits of selected species of benthonic foraminifera in reconstructing paleobathymetry of each of six sequences analyzed, with integrated assessment of modern microfaunal and sedimentologic patterns allowing identification of up to 40 lower bathyal through littoral paleoenvironmental boundaries. Each sedimentary column and associated paleobathymetric-paleoenvironmental curve is plotted both in relation to maximum unit thickness and to an updated Cenozoic time scale utilizing available planktonic zonal criteria, radiometric ages, and magnetostratigraphy. The lithostratigraphic-chronostratigraphic plots yield estimated rates of uplift, subsidence, and sediment accumulation for each paleoenvironmental segment identified (basin plain, slope, shelf, etc.), reflecting interplay between tectonic and depositional events during Paleogene and Neogene basin-filling episodes in the northern and eastern portions of the borderland. Paleogene deep marine sedimentation in this region was focused in an east-west trough (Santa Barbara Embayment) in the area of the present Santa Ynez Mountains and northern Channel Islands. Filling of this depocenter was slow during Late Cretaceous through early Eocene time when lower bathyal (≥2,000 m) basin plain and distal fan deposits accumulated at rates of 20–50 m/m.y. balanced by equally slow subsidence. Subsequently, great wedges of outer, middle, and supra fan sediments filled the trough from the north and east at rates of 200–300 m/m.y. during the middle Eocene. This accelerated to 500 m/m.y. during the late Eocene as subsidence waned to less than 100 m/m.y. and slope, shelf, and littoral facies transgressed westward over proximal fan and base-of-slope deposits. A tectonic pause accompanied by widespread nonmarine deposition and erosion occurred over the southern California margin during the Oligocene aided by a global eustatic event. Nonmarine deposition was terminated by abrupt and widespread subsidence (150–500 m/m.y.) during the latest Oligocene-early Miocene coincident with initiation of equally dramatic tectonic events elsewhere around the Pacific rim. Rapid subsidence produced a series of effectively silled middle bathyal Miocene basins momentarily deficient in terrigenous debris allowing relatively undiluted deposition of prolific numbers of diatom frustules from highly productive surface waters. Most middle to late Miocene basin sills hovered at depths within the oxygen minimum zone creating oxygen deficient (0.1–0.5 ml/l.) subsill water, effectively excluding well-developed megainvertebrate faunas capable of destroying bedding and thus facilitating accumulation and preservation of diatomaceous muds and laminated diatomites (Monterey Formation). Tectonic reorganization of the Miocene borderland basins began in late Miocene-early Pliocene time with further subsidence to lower bathyal depths in some synclinal areas. In addition, an increasing influx of terrigenous material in the form of local fan lobes and fine-grained detritus diluted diatom frustules and capped underlying diatomites with early Pliocene mudstones and distal sands. Major flexing of the borderland occurred about 3 m.y. ago (middle Pliocene) marked by rapid uplift (400–1,000 m/m.y.) of anticlinal interbasin ridges and borderland margins as illustrated in the Palos Verdes Hills and Santa Ana Mountains-San Joaquin Hills sequences. This same event was accompanied by dramatic increases in rates of sedimentation (>2,000 m/m.y.) and subsidence (> 1,000 m/m.y.) in synclinal nearshore depocenters such as the Los Angeles and Ventura basins. Both of these basins were filled to capacity by the late Pleistocene as signaled by rapid reductions in rates of sediment accumulation and subsidence (<1,000 m/m.y.). A major late Pleistocene tectonic episode then deformed borderland margins, basin sills, and interbasin ridges to their present configuration initiating modern depositional patterns.

INTRODUCTION

The spectacularly thick sequences of Cenozoic marine sediments housed within the coastal mountains and basins of southern California have been scrutinized via pick and drill for more than a century. These studies have resulted in an impressive body of data bearing on the tectonic and depositional history of this region. Moreover, it was early recognized that these deposits have their direct analogues within the complex of submarine environments forming the modern continental borderland of southern California (Bagg, 1907; Natland, 1933); this relationship has been vigorously exploited during the past 40 years to the point where the region effectively serves as a natural geologic laboratory. Emery's 1960 summary of the borderland still stands as a prime source of information on the marine geology and oceanography of this region; however, the appearance of new geologic, geophysical, and paleontologic concepts, tools, and techniques continues to force a recasting of older ideas concerning the evolution of this complex margin. The emergence of seismic reflection profiling and the paradigm of plate tectonics have been especially critical in this respect (e.g., Yeats, 1968; Moore, 1969; Atwater, 1970; Crowell, 1974; Vedder and others, 1974; Snyder, Dickinson, and Silberman, 1976). In addition, advances in local and worldwide planktonic biostratigraphy, magnetostratigraphy, and chronostratigraphy (Berggren, 1969, 1972; Berggren and Van Couvering, 1974) necessitate a recalibration of provincial biostratigraphic units including those in use in California that ultimately affect estimates of timing and duration of tectonic and depositional events. Finally, recent concepts of paleoenvironmentally diagnostic lithofacies packages (e.g., Selley, 1970; Walker and Mutti, 1973; Dott and Shaver, 1974) and stratigraphic/depositional cycles (Dickinson and Graham, 1975) provide powerful interpretive models with which to analyze margin history.

This report represents an attempt to utilize aspects of all these interpretative tools and insights to reconstruct depositional histories of six well-studied Cenozoic surface sections exposed along the margin of southern California (Fig. 1). Methods of analysis are briefly reviewed and particular emphasis is placed on the use of benthonic foraminiferal assemblages, lithofacies trends, and an updated chronostratigraphy to illustrate the dynamic interplay between estimated rates of sediment accumulation, subsidence, and paleobathymetric/paleoenvironmental history of the northern and eastern portions of the Southern California Continental Borderland in a series of summary diagrams.

BIOSTRATIGRAPHIC AND CHRONOSTRATIGRAPHIC FRAMEWORK

The provincial Neogene and Paleogene benthonic foraminiferal stages and zones erected by Kleinpell (1938), Natland (1952), and Mallory (1959) comprise the most widely applied means of biostratigraphic age assignment and correlation within Tertiary and Quaternary marine sediments of California. However, recent advances in planktonic biostratigraphy and attendant correlations with the paleomagnetic and radiometric time scales are providing an alternative Cenozoic time scale against which to view regional and worldwide marine events, as ably summarized by Berggren (1972) and Berggren and Van Couvering (1974). The past decade has seen increasing study of planktonic foraminifera and calcareous nannofossils in bathyal marine sequences along the Pacific Coast allowing partial to full recognition of the now well-established low-latitude Cenozoic planktonic biozones in California (Lipps, 1967; Ingle, 1967a, 1973a, 1977a; Bramlette and Wilcoxin, 1967; Wilcoxin, 1969; Schmidt, 1970; Steineck and Gibson, 1971; Lipps and Kalisky, 1972; Bandy, 1972a, b; Bukry, Brabb, and Vedder, 1973; McKeel and Lipps, 1975; Poore and

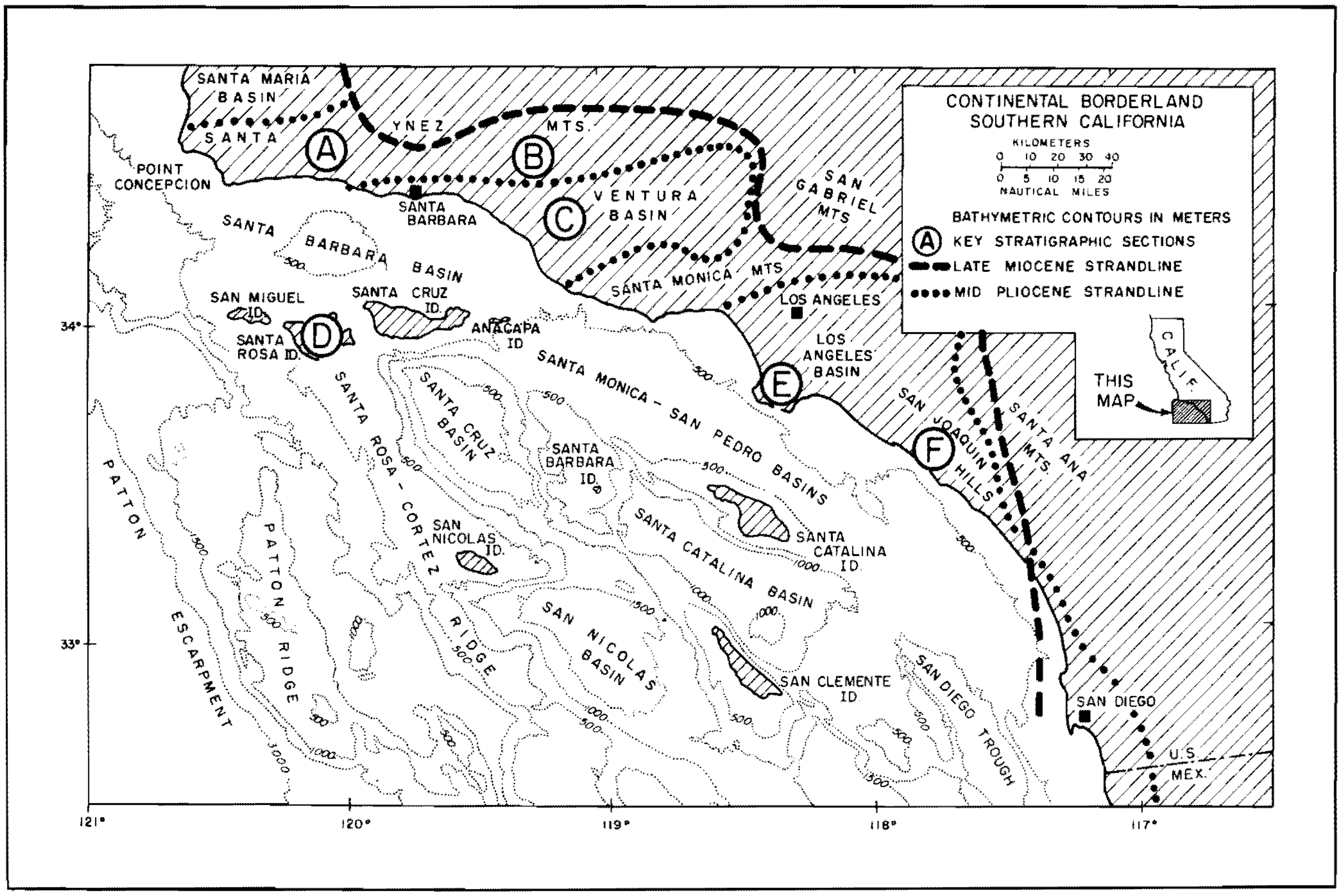


FIGURE 1

Location map illustrating the present bathymetry of the Southern California Continental Borderland, important Cenozoic surface sections referred to in this report, and the approximate positions of the late Miocene and middle Pliocene strandlines.

Brabb, 1977). In addition, studies of the more common mid- to high-latitude calcareous and siliceous plankton within these same sediments have identified a number of useful indices and climatically induced planktonic biofacies trends which allow correlation of both deep sea and marginal basin Neogene sequences from California north to Alaska (Bandy, 1960a, 1967; Ingle, 1967a, 1973a, b, 1976, 1977a; Bandy and Ingle, 1970; Casey, 1972; Schrader, 1973; Casey and Price, 1973; Barron, 1973, 1975; Keller and Ingle, 1977).

One of the more significant and at the same time controversial (Phillips, 1972) results of the increased application of planktonic biostratigraphy in the Pacific Coast region is the recognition by some authors that many if not all of the provincial Cenozoic benthonic foraminiferal stages are time transgressive when viewed against a planktonic biostratigraphic framework (Bandy, 1960a, 1967; Ingle, 1967a; Bandy, 1971; Bukry, Brabb, and Vedder, 1973, 1977; Steineck and Gibson, 1971, 1972; Gibson, 1973). Facies control of benthonic foraminiferal faunas indicative of various Paleogene stages is also suggested by apparent extension, broad overlap, and inversion of ranges of key species (Vedder, 1972; Gibson, 1973). Although more study is needed to establish the magnitude of these discrepancies, the general time-transgressive character of the provincial benthonic foraminiferal stages is implied by slanted stage boundaries in the time scale presented on Figure 2.

Use of planktonic zonal criteria in California has also led to reassessment of provincial Cenozoic epoch and subepoch boundaries with respect to their traditional positions vis-à-vis provincial microfaunal stages. In turn, continuing realignment of various planktonic zones with the paleomagnetic-radiometric scale and the appearance of radiometric dates of vary-

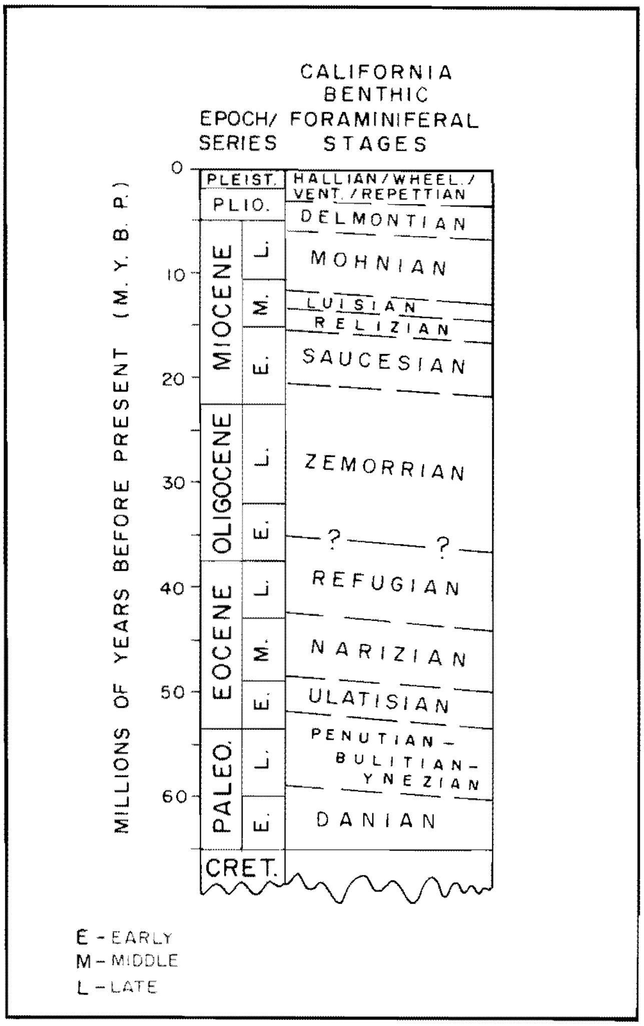


FIGURE 2

Suggested alignment of the provincial Cenozoic microfaunal stages of Kleinpell (1938), Natland (1952), and Mallory (1959) with the radiometric time scale. Placement of series/epoch boundaries as well as chronostratigraphy is based on pertinent radiometric dates in southern California sequences and current correlations of provincial stages with planktonic zonations and, in turn, the paleomagnetic-radiometric time scale of Berggren and Van Couvering (1974). Dashed lines separating the stage boundaries are placed at an angle to the radiometric time scale reflecting accumulating evidence of the time-transgressive nature of faunas defining these units (Ingle, 1967a; Bandy, 1971; Bukry, Brabb, and Vedder, 1973; Gibson, 1973; Bukry, Brabb, and Vedder, 1977; Poore and Brabb, 1977). This figure should be viewed as a working correlation destined for further adjustment as new microfaunal, radiometric, and paleomagnetic data become available. See text for references used in compiling this figure.

ing reliability in the marine Cenozoic of California (Evernden, Savage, Curtis, and James, 1964; Berggren, 1969, 1972; Ingle, 1967a; Bandy and Ingle, 1970; Turner, 1970; Berggren and Van Couvering, 1974) have led to continuing recalibrations of epoch and subepoch boundaries with profound implications for the assessment of timing and duration of Cenozoic tectonic and depositional histories in the Southern California Continental Borderland and elsewhere. Therefore, a state-of-the-art correlation of provincial stages, epoch and subepoch boundaries, and alignment of the radiometric time scale is provided on Figure 2. It is important to emphasize that this biostratigraphic-chronostratigraphic compilation represents a working time scale which will no doubt undergo further adjustments and revisions as new microfaunal, radiometric, and paleomagnetic data become available. This diagram follows the current alignment of standard planktonic biozones and datum planes with the radiometric and paleomagnetic time scales by Berggren and Van Couvering (1974) and, in turn, correlations of the standard planktonic biozones with the provincial benthonic foraminiferal stages of California, incorporating analyses by Lipps (1967, 1972), Bandy and Ingle (1970, Ingle (1973b, 1976, 1977a, c), Schmidt (1970), Steineck and Gibson (1971), Bukry, Brabb, and Vedder (1973), Schrader (1973, 1974), and Gibson (1973).

Radiometric calibration of the provincial benthonic stages includes consideration of the planktonic correlations noted above as well as pre-1973 radiometric Neogene dates from California summarized by Berggren and Van Couvering (1974). The recent fission-track ages reported by Izett, Naeser, and Obradovich (1974) and Boellstorff and Steineck (1975) have particular significance for placement of the Pleistocene-Pliocene and Pliocene-Miocene boundaries with respect to the late Tertiary-Quaternary benthonic stages of Natland (1952) and the Delmontian[1] stage of Kleinpell (1938). These latter dates corroborate planktonic evidence (Ingle, 1973b, 1977a, c), indicating that the base of the Pleistocene, defined in terms of the initial appearance of *Globorotalia truncatulinoides* and the Olduvai paleomagnetic event at 1.8 m.y.B.P.,[2] occurs variously within the Wheelerian, Venturian, and Repettian stages, depending on individual rates of basin subsidence and sedimentation due to the paleoecologic control of foraminiferal assemblages characterizing each of these stages (e.g., Bandy, 1972b; Ingle, 1976). Additional paleomagnetic evidence for these relationships has been recently provided by Blackie and Yeats (1976). The Miocene-Pliocene boundary as defined on the basis of planktonic criteria occurs in the middle

---

[1] The validity of the Delmontian stage has been questioned by Pierce (1972) due to the apparent Mohnian age of the type section of the lower Delmontian stage.

[2] Millions of years before the present.

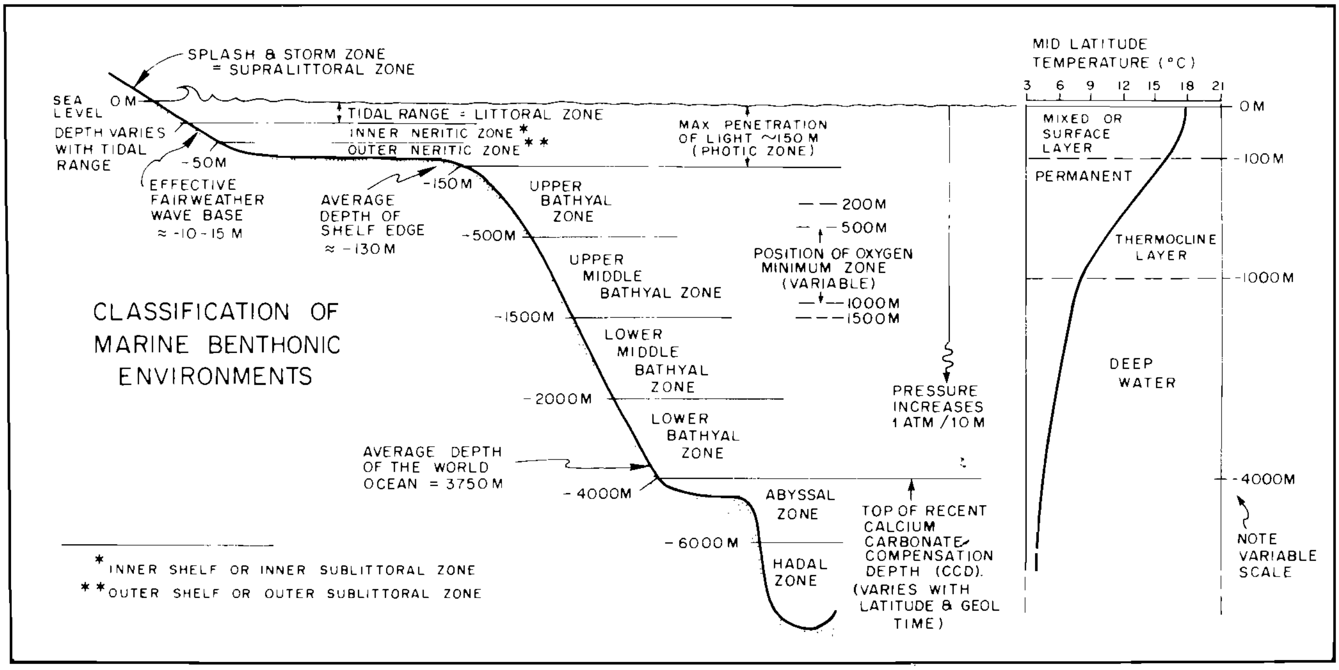


FIGURE 3

Classification of benthonic marine environments in terms of depth and positions of critical oceanographic boundaries or transitional zones in the modern world ocean. Note that water depths are given in meters. This classification is a modification of that presented by Hedgpeth (1957); from Ingle (1975a).

portion of the Delmontian stage (Casey, 1972; Casey and Price, 1973; Ingle, 1973b; Boellstorff and Steineck, 1975) correlative with a radiometric age of 5 m.y.B.P. (Berggren and Van Couvering, 1974). Both revisions have special importance for any analysis or borderland history due to the episodic increases in rates of uplift, subsidence, and sedimentation experienced in this region during the later Neogene (Yeats, 1977).

PALEOENVIRONMENTAL AND PALEOBATHYMETRIC ANALYSIS

Benthonic Marine Environments

The recognition of ancient marine environments in the Cenozoic of southern California and elsewhere is largely dependent on our understanding of the relationships between physical and biologic systems in the modern world ocean, especially those peculiar to continental margin settings. Fortunately, the water mass filling the oceanic "bowl" at any given moment is density stratified due to variations in temperature and salinity with depth produced by latitudinal differences in surface temperature, precipitation, zonal winds, and the production of relatively cold and dense bottom water in polar regions (Sverdrup, Fleming, and Johnson, 1942; Neuman and Pierson, 1966). Additional layers or parcels can be recognized on the basis of the effective penetration of sunlight (photic zone), effective wave base, variations in the amount of dissolved oxygen, etc. (Fig. 3). Ultimately, each of these water mass boundaries or gradients impinges against the continental margin at a known depth or depth range forming key bathymetric horizons which are commonly marked by sharp variations in faunal and sedimentologic parameters, imprinted in the sedimentary record, and preserved. Thus, both modern and fossil biofacies and lithofacies mirror the stratified nature of the marine water column providing readily accessible paleobathymetric/paleoecologic tools.

The stratified character of the world ocean also aids in the classification of benthonic marine environments. The scheme used in this report represents a modified version of the classification proposed by Hedgpeth (1957) with the majority of zonal boundaries drawn at the top or base of important water mass boundaries (Ingle, 1975a; Fig. 3). Consequently, bathymetric terminology (upper bathyal, abyssal, etc.) applied to both

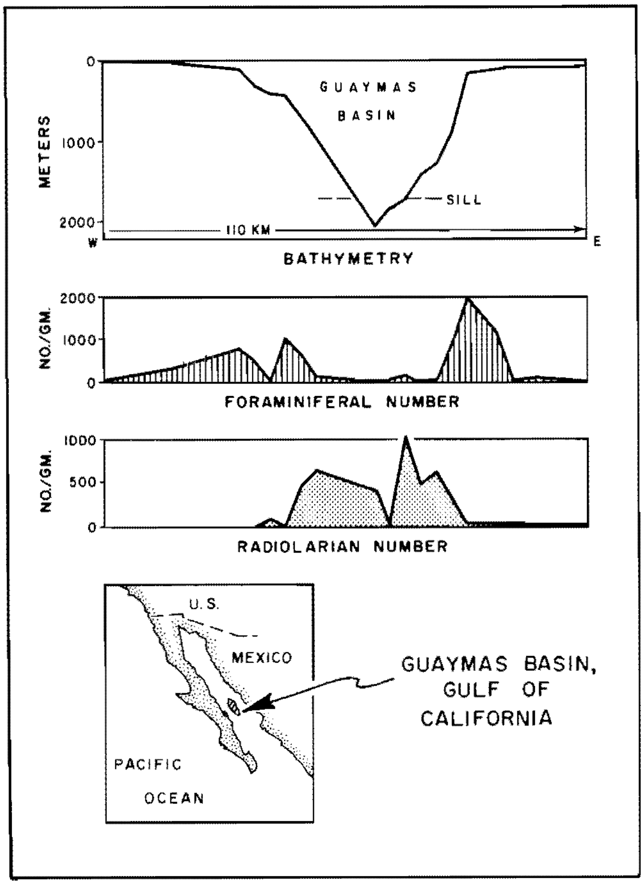


FIGURE 4

Variation in numbers of foraminifers and radiolarians per gram of dry sediment across Guaymas Basin, Gulf of California, Mexico; adapted from Ingle (1967b).

modern and ancient environments takes on some precision with each term implying not only a specific range of water depth but also variations of other parameters as well (Figs. 3 and 4). An example of this relationship is inherent in the definition of the upper middle bathyal zone (500 to 1,500 m) which effectively coincides with the oxygen minimum zone, a parcel of water containing only marginal amounts of dissolved oxygen (0.1–0.5 ml/l) due to oxidation of organic debris derived from high productivity in the overlying photic zone (Richard, 1957). Intersection of this unique water mass with the continental slope and/or basin sills leads to a reduction or exclusion of macrofaunal invertebrates and minimal bioturbation of sediments, resulting in preservation of conspicuously thin-bedded or laminated sediment enriched in organic matter (e.g., Hulesmann and Emery, 1961; Calvert, 1964; Rhodes and Morse, 1971). Critical deeper

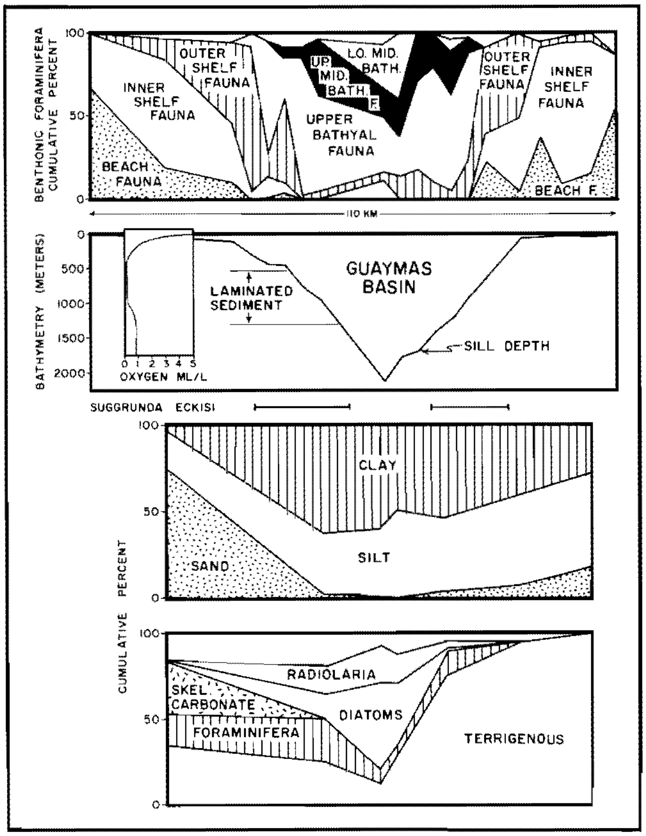


FIGURE 5

Variation of Recent benthonic foraminiferal biofacies, sediments, and dissolved oxygen with depth in Guaymas Basin, Gulf of California, Mexico (Fig. 4), as plotted from data of Bandy (1961), van Andel (1964), and Calvert (1964); figure from Ingle (1967b, 1975a). Note that the limits of the oxygen minimum zone in this basin coincide with the distribution of laminated diatomaceous sediments analogous to Miocene diatomites and siliceous shales assigned to the Monterey, Modelo, and Capistrano formations of southern California. The benthonic foraminifer *Suggrunda eckisi* Natland serves as an index to this oxygen minimum facies (Ingle, 1967a; Phleger and Soutar, 1973) with homeomorphic equivalents such as *S. californica* (Kleinpell) present in analogous Miocene deposits. The horizontal biofacies and lithofacies trends illustrated in this Recent basin are clearly analogous to the vertical (time) trends established in Paleogene and Neogene basinal sequences of southern California and elsewhere around the North Pacific rim.

boundaries include the lysocline (LCD) and the calcium carbonate compensation depth (CCD) at 3,000 to 4,000 m (Berger, 1970, 1974); the top of the abyssal zone (4,000 m) is essentially coincident with the top of the CCD in mid-latitude oceanic areas today. However, the effects of this chemical threshold as well as those expressed by the LCD can be masked or modified by (a) rapid deposition of terrigenous debris in base-of-slope deposits and/or (b) a shallowing of the

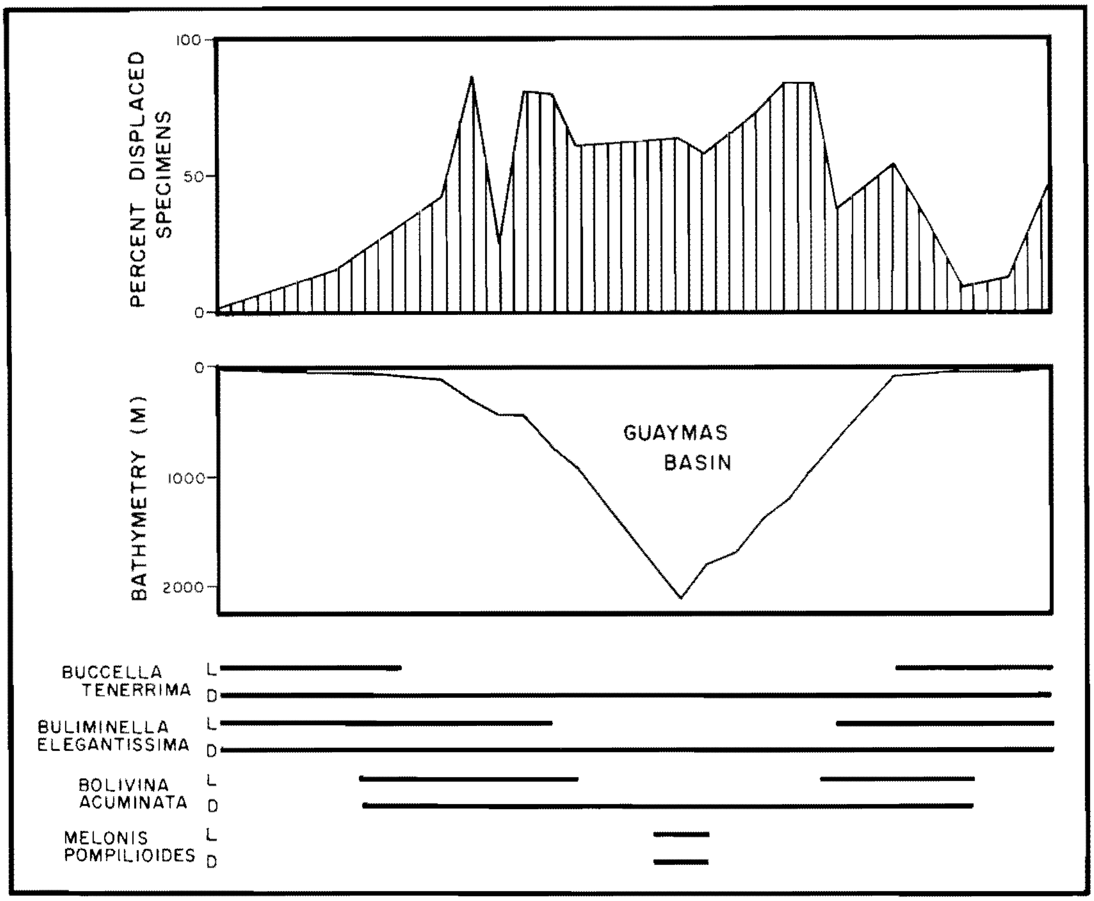


FIGURE 6

Percentages of displaced (redeposited) benthonic foraminifers, distribution of live (L) and dead (D) specimens of selected benthonic foraminifers, and bathymetry across Guaymas Basin, Gulf of California, Mexico (Fig. 4), as plotted from data of Bandy (1961) and Phleger (1964). The importance of upper depth limits in paleobathymetric interpretation are emphasized by the live-dead distributions illustrated.

LCD and CCD surfaces along continental margins (Berger, 1974). Moreover, the CCD and LCD have experienced considerable vertical migration with time (van Andel, 1975) due to major variations in productivity, bottom water migration, and paleoclimatic history, with obvious consequences for paleobathymetric interpretations based on recognition of this facies boundary in the stratigraphic record (e.g., Garrison and Fisher, 1969).

MICROFAUNAL TRENDS

Many microfaunal parameters display systematic trends with depth and distance from strandline as a function of major physical boundaries in the modern ocean as illustrated by patterns in the Gulf of California (Figs. 4–6). Importantly, variations in abundance and character of foraminifera, radiolaria, etc., can be readily assayed in a qualitative or quantitative manner in fossil deposits allowing general differentiation of major paleoenvironments. Trends established at this faunal level reflect large-scale biologic responses and consequently have broad application independent of age and differences expressed at the generic or species level.

Foraminiferal number (number of tests/gram of dry sediment) varies as a function of rate of reproduction and rate of sedimentation, with highest abundances generally associated with the shelf-slope transition where low rates of sedimentation, upwelling, and high productivity combine to form an unusually rich benthonic habitat (Ingle, 1975a). Significantly, the diversity (number of species) of benthonic foraminifera also increases to a maximum in the outer shelf and upper bathyal zones in response to these same optimal conditions. Deeper continental margin environments are characterized by decreasing foraminiferal numbers and diversity; however, anomalously high numbers often occur within individual turbidite units due to downslope redeposition of tests (Figs. 4–6). The relative abundance of planktonic foraminifera represents an additional readily scrutinized parameter, with tests of planktonic species commonly absent or rare in neritic (shelf) deposits. An abrupt increase in abundance and diversity of planktonic foraminifera commonly marks the shelf-slope juncture representing an easily identified biofacies boundary in both modern and ancient sequences (Bandy, Ingle, and Resig, 1964; Ingle, 1975b; Bandy and Arnal, 1969). Additional gross foraminiferal trends include variations in abundance of arenaceous, porcelaneous, and hyaline forms with depth and environment (Bandy, 1960a; Bandy and Arnal, 1960, 1969).

The abundance of radiolarian tests also represents a reliable guide to lower bathyal-abyssal paleodepths (Bandy and Arnal, 1960; Ingle, 1967a, 1975a). Both the relative and absolute abundance of radiolarian tests increase in middle bathyal depths, with radiolarians becoming major faunal constituents at depths greater than 2,000 m (Fig. 4). Dissolution of calcareous foraminiferal tests below the LCD and CCD further exaggerates this ratio below 3,000 m and increases the relative abundance of arenaceous foraminifera.

BENTHONIC FORAMINIFERAL BIOFACIES

Modern foraminiferal faunas have been analyzed from a wide spectrum of Recent marine environments[3] and, although we are still investigating the complex of physical and biologic controls on their distribution, it is apparent that well-established biofacies patterns reflect significant physical boundaries in both Recent and fossil deposits spanning the littoral-to-abyssal gradient (Fig. 5). Distributional patterns reported from mid and low latitudes in the marginal eastern Pacific (e.g., Bandy, 1953, 1961; Bandy and Rodolfo, 1964; Smith, 1964) have particular significance for interpretation of faunas reported from Cenozoic deposits in southern California. Indeed, the pioneering reports of Natland (1933, 1952, 1957) and Bandy (1953) continue to provide premier examples demonstrating the direct relationship between the bathymetric distribution of living benthonic foraminifera off California and the sequential appearance of similar biofacies in late Cenozoic basin through shelf deposits in this same region. Moreover, general morphologic trends established with depth and environment among living benthonic foraminifera have led to the recognition that the structure, composition, and morphology of this group exhibit convergent environmental adaption and evolutionary trends through time (Bandy, 1960b, 1963; Harman, 1964; Theyer, 1971) in turn allowing identification and use of paleoecologically significant homeomorphs and isomorphs for paleobathymetric interpretation of Cenozoic and Mesozoic faunas (Bandy and Arnal, 1960, 1969; Ingle, 1967a, 1972; Sliter and Baker, 1972; Sliter, 1972, 1975).

During this investigation, selected species of benthonic foraminifera commonly reported from the Cenozoic sediments of southern California were assigned to six Neogene and six Paleogene faunal groups representing inner shelf through lower bathyal paleoenvironments (Tables 1 and 2). Assignment of species to bathymetrically defined biofacies is based on the concepts of adaptive morphology and use of isomorphic and homeomorphic relationships proposed by Bandy (1960b), fossil occurrences of living species with known bathymetric tolerances, and recurrent species associations within well-established bathyal deposits (e.g., Anita Formation, Kreyenhagen Shale, Monterey Shale). In addition, the recognition of middle and lower bathyal Paleogene species was aided by reports on Paleogene and Neogene deep-sea assemblages by Beckmann (1953) and Douglas (1973).

It is important to note that there is accumulating evidence demonstrating that deeper bathyal biofacies have undergone vertical and horizontal migration in response to climatically induced changes in bottom water temperature, structure, and flow (Streeter, 1973; Schnitker, 1974); the patterns and limits of these adjustments have significant implications for paleodepth and paleoenvironmental interpretations (Douglas, 1973). In turn, both paleontologic and isotopic evidence indicate that the Cenozoic climatic record is punctuated by major warmings and refrigerations with (a) pervasively warm temperatures during the early Paleogene (late Paleocene-early Eocene), (b) a profound refrigeration and restructuring of surface and deep oceanic circulation during the Oligocene, and (c) a fluctuating but deteriorating climatic pattern in the Neogene produced by high latitude glaciation (Emiliani, 1954, 1956; Dorf, 1955; Bandy, 1960a, 1968; Dorman, 1966, 1968; Devereux, 1967; Ingle, 1967a, 1973b, 1977a, c; Kennett, 1968; Margolis and Kennett, 1971; Saito and van Donk, 1974; Kennett and others, 1975; Shackleton and Kennett, 1975a; Savin, Douglas, and

---

[3] See Ingle (1967a) for a review of pre-1967 studies in the eastern North Pacific and Murray (1973) for a general overview.

TABLE 1

Species composition of Neogene benthonic foraminiferal biofacies.[1]

INNER SHELF[2] BIOFACIES[3]: 0–50 m; 0–150 ft.

Ammonia becarri (Cushman)
Buliminella elegantissima (d'Orbigny)
Buccella frigida (Cushman)
Buccella tenerrima (Bandy)
Cancris auricula (Fichtel and Moll)
Cibicides lobatus (Montagu)
Cibicides fletcheri Galloway & Wissler
Elphidium crispum (Linné)
Elphidium incertum (Williamson)
Elphidium poeyanum translucens Natland
Elphidium granti Kleinpell
Florilus ("Nonion") costiferum (Cushman)
Florilus ("Nonionella") incisus (Cushman)
Hanzawaia basiloba (Cushman)
Nonionella basispinata (Cushman & Moyer)
Nonionella miocenica miocenica Cushman
Nonionella miocenica stella Cushman & Moyer
Nonionella pizarrensis (Berry)
Quinqueloculina akneriana d'Orbigny
Quinqueloculina angulostriata Cushman & Valentine
Quinqueloculina costata d'Orbigny
Quinqueloculina lamarckiana d'Orbigny
Quinqueloculina spp.
Trochammina inflata (Montagu)
Trochammina pacifica Cushman

OUTER SHELF BIOFACIES: 50–150 m; 150–470 ft.

Bolivina acutula Bandy
Bolivina acuminata Natland
Bolivina rhomboidalis (Millett)
Bolivina tongi tongi Cushman
Bolivina tongi filicostata Cushman & McCulloch
Bolivina vaughani Natland
Bulimina marginata denudata Cushman
Buliminella curta Cushman & Parker
Buliminella californica Cushman
Buliminella dubia Barbat & Johnson
Buliminella ecuadorana Cushman & Stevenson
Buliminella semihispida Kleinpell
Buliminella spp.
Cassidulina minuta Cushman[4]
Cassidulina oblonga Reuss[4]
Discorbinella valmonteensis Kleinpell
Gandryina arenaria Galloway & Wissler
Hanzawaia crassisepta (Cushman & Laiming)
Hanzawaia illingi (Nuttal)
Hanzawaia nitidula (Bandy)
Hanzawaia relizensis (Kleinpell)
Loxostomum baculum Bandy
Planulina ariminensis (d'Orbigny)
Planulina baggi Kleinpell
Planulina ornata (d'Orbigny)
Pullenia malkinae Coryell & Mossman
Pullenia salisburyi Stewart & Stewart
Saracenaria beali (Cushman)
Saracenaria spp.
Sigmoilina tenuis (Czjzek)
Trifarina angulosa (Williamson)[4]

TABLE 1

Continued

Trifarina baggi (Galloway & Wissler)[4]
Trifarina occidentalis (Cushman)[4]
Trifarina spp.[4]
Uvigerina juncea Cushman & Todd[4]
Valvulineria casitasensis Kleinpell
Valvulineria depressa Cushman
Valvulineria miocenica Cushman

UPPER BATHYAL BIOFACIES: 150–500 m; 460–1,560 ft.

Baggina california Cushman[4]
Baggina cancriformis Kleinpell[4]
Baggina robusta robusta Kleinpell[4]
Baggina robusta globosa Kleinpell[4]
Baggina subinequalis Kleinpell[4]
Bolivina acuminata Natland
Bolivina advena advena Cushman
Bolivina advena gracilis Cushman & Kleinpell
Bolivina advena ornata Cushman
Bolivina advena striatella Cushman
Bolivina barbarana Cushman & Kleinpell
Bolivina benedictensis Pierce
Bolivina bramletti Kleinpell
Bolivina brevior Cushman
Bolivina californica Cushman
Bolivina davisi Cushman & Ellison
Bolivina decurtata Cushman
Bolivina dunlapi Kleinpell
Bolivina interjuncta Galloway & Wissler
Bolivina marginata Cushman
Bolivina modeloensis Cushman & Kleinpell
Bolivina obliqua Barbat & Johnson
Bolivina pacifica Cushman & McCulloch
Bolivina parva Cushman & Galliher
Bolivina perrini Kleinpell
Bolivina pseudoplicata Heron-Allen and Earland[4]
Bolivina rankini Kleinpell[5]
Bolivina seminuda humilus Cushman & McCulloch[5]
Bolivina spissa Cushman
Bolivina ticensis Kleinpell
Bolivina tumida tumida Cushman
Bolivina tumida cuneata Kleinpell
Buliminella subfusiformis Cushman[5]
Cancris baggi Cushman and Kleinpell[4]
Cassidella bramletti (Galloway and Morrey)
Cassidella californiensis californiensis (Cushman)
Cassidella californiensis grandis (Cushman and Kleinpell)
Cassidella delmonteensis (Cushman and Galliher)
Cassidulina barbarana Cushman and Kleinpell[4]
Cassidulina californica Cushman and Hughes[4]
Cassidulina limbata Cushman and Hughes[4]
Cassidulina lomitensis Galloway and Wissler[4]
Cassidulina margareta Karrer[4]
Cassidulina modeloensis Rankin[4]
Cassidulina monicana Cushman and Kleinpell[4]
Cassidulina norcrossi Cushman[4]
Cassidulina panzana Kleinpell[4]
Cassidulina subglossa quadrata Cushman and Hughes[4]
Cassidulina tortuosa Cushman and Hughes[4]
Cassidulina translucens Cushman and Hughes

TABLE 1

Continued

Cassidulina williami Kleinpell[4]
Cassidulina cornuta (Cushman)
Cibicides mckannai Galloway and Wissler
Cibicides pseudoungerianus (Cushman)
Ehrenbergina compressa Cushman
Eilohedra levicula (Resig)
Epistominella exigua (Brady)
Epistominella subperuviana (Cushman)[4]
Globobulimina pacifica Cushman[5]
Gyroidina altiformis R. E. and K. C. Stewart
Gyroidina subtener (Galloway and Wissler)
Hoeglundina elegans (d'Orbigny)
Loxostomum pseudobeyrichi (Cushman)
Suggrunda californica Kleinpell[5]
Suggrunda eckisi Natland[5]
Suggrunda kleinpelli Bramlette[5]
Trifarina carinata (Cushman)[4]
Uvigerina foxensis Woodring and Bramlette
Uvigerina kernensis Barbat and von Estorff
Uvigerina peregrina Cushman
Uvigerina segundoensis Cushman and Galliher
Uvigerina sparsicostata Cushman and Laiming
Uvigerina subperegrina Cushman and Kleinpell
Uvigerinella californica californica Cushman
Uvigerinella californica appressa Cushman[4]
Uvigerinella californica ornata Cushman
Uvigerinella obesa obesa Cushman
Uvigerinella obesa impolita Cushman and Laiming
Valvulineria californica californica Cushman[4]
Valvulineria californica appressa Cushman[4]
Valvulineria californica obesa Cushman[4]
Valvulineria williams Kleinpell[4]

UPPER MIDDLE BATHYL BIOFACIES:
500–1,500 m; 1,560–4,700 ft.

Ambitropus evax (Bandy)
Bolivina argentea Cushman
Bolivina conica Cushman
Bolivina cuneiformis Kleinpell
Bolivina floridana Cushman
Bolivina girardensis Rankin
Bolivina goudkoffi Rankin
Bolivina granti Rankin
Bolivina hughesi Cushman
Bolivina imbricata Cushman
Bolivina interjuncta Galloway and Wissler
Bolivina marginata multicostata (Cushman)
Bolivina pisciformis Galloway and Morrey
Bolivina pseudospissa Kleinpell
Bolivina salinasensis Kleinpell
Bolivina seminuda seminuda Cushman[5]
Bolivina seminuda foraminifera R. E. and K. C. Stewart[5]
Bolivina semiperforata Martin
Bolivina sinuata Galloway and Wissler
Bolivina spissa Cushman
Bolivina subadvena sulphurensis Cushman and Adams
Bolivina woodringi Kleinpell
Bulimina affinis d'Orbigny
Bulimina carnerosensis Cushman and Kleinpell
Bulimina inflata inflata Sequenza
Bulimina inflata alligata Cushman and Laiming

TABLE 1

Continued

Bulimina microcostata Cushman and Parker
Bulimina pagoda hebespinata R. E. and K. C. Stewart
Bulimina pseudoaffinis Kleinpell
Bulimina rinconensis Cushman and Laiming
Bulimina subacuminata Cushman and Stewart
Bulimina subcalva Cushman and Stewart
Buliminella tenuata (Cushman)
Cassidulina crassa d'Orbigny
Cassidulina delicata Cushman[7]
Cassidulina laevigata laevigata d'Orbigny[7]
Cassidulina laevigata carinata Cushman[7]
Chilostomella ovoidae Reuss[5]
Cibicides spiralis Natland
Concavella (Epistominella) gyroidinaformis (Cushman and Goudkoff)
Dentalina communis (d'Orbigny)
Epistominella capitanensis (Cushman[7] and Kleinpell)
Epistominella pacifica (Cushman)[7]
Glandulina laevigata d'Orbigny
Globobulimina galliheri (Kleinpell)[5]
Globobulimina ovula ovula (d'Orbigny)[5]
Globobulimina ovula pedroana (Kleinpell)[5]
Globobulimina pyrula (d'Orbigny)
Oridorsalis tener (Brady)
Oridorsalis umbonatus (Reuss)
Pullenia quinqueloba (Reuss)
Sighogenerina branneri (Bagg)[6]
Siphogenerina collomi Cushman[6]
Siphogenerina hughesi Cushman[6]
Siphogenerina multicostata Cushman[6] and Jarvis
Siphogenerina nodifera Cushman[6] and Kleinpell
Siphogenerina reedi Cushman[6]
Siphogenerina transversa Cushman[6]
Sphaeroidina bulloides d'Orbigny
Sphaeroidina variabilis Reuss
Uvigerina gallowayi Cushman
Uvigerina gesteri Barbat and von Estorff
Uvigerina hispidocostata Cushman and Todd
Uvigerina hootsi Rankin
Uvigerina joaquinensis Kleinpell
Uvigerina peregrina dirupta Todd
Valvulineria araucana araucana (d'Orbigny)
Valvulineria araucana malagensis Kleinpell

LOWER MIDDLE BATHYAL BIOFACIES:
1,500–2,000 m; 4,700–6,250 ft.

Anomalina salinaensis Kleinpell
Bulimina corrugata Cushman and Siegfus
Bulimina rostrata Brady
Cibicides floridanus (Cushman)
Gyroidina gemma Bandy
Gyroidina heddi (R. E. and K. C. Stewart)
Gyroidina keenani (Cushman and Kleinpell)
Gyroidina multicamerata (Kleinpell)
Gyroidina multilocula Coryell and Mossman
Gyroidina rosaformis (Cushman and Kleinpell)
Gyroidina rotundimargo R. E. and K. C. Stewart
Laticarinata pauperata (Parker and Jones)
Melonis barleeanus (Williamson)[8]
Pullenia bulloides (d'Orbigny)[8]
Pullenia miocenica miocenica Kleinpell[8]

TABLE 1

Continued

Pullenia miocenica globula Kleinpell
Pullenia moorei Kleinpell
Stilostomella adolphina (d'Orbigny)
Stilostomella advena (Cushman and Laiming)
Stilostomella irregularis (Kleinpell)
Stilostomella lepidula (Schwager)
Stilostomella spp.
Uvigerina hispida Schwager
Uvigerina proboscidea Schwager

LOWER BATHYAL BIOFACIES: 2,000 m+; 6,250 ft.+

Cibicides floridanus cushmani Barbat and von Estorff
Cibicides pseudoungerianus evolutus Cushman and Hobson
Gyroidina soldani (d'Orbigny)
Melonis pompilioides (Fitchel and Moll)[9]
Plectofrondicularia advena (Cushman)
Plectofrondicularia californica Cushman and Stewart
Plectofrondicularia miocenica laimingi Kleinpell
Uvigerina senticosa Cushman
Uvigerina senticosa var.

---

[1] Arrangement and interpretation of biofacies follows procedures and principles described by Bandy (1960b, 1961), Bandy and Arnal (1960, 1969), and Ingle (1967a, 1967b, 1973a) with modifications and additions based on reinterpretations of recurring species associations and incorporating additional (post-1972) information on the bathymetric distribution of living species. Each biofacies includes important and/or common late Oligocene, Miocene, Pliocene, and Pleistocene-Holocene benthic species associated with each respective biofacies in surface exposures of Neogene continental borderland sediments. Thus, not all species included within each biofacies are encountered in any given sample nor are all of the species identified to date in Neogene sections included in one of the six biofacies.

[2] The term *shelf* is equivalent to the neritic or sublittoral zone of many authors.

[3] Includes littoral species.

[4] Species exhibiting a transitional distribution from outer shelf to upper bathyal depths and generally indicative of the shelf-edge environment.

[5] Species thought to be indicative of the anaerobic bottom conditions produced by low-oxygen content (less than 0.2 ml/l of oxygen) of ambient water overlying slopes or basin plains and associated with the effects of the oxygen minimum layer (Hulesmann and Emery, 1961; Harman, 1964; Ingle, 1967a; Phleger and Soutar, 1973; Sliter, 1975). The genus *Suggrunda* appears to have a particular affinity for these conditions.

[6] The paleobathymetric significance of middle Tertiary costate-striate species of *Siphogenerina* is not fully resolved. Recurring species associations within progressively shoaling middle Tertiary stratigraphic sequences (e.g., Renz, 1948; Ingle, 1972) suggest that the more heavily costate forms are characteristic of middle bathyal depths with striate forms indicative of upper bathyal-outer shelf depths.

[7] Species exhibiting a transitional distribution from upper bathyal to upper middle bathyal depths.

[8] Species exhibiting transitional distributions from upper middle to lower middle bathyal depths.

[9] Forms commonly assigned to *Anomalina californiensis* Cushman and Hobson are included with *Melonis pompilioides* in this report.

Stehli, 1975; Kennett and Shackleton, 1976; Kennett, 1977; Savin, 1977). Each major paleoclimatic-paleoceanographic event was accompanied by poleward or equatorward adjustment of surface isotherms in the eastern Pacific and associated latitudinal migrations of temperature-sensitive biofacies documented by the appearance of subtropical-tropical faunas in southern California during late Paleocene-early middle Eocene, latest Oligocene, and middle Miocene time and cool temperate-subarctic faunas during late Eocene-early Oligocene, late Miocene, and late Pliocene-Pleistocene time (Arnold, 1909; Kleinpell, 1938; Durham, 1950; Ingle, 1967a, 1973b, 1977b; Addicott, 1969; Schmidt, 1971; Steineck, 1971). Brief appearances of larger foraminifera mark the two warmest Cenozoic events in this region during the Paleocene (Schenck, 1929) and late Oligocene (Hornaday, 1972). Thus, differences in species composition between Neogene and Paleogene benthonic biofacies utilized in this report (Tables 1 and 2) are assumed to reflect not only variations due to evolution but also major differences in paleoclimatic-paleoceanographic settings during these two phases of the Cenozoic along with attendant changes in shallow as well as deep water mass structure and character (Savin, Douglas, and Stehli, 1975). Recent high- and mid-latitude benthonic foraminiferal biofacies in the northeastern Pacific serve as appropriate models for temperate through subarctic faunas and conditions encountered in late Neogene deposits (Ingle, 1967a, 1972). Alternately, modern lower latitude biofacies within the eastern Pacific and Gulf of Mexico (e.g., Phleger, 1951, 1960; Bandy and Arnal, 1957; Bandy, 1961; Bandy and Rodolfo, 1964; Smith, 1964) serve as crude but useful models for paleobathymetric analysis of temperate through tropical faunas encountered in Paleogene deposits of southern California.

Biofacies analysis per se involves arranging species with similar *upper* depth limits into faunal groups (biofacies) indicative of major bathymetric increments and benthonic environments (Bandy, 1961) which, in turn, reflect major water mass and substrate boundaries in a given area. Use of upper depth limits in defining these groups is of critical importance because of continual downslope displacement and redeposition of specimens resulting in artificial extension of shallow biofacies into deeper water (Fig. 5). In fact, displaced specimens commonly constitute well over 50 percent of assemblages within middle and lower bathyal continental margin deposits as illustrated by Recent foraminiferal distributions in the Gulf of California (Figs. 5, 6). Consequently, paleobathymetric curves should be constructed using the *deepest dwelling forms* pres-

TABLE 2

Species composition of Paleogene benthonic foraminiferal biofacies.[1]

INNER SHELF[2] BIOFACIES[3]: 0–50 m; 0–150 ft.

Amphistegina spp.
Asterigerina spp.
Buccella spp.
Cibicides hodgei Cushman & Schenck
Cibicides sandiegoensis Cushman & Hanna
Discocyclina spp.
Discorbis spp.
Elphidium californicum Cook
Elphidium smithi Cushman & Dusenberg
Eponides gaviotaensis Wilson
Eponides kleinpelli Cushman & Frizzell
Eponides patelliformis Stadnichenko
Florilus spp.
Hanzawaia blanpiedi (Toulmin)
Hanzawaia hodgei (Cushman & Schenck)
Hanzawaia walli (Bandy)
Haplophragmoides obliquicameratus Marks
Nonionella applini Howe & Wallace
Nonionella frankei Cushman
Nonionella jacksonensis Cushman
Nonionella labradoricum Dawson
Nonionella miocenica Cushman
Operculina spp.
Siphonina spp.
Quinqueloculina minuta Beck
Quinqueloculina triangularis d'Orbigny

OUTER SHELF BIOFACIES: 50–150 m; 140–470 ft.

Alabamina kernensis Smith
Allomorphina macrostoma Karrer
Allomorphina paleocenica Cushman
Anomalina acuta Plummer
Bolivina jacksonensis Cushman & Applin
Bolivina pisciformis Galloway & Morrey
Buliminella curta Cushman
Buliminella robertsi Howe & Ellis
Cancris mexicana Cushman & Todd
Cassidulina globosa Hantken
Cassidulina kernensis Smith
Cassidulina zetina indirecta Mallory
Cibicidoides coalingensis Cushman & Hanna
Clavulinoides spp.
Eggerella advena (Cushman)
Eggerella inhungia Finlay
Eggerella trochoides (Reuss)
Gaudryina laevigata Franke
Gaudryina pachecoensis Smith
Guttulina problema d'Orbigny
Hanzawaia involuta (Cushman & Dusenburyi)
Hanzawaia joaquinensis (Smith)
Marginulina laeviuscula Cushman & Bermudez
Planulina haydoni Cushman & Schenck
Planulina truncana (Gumbel)
Pullenia quinqueloba (Reuss)
Pullenia salisburyi Cushman & Stewart
Robertina wilcoxensis Cushman & Ponton
Spiroplectammina gryzbowski Frizzell
Spiroplectammina richardi Martin
Textularia recta Cushman

TABLE 2

Continued

Trifarina spp.[4]
Uvigerina atwilli Cushman & Simonson[4]
Vaginulinopsis asperuliformis (Nuttall)
Valvulineria tumeyensis Cushman & Simonson[4]
Verneuilina triangulata Cook

UPPER BATHYAL BIOFACIES: 150–500 m; 460–1,560 ft.

Bolivina alazarensis Cushman
Bolivina aragonensis (Nuttall)
Bolivina basiscurta Cushman & Stone
Bolivina basiscurta oregonensis Cushman, Stewart & Stewart
Bolivina gracilis gracilis Cushman & Applin
Bolivina gracilis inciscurata Cushman
Bolivina marginata Cushman
Bolivina midwayensis betteae (Weaver & Weaver)
Bolivinoides mexicana (Cole)
Bulimina bradburyi Martin
Bulimina decurtata Cushman & Stainforth
Bulimina guayabalensis Cole
Bulimina kugleri Cushman & Renz
Bulimina ovata cowlitzensis Beck
Bulimina ovata ovata d'Orbigny
Bulimina pupoides d'Orbigny
Cassidulina crassipunctata Cushman & Hobson
Cassidulina galvinensis Cushman & Frizzell
Chilostomella cylinderoides Reuss
Cibicides fortunatus Martin
Cibicides pseudowuellorstorffi Cole
Cibicides spiropunctatus Galloway & Morrey
Epistomina eocenica (Cushman & Hanna)
Epistomina helicello Hanna
Globobulimina ovula (d'Orbigny)
Globobulimina pacifica compressa Hornaday
Globobulimina pacifica oregonensis (Stewart & Stewart)
Gyroidina guayabalensis Cole
Gyroidina octocamerata Cushman & Hanna
Gyroidina orbicularis d'Orbigny
Gyroidina orbicularis obliquata Cushman & McMasters
Gyroidina orbicularis planata Cushman
Hoeglundina spp.
Loxostomum applinae (Plummer)
Oridorsalis umbonatus (Reuss)
Pseudoglandulina manifesta Reuss
Uvigerina cocoaensis Cushman
Uvigerina gallowayi Cushman
Uvigerina jacksonensis Cushman
Uvigerina kernensis Barbat & von Estorff
Uvigerina weaveri Smith
Uvigerina yazooensis Clark
Uvigerinella obesa impolita Cushman & Laiming
Valvulineria martinezensis Smith[4]
Valvulineria palmarealensis (Nuttall)[4]
Valvulineria thomasi Cushman & Simonson[4]
Valvulineria wilcoxensis Cushman & Ponton

UPPER MIDDLE BATHYAL BIOFACIES:
500–1,500 m; 1,560–4,700 ft.

Anomalina garzaensis Cushman & Siegfus
Bulimina callahani Galloway & Morrey
Bulimina consaguinea Parker & Bermudez
Bulimina instabilis Cushman & Parker

TABLE 2

Continued

Bulimina jacksonensis welcomensis Mallory
Bulimina lirata Cushman & Parker
Bulimina macilenta Cushman & Parker
Bulimina microcostata Cushman & Parker
Bulimina pachecoensis Smith
Bulimina rinconensis Cushman & Laiming
Bulimina sculptilus Cushman
Bulimina semicostata lacrima Mallory
Bulimina semicostata semicostata Nuttall
Cibicides laimingi Mallory
Cibicides pachyderma (Rzehak)
Eggerella bradyi Cushman
Eponides duprei Cushman & Schenck
Eponides lodoensis Martin
Karreriella chapapotensis Cole
Glandulina laevigata ovata (Cushman & Applin)
Gyroidina condoni (Cushman & Schenck)
Martinotiella eocenica Cushman & Bermudez
Martinotiella petrosa (Cushman & Bermudez)
Melonis regina minor (Smith)
Melonis regina regina Martin
Melonis tennesseensis (Berry)
Osangularia culter midwayana (Cushman & Todd)
Osangularia mexicana (Cole)
Pullenia bulloides (d'Orbigny)
Pullenia eocenica Cushman & Siegfus
Pullenia quinqueloba (Reuss)
Pseudoglandulina ovata (Cushman & Applin)
Rhabdammina eocenica Cushman & Hanna
Uvigerina churchi churchi Cushman & Siegfus
Uvigerina churchi demicostata Mallory
Uvigerina gardnerae Cushman

LOWER MIDDLE BATHYAL BIOFACIES:
1,500–2,000 m: 4,700–6,250 ft.

Boldia (Anomalina) crassisepta (Cushman & Siegfus)
Bulimina adamsi Cushman & Parker
Bulimina corrugata Cushman & Siegfus
Bulimina truncana Gumbel
Bulimina truncanella Finlay
Bulimina whitei Martin
Cibicides coalingensis (Cushman & Hanna)
Cibicides ouachitaensis Howe & Wallace
Cibicidoides coalingensis (Cushman & Hanna)
Cibicidoides grimsdelei (Nuttall)
Cibicidoides perlucidus (Nuttall)
Cyclammina cancellata Brady
Cyclammina clarki (Hanna)
Cyclammina incisa Starke
Cyclammina pacifica Beck
Cyclammina somanica Berry
Gavelinella spp.
Karreriella elongata (Mallory)
Karreriella washingtonensis Rau
Melonis durhami (Mallory)
Plectofrondicularia gracilis Smith
Plectofrondicularia spp.
Stilostomella advena (Cushman & Laiming)[6]
Stilostomella adolphina (d'Orbigny)
Stilostomella irregularis (Kleinpell)
Stilostomella lepidula (Schwager)

TABLE 2

Continued

Stilostomella plummerae (Cushman)
Stilostomella sanctaecrucis (Kleinpell)
Uvigerina garzaensis nudo-robusta Mallory
Valvulina curta Cushman & Siegfus

LOWER BATHYAL BIOFACIES[7]: 2,000 m+; 6,250 ft.+

Anomalinoides dorri aragonensis (Nuttall)
Anomolinoides pompilioides (Galloway & Hemingway)
Bathysiphon spp.
Glomospira charoides (Jones & Parker)
Gyroidina soldani d'Orbigny
Melonis pompilioides (Fitchell & Moll)[8]
Nuttalides trumpyi (Nuttall)
Pleurostomella acuta Hantken
Pleurostomella alazarensis Cushman
Pleurostomella alternans Schwager
Pleurostomella nuttali Cushman & Siegfus
Pleurostomella paleocenica Cushman
Psammosphaera spp.
Uvigerina gardnerae pachecoensis Smith
Uvigerina garzaensis Cushman & Siegfus

---

[1] Arrangement and interpretation of biofacies follows procedures and principles described by Bandy (1960b, 1961), Bandy and Arnal (1960, 1969) and Ingle (1967a, 1967b, 1973a) with modifications based on analysis of Recent tropical-subtropical benthic foraminiferal distributions thought to be analogous to the Paleogene faunas of the marginal mid-latitude Pacific, recurring species associations within unequivocal bathyal deposits (e.g., Kreyenhagen Shale), and established lower bathyal-abyssal assemblages (e.g., Beckmann, 1953, Douglas, 1973). Not all species listed within each biofacies are present in any given sample due to various age ranges of the component species.

[2] The term *shelf* is equivalent to the neritic or sublittoral zone of many authors.

[3] Includes littoral species.

[4] Species thought to exhibit a transitional distribution from shelf to upper bathyal depths. In many tropical areas, a minute hispid species of *Uvigerina* (usually assigned to *U. auberiana* d'Orbigny) characterizes shelf-edge biofacies; *U. elongata* Cole may represent a Paleogene homeomorph of this species.

[5] The assumed Paleogene homeomorph of *Bulimina rostrata* Brady which exhibits heterobathyal upper middle to lower bathyal upper depth limits in the modern ocean.

[6] Ornamented species of *Stilostomella* are thought to exhibit a transitional distribution from lower middle bathyal to lower bathyal depths based on modern distributional patterns (e.g., Bandy and Rodolfo, 1964).

[7] In situ lower bathyal-abyssal faunas indicative of depths approaching or below the calcium carbonate compensation depth (Fig. 5; van Andel, 1975) are composed primarily of arenaceous species and radiolaria as exemplified by assemblages from portions of the Oceanic Formation of Barbados (Beckmann, 1953) and similar arenaceous faunas reported from portions of the Anita Formation in southern California and correctly surmised to represent a sub-lysocline biofacies by Gibson (1973); common genera in this particular biofacies include *Bathysiphon*, *Cyclammina*, *Eggerella*, *Glomospira*, *Haplophragmoides*, *Hormosina*, *Hyperammina*, *Psammosphaera*, *Rhabdammina*, *Trochamminoides*, and *Vulvulina*.

[8] Forms commonly assigned to *Anomalina californiensis* Cushman and Hobson are included with *Melonis pompilioides* of this report.

ent in a given sample yielding estimated *minimum depths of deposition*; correct paleodepths are not obtained by "integrating" the depth aspect of entire faunas nor by focusing exclusively on the most abundant elements in a fauna to arrive at "average" paleodepths. Paleobathymetric curves presented in this report were constructed following this concept with estimated paleodepths derived by analysis of deepest dwelling members of Paleogene or Neogene paleobathymetric biofacies (Tables 1, 2) reported by various authors from each section studied. No attempt was made to compare taxonomic assignments of each author; all taxa listed in any given report are accepted as valid identifications. Moreover, most microfaunal reports utilized tabulate relative abundances of species in qualitative terms preventing quantitative analysis of biofacies trends; those reports utilizing quantitative faunal data serve to emphasize the direct analogies between modern and fossil biofacies (e.g., Bandy and Kolpack, 1963; Ingle, 1967a, 1972, 1976).

Paleoenvironmental Models

Variations of general microfaunal parameters, benthonic foraminiferal biofacies, and sedimentologic patterns across Guaymas Basin in the Gulf of California illustrate important qualitative and quantitative trends with depth in a marginal basin setting and provide striking analogues of facies trends characteristic of Cenozoic basinal cycles of the Southern California Continental Borderland. Indeed, by simply turning Figures 4 to 6 on end, the horizontal Recent trends within the modern gulf can be viewed "stratigraphically" with vertical variations duplicating a typical cycle of basin evolution from initial subsidence through filling of the resulting basin. When Figure 5 is viewed in this context, (1) the nonmarine bajadas of the Baja California peninsula are analogous to the Eocene-Oligocene deposits of the Sespe Formation, (2) the bioclastic deposits of the western gulf shelf are analogous to the Oligocene Vaqueros Formation, (3) the western shelf edge through upper slope deposits are analogous to the Miocene Rincon Shale, (4) the laminated diatomites and diatomaceous muds associated with the slope and the oxygen minimum zone are analogous to the Miocene Monterey Shale, and (5) the terrigenous deposits forming the fan, slope, and shelf of the eastern gulf are analogous to the Plio-Pleistocene basin-filling phase of the eastern borderland usually assigned to the Fernando and Pico Formations. Major variations of these trends within Cenozoic borderland sequences are related to differences in position of effective basin sills, proximity of the Cenozoic strandline, and variations in rates of subsidence and uplift.

A generalized model of characteristic physical, microfaunal, and sedimentologic trends across a schematic continental margin is provided on Figure 7, incorporating many of the major lithologic and microfaunal boundaries utilized in paleoecologic and paleobathymetric interpretation of the southern California Cenozoic sequences presented in this report. Each of the more than 40 paleoenvironmental boundaries identified in this model is tied directly to significant variations of major physical parameters governed by the stratified nature of the marine water column providing multiple criteria for analyzing Cenozoic paleobathymetric and depositional history. In addition, a summary of terminology applied to the complex of depositional environments associated with slope, base-of-slope, and submarine fan environments is included for clarity because of the predominance of these particular lithofacies in marginal basin sequences of the borderland (Fig. 8). Thus, the hindcasting of Cenozoic paleobathymetry was essentially a search for microfaunal and lithologic signatures of major paleoenvironmental trends, boundaries, and biofacies (Fig. 7) through scrutiny of previously published reports on the portions of the borderland selected for study. Reconstructions were also aided by earlier paleoenvironmental analyses by Natland (1952, 1957), Bandy (1953), Bandy and Kolpack (1963), Ingle (1967a, 1972), Weaver and others (1969), and Gibson (1973); however, paleobathymetric trends presented herein represent revaluations of previously presented data and interpretations in light of the current concepts and models discussed earlier. Estimated paleobathymetric curves are based primarily on analyses of the deepest dwelling members of foraminiferal assemblages reported from each unit in each of the six sequences studied following biofacies assignments noted in Tables 1 and 2. Identifications of specific paleoenvironmental facies (i.e., shelf, slope, anaerobic basin plain, etc.) represent integrated assessments of available microfaunal and lithologic data interpreted in light of basic depositional models (Figs. 7, 8) based on patterns established in the modern borderland (Emery, 1960; Moore, 1969) and in the Gulf of California (van Andel and Shor, 1964).

ANALYSIS OF SUBSIDENCE, UPLIFT, AND RATES OF SEDIMENT ACCUMULATION

One of the more speculative but interesting aspects of this study concerns variations in estimated rates of sediment accumulation, subsidence, and uplift. In or-

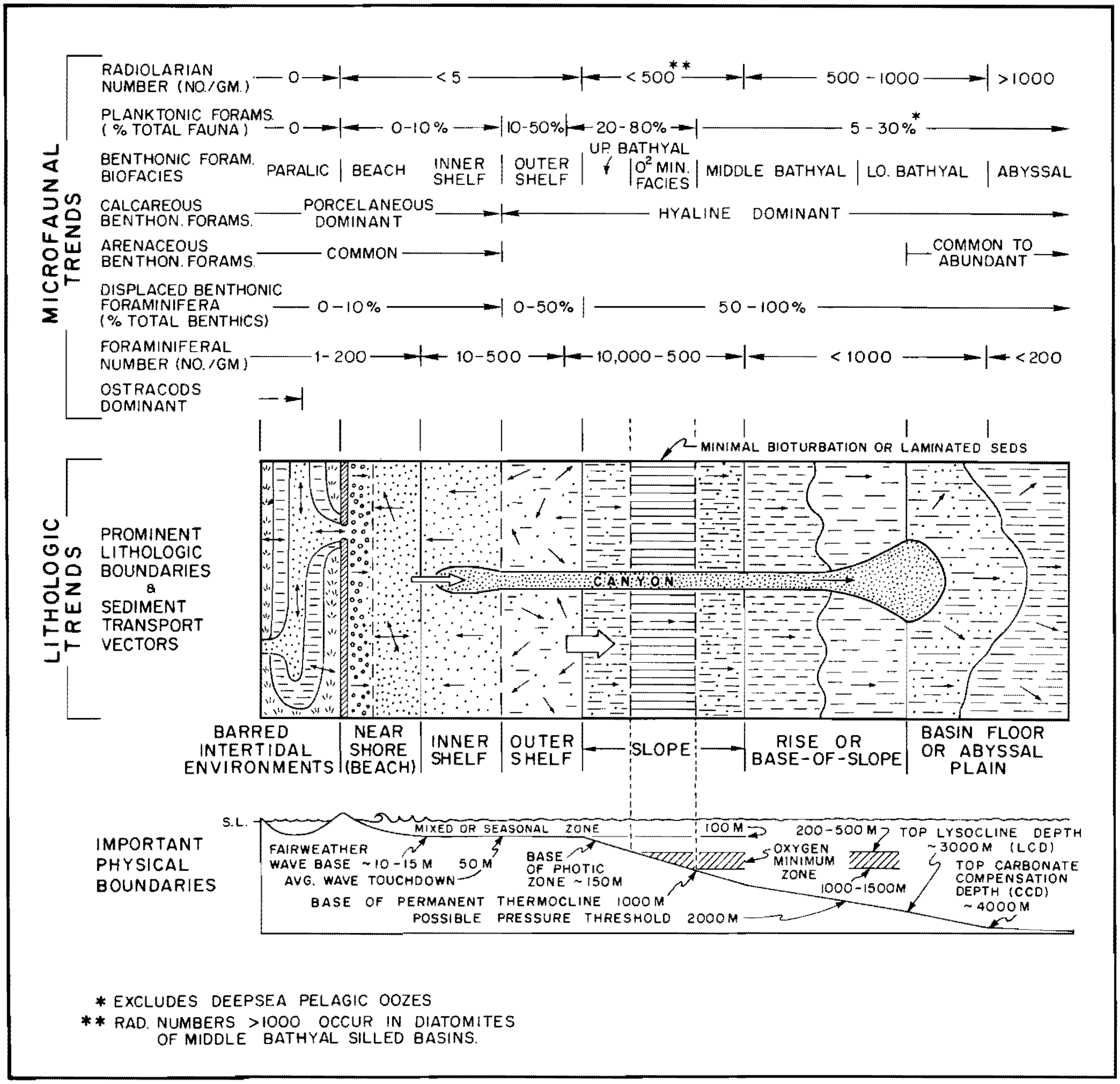


FIGURE 7

Mode of significant microfaunal and sedimentologic trends across a schematic littoral to abyssal bathymetric gradient along with associated major physical oceanographic boundaries. Arrows indicate general direction of sediment transport with large open arrows indicating transport of suspensates. Foraminiferal trends are based on late Neogene and Recent distributional patterns and abundances. Lithologic patterns modified from Emery (1969); figure from Ingle (1975b).

der to gain a clearer understanding of these parameters, five of the six sequences are plotted in terms of both stratigraphic thickness and estimated duration of each stratigraphic unit in time (e.g., Fig. 9) through correlation of planktonic zonal data, provincial stages, and the radiometric time scale (Fig. 2). These contrasting but complementary columns emphasize the inherent differences in the lithostratigraphic versus chronostratigraphic perspective and provide basic information necessary to calculate estimated rates of

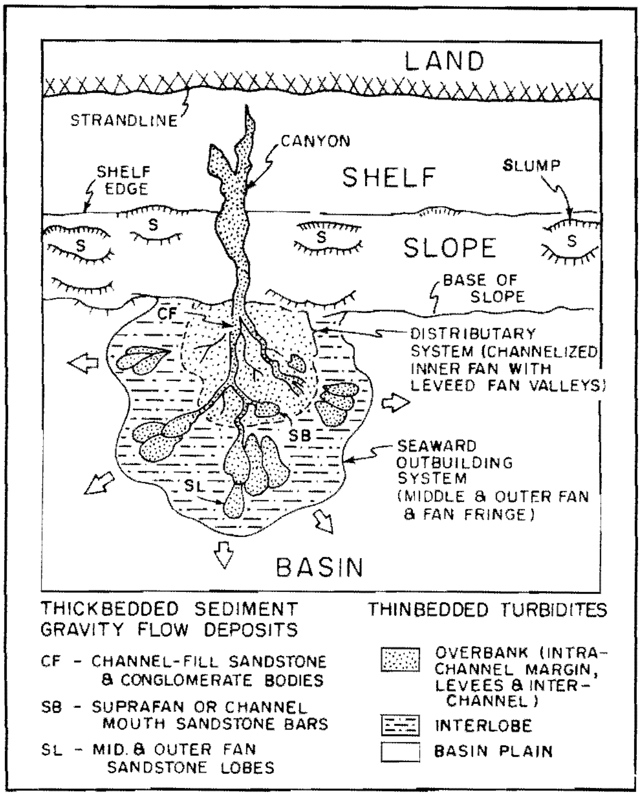


FIGURE 8

Schematic distribution of distinctive proximal and distal sedimentary facies characterizing various portions of a typical submarine fan deposit; adapted from Normark (1974), Nelson (1975), and Ricci-Lucchi (1975).

sedimentation and subsidence. *Amounts* of subsidence and uplift were calculated using the following technique modified from Bandy and Arnal (1960): (a) if estimated water depth increases from the stratigraphic base of an arbitrary paleoenvironmental unit[4] (i.e., shelf, slope, etc.) to the top of that unit, the amount of deepening is added to the stratigraphic thickness assigned to the unit of interest to obtain total subsidence; (b) if estimated water depth remains the same from the bottom to stratigraphic top of a given paleoenvironmental unit, the amount of subsidence is approximately the thickness of that unit; (c) if water depth decreases from one arbitrary unit to the next, the amount of shoaling is subtracted from the stratigraphic thickness of the unit of interest to obtain a value for subsidence; (d) uplift is indicated if the amount of shoaling is greater than the stratigraphic thickness of the unit of interest. *Rates* of subsidence and uplift were estimated by dividing the amount of subsidence or uplift calculated for an arbitrary paleoenvironmental unit by the estimated duration of that unit in time in millions of years as deduced from the appropriate chronostratigraphic plot (e.g., Fig. 9). Estimated rates of sediment accumulation were computed in a similar manner by dividing the maximum stratigraphic thickness of a given paleoenvironmental unit (shelf, slope, etc.) by the estimated duration of the unit in time. No attempt was made to correct estimated rates of sediment accumulation for compaction.

PALEOBATHYMETRIC AND PALEOENVIRONMENTAL HISTORY

Even a cursory review of the now substantial literature dealing with the Cenozoic marine history of southern California quickly reveals the rather tidy partitioning of Paleogene and Neogene basinal sedimentation in this region with a third depositional phase characterizing Plio-Pleistocene time. This tripartite division of the stratigraphic record is clearly the product of the unusually dynamic but episodic tectonic history of this portion of the Pacific rim, initially delineated in classic syntheses by Reed (1933) and Reed and Hollister (1936). Newer tectonic insights indicate that major adjustments of the Pacific-Farallon and Pacific-American plate boundary have been responsible for the respective Paleogene and Neogene cycles of basin formation and filling in this region (Atwater, 1970; Nilsen and Clarke, 1975; Silver, 1974; Snyder, Dickinson, and Silberman, 1976). The following discussions and summary diagrams focus on the paleobathymetric and paleoenvironmental history of six key stratigraphic sequences arrayed along the northern and eastern edges of the present borderland (Fig. 1) representing end products of these complex tectonic and sedimentary events. Each column represents a generalized history of a restricted portion of the evolving borderland margin emphasizing the deepest depositional environments envisioned for any given unit and maximum stratigraphic thicknesses. Thus, the report is interpretive in character; no attempt is made to reprint basic geologic and paleontologic data readily accessible in the many references duly cited and utilized in the analysis. In effect, the six diagrams presenting paleobathymetric, paleoenvironmental, and depositional histories of individual areas constitute the summary and conclusions of this study with the following text discussion highlighting regional trends and events.

---

[4] Bandy and Arnal (1960) utilize differences in water depth between stages.

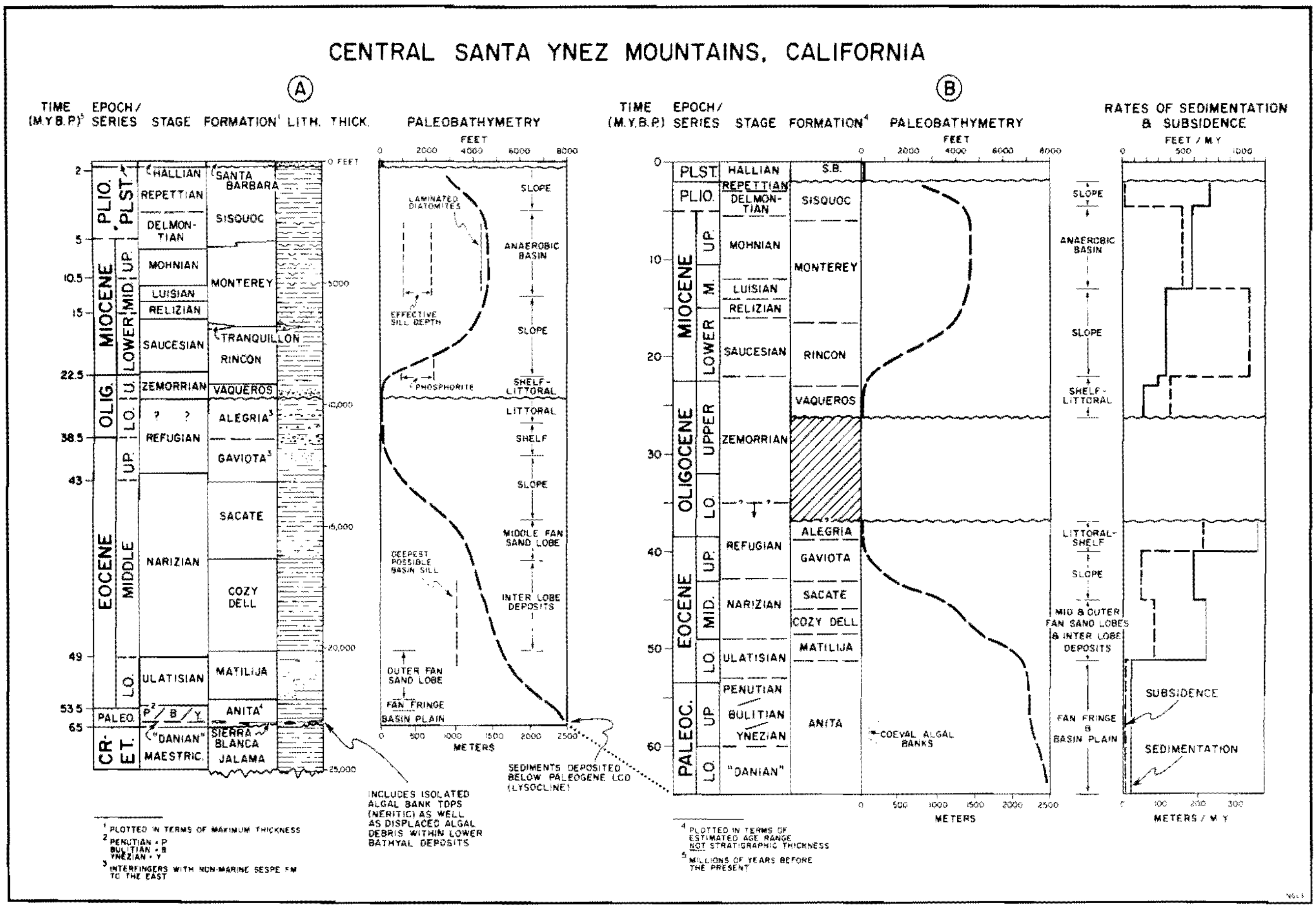
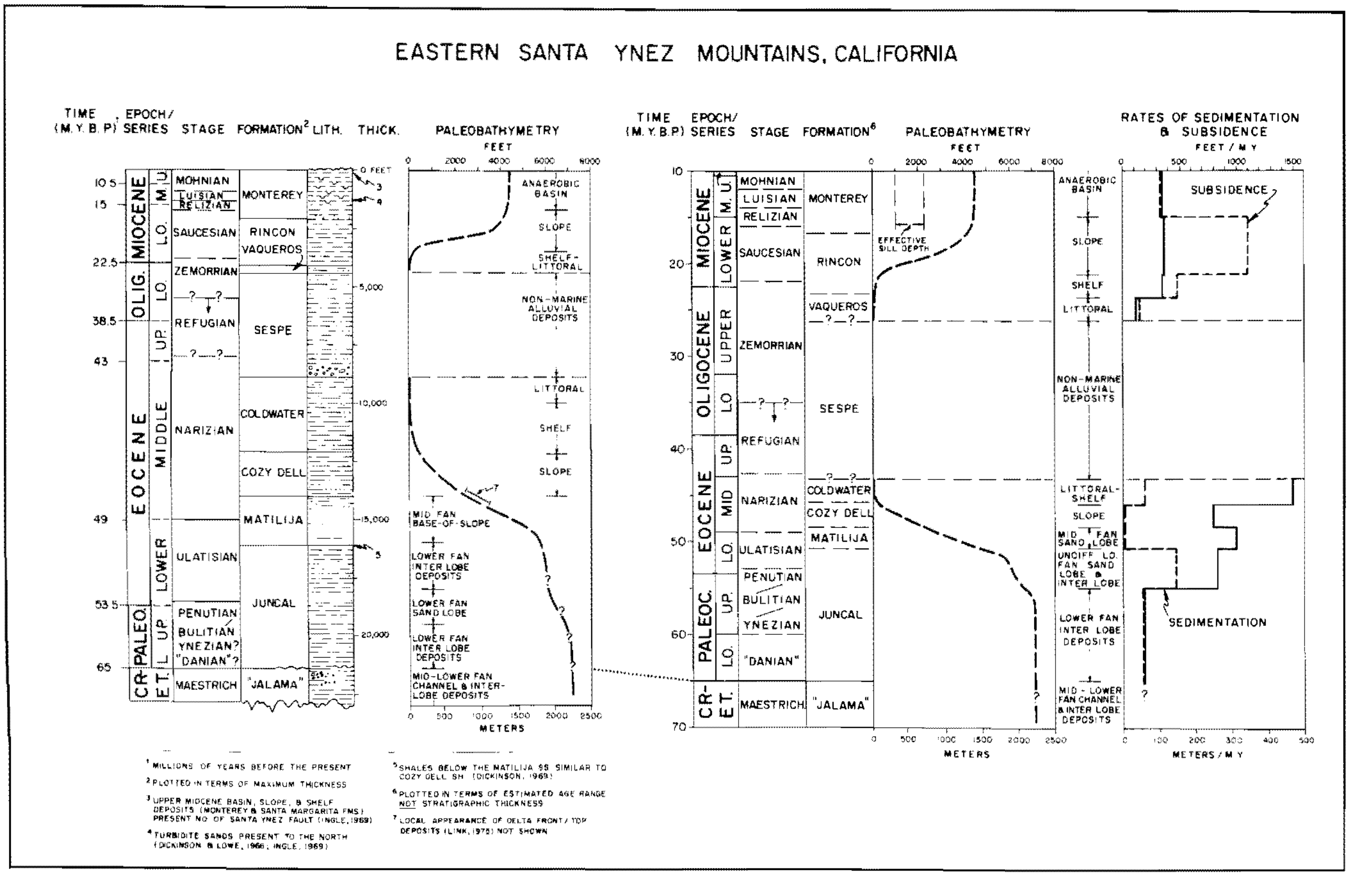


FIGURE 9

Paleobathymetry, marine paleoenvironments, and estimated rates of sedimentation and subsidence within Cenozoic deposits exposed in the central Santa Ynez Mountains, California. Note that paleobathymetry is plotted in terms of maximum stratigraphic thickness of each formation (A) and alternately in terms of estimated duration of each unit in time (B) based on correlations of provincial stages with the radiometric time scale presented on Figure 2. The stratigraphic column is adapted from Dibblee (1950, 1966) and Kleinpell and Weaver (1963). Estimated paleobathymetry is based on an analysis of benthonic foraminifera reported in these units by Woodring and Bramlette (1950), Wilson (1954), Mallory (1959), Hornaday (1961), Weaver and Weaver (1962), Kleinpell and Weaver (1963), Bandy and Kolpack (1963), Weaver and Molander (1964), Edwards (1972), and Gibson (1973), utilizing methods discussed in text and biofacies detailed in Tables 1 and 2; stage assignments follow these same authors. However, it is important to note that Gibson (1973) documents early as well as early middle Eocene ages for portions of the upper Anita Formation based on planktonic criteria implying facies control of Ulatisian benthonic foraminiferal faunas within these beds; these discrepancies, as well as similar facies problems in older and younger strata, are not fully documented in this generalized column but are noted in text and Figure 2. Interpretation of sediment character and structures is based on descriptions in these same reports. Rates of subsidence and sedimentation were computed for each depositional-paleoenvironmental unit (shelf, slope, etc.) following the method outlined by Bandy and Arnal (1960).

PALEOGENE HISTORY AND THE SANTA BARBARA EMBAYMENT

A total of more than 18,000 m of Upper Cretaceous and Cenozoic marine strata are displayed in the Santa Ynez Mountains, adjacent Channel Islands, and the western Ventura Basin (Fig. 1) comprising a remarkable record of deposition along the northern margin of southern California from Turonian through Holocene time (Figs. 9–12). The east-west structural trough forming this major depocenter is commonly referred to as the Santa Barbara Embayment (Reed and Hollister, 1936) and contains clear evidence of both Paleogene and Neogene cycles of basin evolution. The late Mesozoic-Paleogene basinal history experienced in this northern area stands in striking contrast to the mild subsidence and paralic marine history recorded



EASTERN SANTA YNEZ MOUNTAINS, CALIFORNIA

¹MILLIONS OF YEARS BEFORE THE PRESENT

²PLOTTED IN TERMS OF MAXIMUM THICKNESS

³UPPER MIOCENE BASIN, SLOPE, & SHELF DEPOSITS (MONTEREY & SANTA MARGARITA FMS.) PRESENT NO. OF SANTA YNEZ FAULT (INGLE, 1969)

⁴TURBIDITE SANDS PRESENT TO THE NORTH (DICKINSON & LOWE, 1966; INGLE, 1969)

⁵SHALES BELOW THE MATILIJA SS SIMILAR TO COZY DELL SH (DICKINSON, 1969)

⁶PLOTTED IN TERMS OF ESTIMATED AGE RANGE NOT STRATIGRAPHIC THICKNESS

⁷LOCAL APPEARANCE OF DELTA FRONT/TOP DEPOSITS (LINK, 1975) NOT SHOWN

FIGURE 10

Paleobathymetry, marine paleoenvironments, and estimated rates of sedimentation and subsidence within Cenozoic sediments exposed in the eastern Santa Ynez Mountains, California. Note that paleobathymetry is plotted both in terms of maximum stratigraphic thickness of each formation and alternately in terms of estimated duration of each unit in time following the time scale and correlations presented on Figure 2. The stratigraphic column was compiled from Dibblee (1966), Stauffer (1967a), and Dickinson (1969). Estimated paleobathymetry is based on biofacies analysis of benthonic foraminifera reported from these strata by authors noted on Figure 10 together with data in Blaisdell (1953) and Ingle (1969); stage assignments follow these same authors.

in sediments of this age along the southern margin of the borderland as typified by exposures in the Santa Ana Mountains-San Joaquin Hills area (Figs. 1, 13). Thus, discussions of Paleogene events center on sequences within the Santa Barbara Embayment lying north of the present-day Channel Islands and precursor highs assigned to "Anacapia" (Reed and Hollister, 1936; Weaver and others, 1969).

Regional overviews of the Cenozoic stratigraphy and evolution of the western Transverse Ranges-Santa Barbara Embayment area have been presented by Bailey and Jahns (1954), Corey (1954), Kleinpell and Weaver (1963), Weaver (1969b), Dickinson (1969), and Vedder and others (1974). All of these authors emphasize the west-trending structural control of depositional patterns in this portion of the borderland during the early and middle Cenozoic and note that uplift of the Santa Ynez Mountains and Santa Monica Mountains ultimately shifted subsidence and sedimentation to the present Santa Barbara Basin-Ventura Basin axis in the late Cenozoic (Fig. 1). The basic stratigraphic and geologic framework of the Santa Ynez Mountains has been worked out by Dibblee (1950, 1966) with the related geology of the Channel Islands described by Weaver and others (1969). Previous studies dwelling primarily on Paleogene paleobathymetric and paleoenvironmental history of portions of the Santa Ynez sequence include reports by Natland (1957) and Bandy and Kolpack (1963); a number of reports by D. W. Weaver and University of California students provide detailed information on Paleogene benthonic foraminiferal faunas in this area

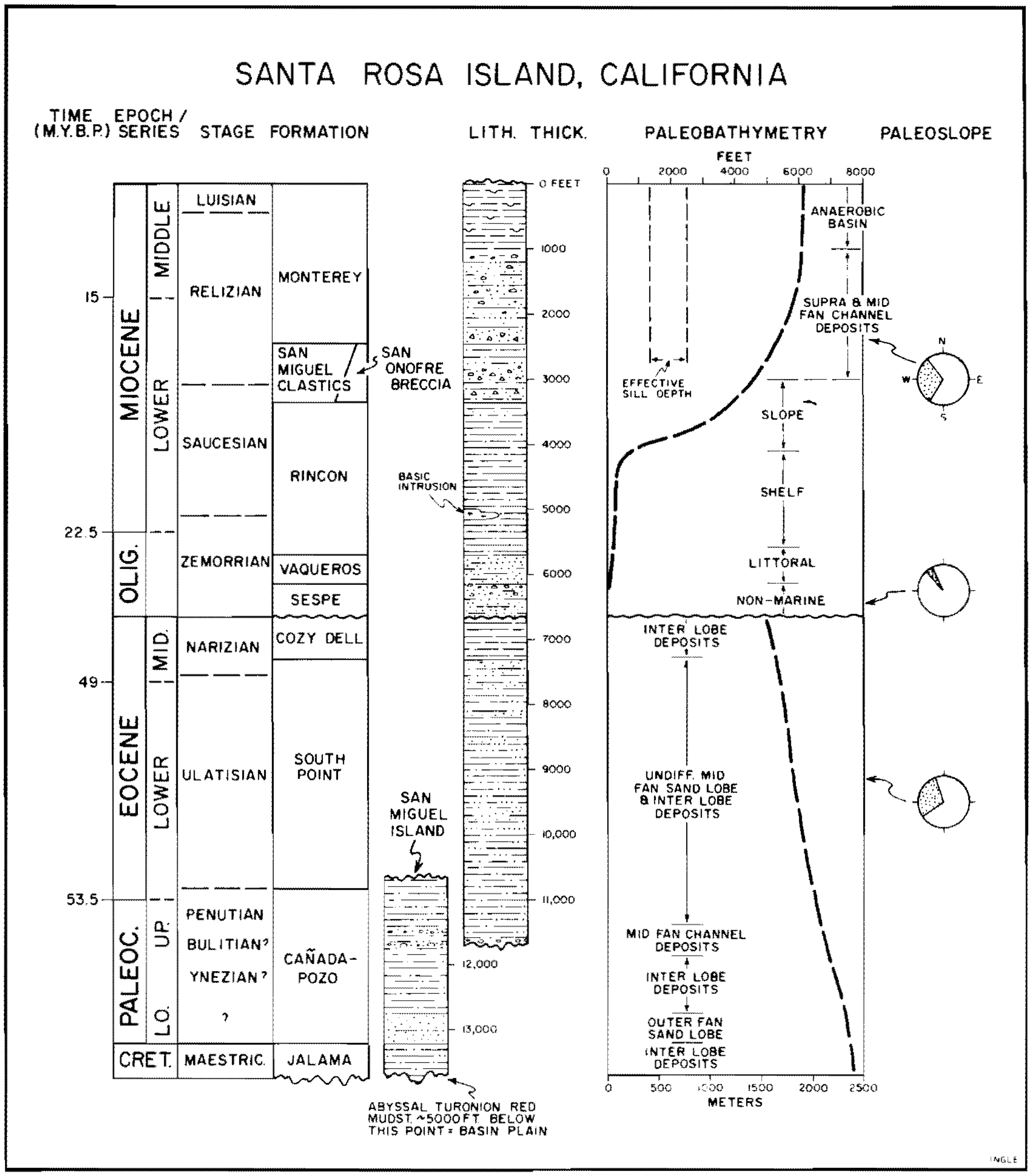


FIGURE 11

Paleobathymetry and marine paleoenvironments within early and middle Tertiary deposits exposed on Santa Rosa Island, California; a supplementary section reported from San Miguel Island (Fig. 1) allows extension of paleoenvironmental trends to the Tertiary-Cretaceous boundary. Estimated paleobathymetry is based on biofacies analysis of benthonic foraminiferal faunas reported from these sediments by Weaver (1969a), Weaver and Doerner (1969), and Avila and Weaver (1969). Sedimentary columns and paleoslope data were taken from these same reports and from McCracken (*in* Weaver and Doerner, 1969). Chronostratigraphy follows correlations presented on Figure 2; stage assignments follow authors noted above.

as cited in text and diagrams to follow. Lithofacies and depositional regimes are emphasized by Stauffer (1967a, b), McCracken (1969), Obrien (1972), Link (1975), and van Kamp and others (1974). Summary diagrams illustrate Cenozoic paleobathymetric and depositional histories of four subareas within the Santa Barbara Embayment in the central and eastern Santa Ynez Mountains (Figs. 9, 10), Santa Rosa-San Miguel

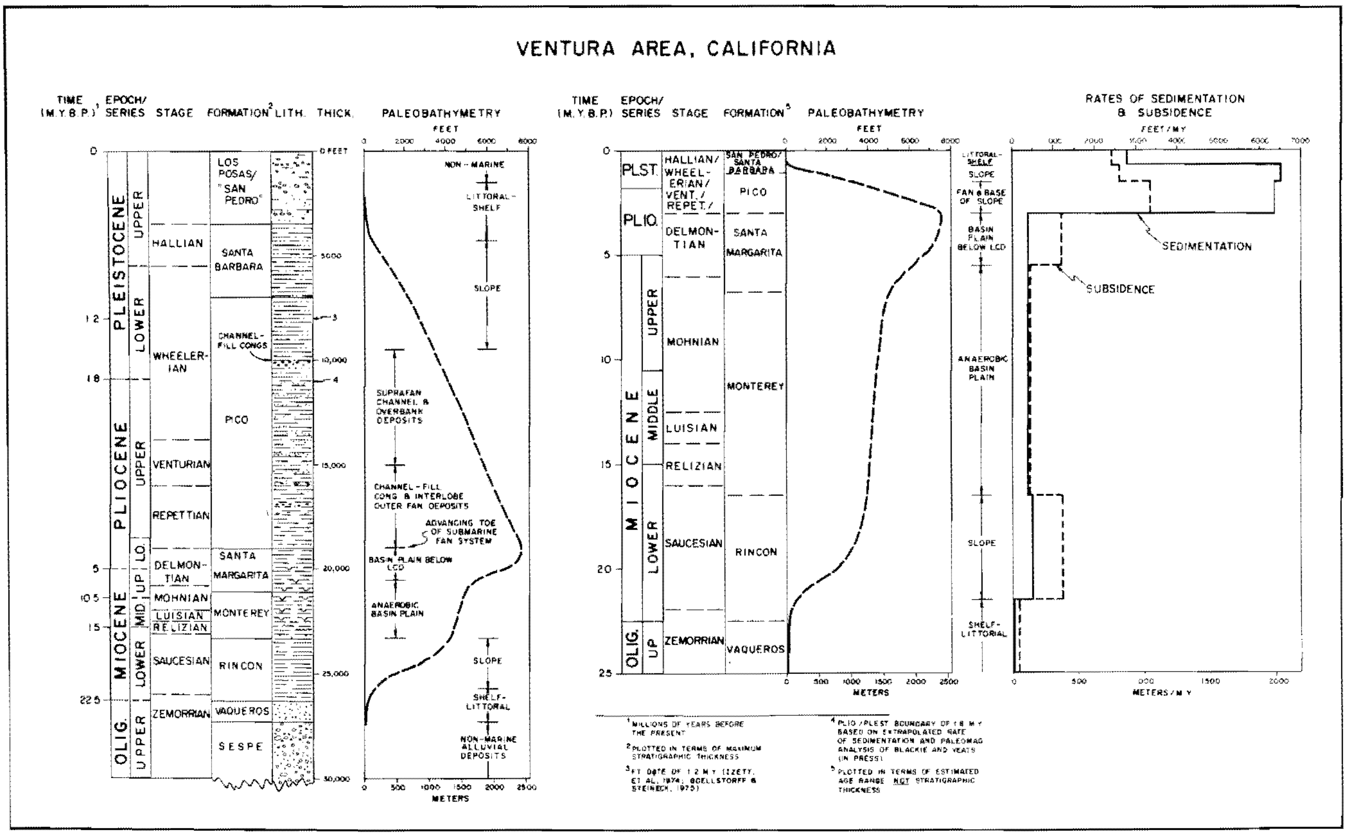


FIGURE 12

Paleobathymetry and marine paleoenvironments within Neogene deposits of the western Ventura Basin, California. Note that paleobathymetry is plotted in terms of maximum stratigraphic thickness of each formation and alternately in terms of the estimated duration of each unit in time following the time scale presented on Figure 2. Chronostratigraphy incorporates fission-track dates reported by Izett, Naeser, and Obradovich (1974) and Boellstorff and Steineck (1975) and the paleomagnetic data of Blackie and Yeats (1976). Estimated paleobathymetry is based on biofacies analysis of benthonic foraminifera reported from these units by Natland (1933, 1952, 1957), Natland and Kuenen (1951), and Ingle (1967a).

Islands (Fig. 11), and the western Ventura Basin (Fig. 12).

Late Mesozoic deposition in this area occurred inboard of a major submarine trench experiencing subduction with wedges of Lower through Upper Cretaceous terrigenous sediments shed generally westward forming abyssal-lower bathyal fans deposited on top of Jurassic deep sea radiolarian oozes and ultramafic crust (Franciscan Formation) moving eastward into the trench (Nilsen and Clarke, 1975). Turonian red mudstones intercalated with coarse fan deposits of the Jalama Formation on San Miguel Island (Weaver, 1969a) likely represent sediments accumulating at or near the Late Cretaceous carbonate compensation depth (Fig. 7). Several species of *Glomospira*, *Pleurostomella*, and other genera common to Late Cretaceous lower bathyal-abyssal biofacies (Sliter, 1972) are present in both the youngest and oldest portions of the Jalama deposits (Akpati, 1966; Weaver, 1969a) indicating paleodepths of 2,000 m and deeper during the some 25 m.y.[5] of Turonian through Maestrichtian deposition represented by this unit. Sedimentary structures and lithologies described from the Jalama and related units are typical of several submarine fan environments (Stauffer, 1967b), including overbank (interlobe) and outer fan sand lobes and channels (e.g., Walker, 1975). Unconformities separate Upper Cretaceous sediments from overlying lower Tertiary shelf and banktop deposits (including the Sierra Blanca Limestone) in the San Raphael uplift area north of the central Santa Ynez sequence (Weaver, 1969a; Gibson,

---

[5] Using the Mesozoic time scale of Berggren, McKenzie, Sclater, and van Hinte (1975).

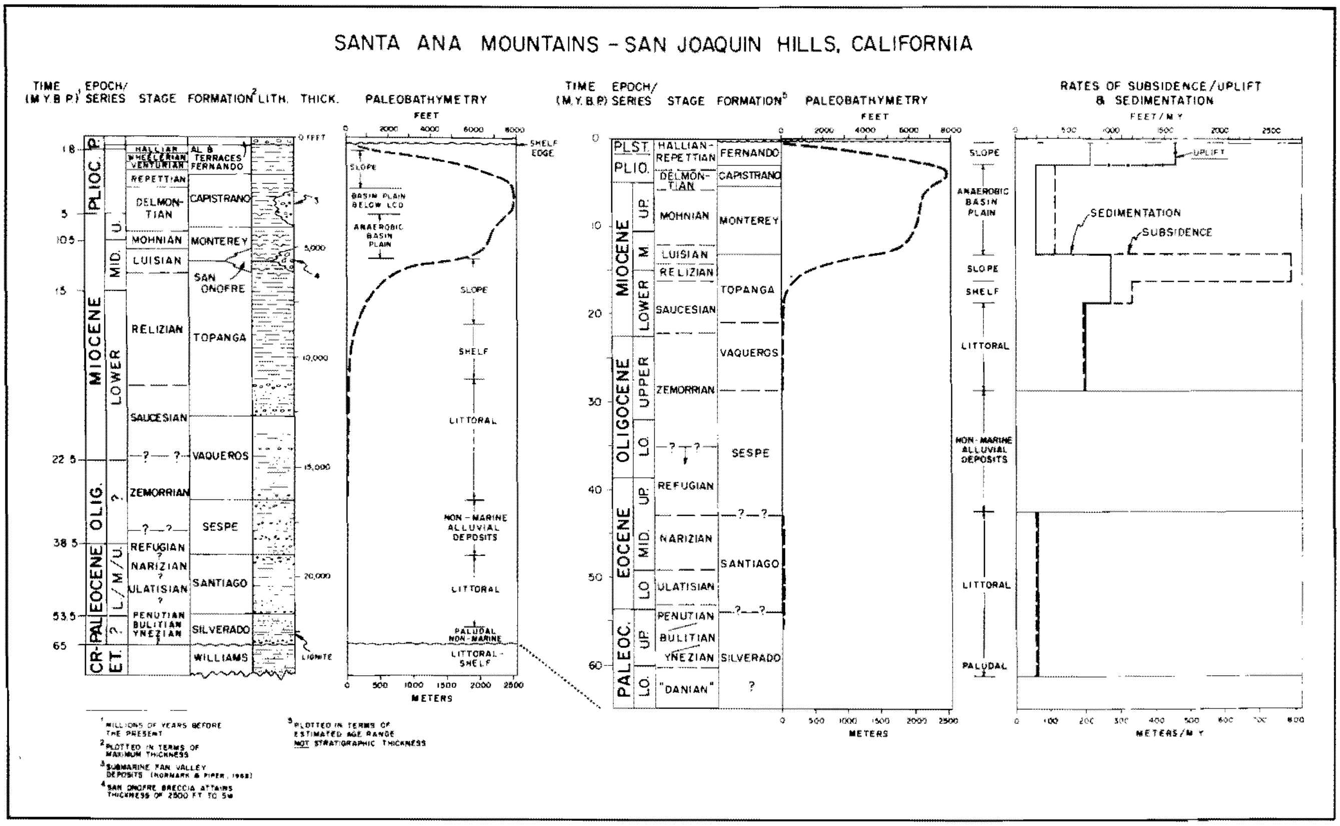


FIGURE 13

Paleobathymetry, marine paleoenvironments, and depositional history of Cenozoic deposits exposed in the Santa Ana Mountains-San Joaquin Hills area, California. Note that paleobathymetry is plotted in terms of maximum thickness of each formation and alternately in terms of estimated duration of each unit in time following the time scale and correlations presented on Figure 2. Estimated Neogene paleobathymetry is based on biofacies analysis of benthonic foraminifera reported from these strata by Natland (1957), Smith (1960), and Ingle (1962, 1972). Paleogene paleobathymetry is based on a summary of these deposits by Woodford, Schollhamer, Vedder, and Yerkes (1954), personal observations, and data in Mallory (1959); stage assignments follow these same authors.

1973; van Kamp and others, 1974), attesting to late Mesozoic flexing of this area. However, sedimentation was apparently continuous across the Mesozoic-Cenozoic boundary in bathyal-abyssal environments south of this major structural high (Weaver, 1969a; Gibson, 1973) as typified by the Jalama/Cañada/Pozo transition of San Miguel Island (Fig. 11) and the Jalama/Anita shale transition in portions of the Santa Ynez Mountains sequence (Figs. 9, 10).

Lower bathyal depths continued to prevail during early Paleogene (Ynezian to Ulatisian) deposition of basin plain and submarine fan deposits represented by the Anita and Juncal formations (Figs. 9 and 10). Abundant radiolarian tests and planktonic foraminifera together with lower bathyal benthonic foraminifera mark the Anita shales in the central Santa Ynez Mountains (Gibson, 1973). Maroon portions of this unit, referred to as the "Poppin Shale," and underlying siltstones, appear to represent deposition at or near the Paleocene CCD at depths in excess of 2,000 m (Van Andel, 1975). A transition from a dominantly arenaceous fauna containing species of *Bathysiphon*, *Cyclammina*, *Hyperammina*, *Rhabdammina*, and *Trochammina*[6] to a calcareous fauna containing lower bathyal-abyssal species of *Stilostomella* and *Pleurostomella*[6] (Table I) recorded in the Anita formation by Gibson (1973) may mark this important paleoceanographic boundary. The 300 m of basinal muds and fan fringe debris comprising the Anita Formation in the central Santa Ynez sequence (Fig. 9) telescope latest Cretaceous through early Eocene time (Gibson, 1973, 1974), reflecting generally low rates of sedimentation and mild subsidence seaward of advancing fans (Fig. 9). In fact, some portions of this unit have been dated

---

[6] Deepest dwelling members of both assemblages are very similar to modern lower bathyal-abyssal faunas reported from the southeastern Pacific (Bandy and Rodolfo, 1964; Keller and Ingle, 1976).

as early middle Eocene in age (Gibson, 1973), representing areas of basin floor free of major fan deposits until this later period. Pods and lenses of detrital limestone and limy mudstones within the lower bathyal portions of this unit represent redeposited bioclastic and glauconitic debris from coeval banktops and shelves fringing the Paleogene San Raphael high (Gibson, 1973; van Kamp and others, 1974).

Packages of thick sands and siltstones forming the Juncal Formation signal the appearance of lower and mid fan deposits in the eastern Santa Ynez sequence during Paleocene-early Eocene time (Fig. 10). West-southwest progradation of these deposits (Stauffer, 1967b) and west-northwest transport of fan debris represented by the Cañada-Pozo formation of San Miguel Island (Fig. 11) spurred dramatic increases in rates of sediment accumulation, subsidence, and shoaling in the Santa Barbara Embayment. The time-transgressive character of Paleogene fan and slope facies is apparent when the eastern and central Santa Ynez sequences are compared (Figs. 9, 10). In general, each successively shallower facies (base-of-slope fan, slope, shelf, etc.) appears later in time toward the west, crudely following Walther's law (Middleton, 1973) but in detail this pattern has led to inevitable controversies over correlation of specific sand and shale units both across and along depositional strike (Bailey, 1952; Stauffer, 1967a; Dickinson, 1969; Vedder, 1972). For example, thick Juncal fan lobes and interlobe deposits were rapidly accumulating in the east at the same time relatively thin basinal muds of the Anita Formation were slowly accumulating to the west as early noted by Kelley (1943). Consequently, rates of sedimentation began to exceed rates of subsidence by latest Paleocene time (Bulitian-Penutian) in the eastern Santa Ynez Basin (Fig. 10), whereas this same event did not occur until early Eocene time (Ulatisian) in the central and western areas (Fig. 9). This depositional scheme continued to accelerate into the middle Eocene with Matilija sands of the central and western Santa Ynez Basin representing the distal margins of major fans (Juncal Formation) initially appearing in Paleocene time (Ynezian-Penutian) in the eastern portion of the basin (Fig. 10). Middle bathyal faunas containing *Bulimina corrugata* have been reported from distal fan deposits of the Matilija Formation as mapped in the Point Conception area (Weaver, 1962; Weaver and Weaver, 1962). Alternately, only meager bathyal assemblages containing several species of *Cyclammina* have been reported from proximal turbidite sands of the type Matilija Formation in the Ojai area to the east (Fig. 10; Blaisdell, 1956), with upper Matilija sediments containing evidence of a short-lived local excursion of a nearby delta front onto the shelf and slope (Link, 1975); however, enclosing Juncal and Cozy Dell shales contain diverse middle bathyal faunas. Similar middle bathyal paleodepths are also indicated by faunas from Paleocene-early Eocene (Penutian-Ulatisian) South Point submarine fan deposits exposed on Santa Rosa Island (Fig. 11) and by foraminifera at the base of coarse fan debris (Jolla Formation) underlying Cozy Dell shales on Santa Cruz Island (Doerner, 1969).

Middle bathyal faunas containing costate buliminids and costate-spinose uvigerinids (Table 1) also occur within interlobe fan deposits and laminated basin mudstones assigned to the Cozy Dell Formation in the central and western Santa Ynez areas (Fig. 9; Weaver, 1962; Bandy and Kolpack, 1963; Weaver and Molander, 1964). In contrast, faunas reported from Cozy Dell shales in the eastern area of the basin (Blaisdell, 1956) are indicative of middle bathyal, upper bathyal, and shelf paleodepths (Fig. 10). A similar paleoenvironmental-paleobathymetric transition from supra or mid fan base-of-slope sands to slope and shelf-edge deposition is represented by middle and upper bathyal faunas within the Sacate Formation of the central Santa Ynez sequence (Fig. 10); corroborating sedimentologic evidence of this transition is detailed by Obrien (1972). Interestingly, common to abundant pyritized foraminifera and/or limonite casts have been reported from both Cozy Dell and Sacate shales (Hornaday, 1961; Bandy and Kolpack, 1963), pointing to anaerobic bottom conditions likely induced by the intersection of a relatively weak oxygen minimum layer[7] with Paleogene basin sills and slopes dictating a maximum sill depth of about 1,000 m (Figs. 7, 9). Gibson (1973) notes pyritized foraminifera in Anita, Matilija, and Cozy Dell sediments in the western Santa Ynez Basin and suggests effective sills were formed in early middle Eocene time. Alternately, basin sills may have been produced during late Mesozoic uplift with effective intersection of the oxygen minimum layer delayed until middle Eocene time due to paleoclimatic events.

---

[7] Tropical-subtropical surface temperatures implied by late Paleocene-early Eocene planktonic foraminifera in this mid latitude area (Schmidt, 1970, 1971; Ingle, 1977b) call for relatively sluggish overturn of the surface layer and, in turn, relatively low rates of primary productivity, a deficiency of organic detritus at depth, and a weakly developed oxygen minimum layer (Figs. 3, 5, 7). Deteriorating Eocene climate (Steineck, 1971; Kennett and others, 1975; Kennett, 1977) was likely accompanied by increased atmospheric transport, increased upwelling, and increased productivity, in turn generating a well-developed oxygen minimum layer.

Rates of sediment accumulation approached 500 m/m.y. as fan, slope, and shelf deposits prograded into the Santa Ynez Basin from north, east, and southeast during middle and late Eocene time (Ulatisian-Refugian). The final phases of Paleogene marine sedimentation in the eastern part of the basin are represented by shelf and intertidal deposits of the Coldwater Formation. Rates of subsidence slackened in the eastern area during this period but increased to the west (Figs. 9, 10), allowing littoral marine deposition (Coldwater Formation) to give way to nonmarine alluvial fans (Sespe Formation) in the eastern portion of the basin about 43 m.y.B.P. with marine sedimentation continuing to at least 35 m.y.B.P. to the west (Fig. 9) as represented by upper bathyal, neritic, and littoral lithofacies and biofacies of the Gaviota and Alegria Formations (Wilson, 1954; Obrien, 1972).

Extensive erosion and nonmarine deposition continued to take place during Oligocene time not only within the Santa Barbara Embayment area but also over most of the southern California margin (Vedder and others, 1974), including the Santa Monica Mountains-San Joaquin Hills area (Fig. 13). Erosion was aided by flexing of older rocks in the northwestern area of the borderland (Dibblee, 1950; Weaver, 1969b), but contacts between Paleogene and Neogene strata bounding Oligocene erosion surfaces and nonmarine deposits are commonly concordant even in areas where major stratigraphic gaps are present (Figs. 9, 11). Thus, it seems almost a certainty that the major change in base level demanded by these events was in part the product of significant eustatic variations of sea level accompanying severe late Eocene-early Oligocene global refrigeration[8] (Kennett and others, 1975; Shackleton and Kennett, 1975; Kennett and Shackleton, 1976; Ingle, 1975c, 1977b; Ingle, Graham, and Dickinson, 1976).

Formation of Neogene Basins

The rather peaceful Oligocene vista of broad alluvial valleys and bajadas formed during a 15-m.y. pause in the tectonic development of southern California was abruptly terminated by widespread subsidence and marine transgression in late Oligocene-early Miocene (Zemorrian) time. This major event initiated a Neogene cycle of basin formation and eastward transgression of the marine strandline from its static Oligocene position west of the present Channel Islands (Reed, 1933). Subsidence was accompanied by increasing volcanism which peaked during late early Miocene time (19 to 16 m.y.B.P.) forming a regional datum of basaltic through andesitic intrusives, flows, and pyroclastics in borderland sediments of this age (Weaver and others, 1969; Vedder and others, 1974). Significantly, this middle Cenozoic tectonic scenario was repeated in many areas around the Pacific rim including the Philippine Islands, Japan, Kamchatka, as well as along the west coast of North America resulting in widespread production of marginal basins in early to middle Miocene time (Dott, 1969), generating amazingly similar Neogene stratigraphies (Ingle, 1973b, 1975c). Essentially synchronous basin formation over this broad a region was likely the product of a middle Cenozoic adjustment of plate margins and a change in vector and rate of subduction of the Pacific plate, resulting in back-arc spreading in the western Pacific and initiation of translational tectonics creating characteristic borderland topography in California (Packham and Falvey, 1971; Jackson and others, 1972; Atwater, 1970; Silver, 1974). An updated view of Neogene plate-edge events along the Pacific coast is provided by Snyder, Dickinson, and Silberman (1976) who demonstrate a remarkable correlation between timing of marginal basin formation, cutoff of volcanic activity, and migrating ridge segments.

The initial blanket of late Oligocene (Zemorrian) marine sediments deposited along the northern and eastern margins of the southern California borderland is commonly assigned to the Vaqueros formation (Loel and Corey, 1932). This unit varies from thin glauconitic and foraminiferal banktop sands in the northeast (Corey, 1965) to thick wedges of coarse terrigenous strandline debris toward the south (Figs. 9–13). Rapid rates of subsidence soon outpaced the relatively low rates of sediment accumulation in the northern borderland giving way to slope deposits of the overlying Rincon formation in early Miocene (Zemorrian-Saucesian) time (Figs. 9–11). Subtropical outer shelf through middle bathyal biofacies (Table 2) occur sequentially in this formation (Avila and Weaver, 1969; Edwards, 1972) and pelletal phosphorite likely marks the intersection of the oxygen minimum zone with the early Miocene slope and shelf edge (Figs. 7, 9).

Estimated early Neogene paleobathymetric histories of all six borderland sequences suggest a progressive north-to-south pattern of subsidence, with basin floors reaching a maximum depth of 1,500 m by early Miocene (Saucesian) time adjacent to the northern strandline (Figs. 10, 11), almost 2,000 m by the early

---

[8] An alternate but less viable explanation of the apparent global Oligocene regressive event involves adjustment of mean depth, volume, and freeboard of the major ocean basins as a function of plate tectonics.

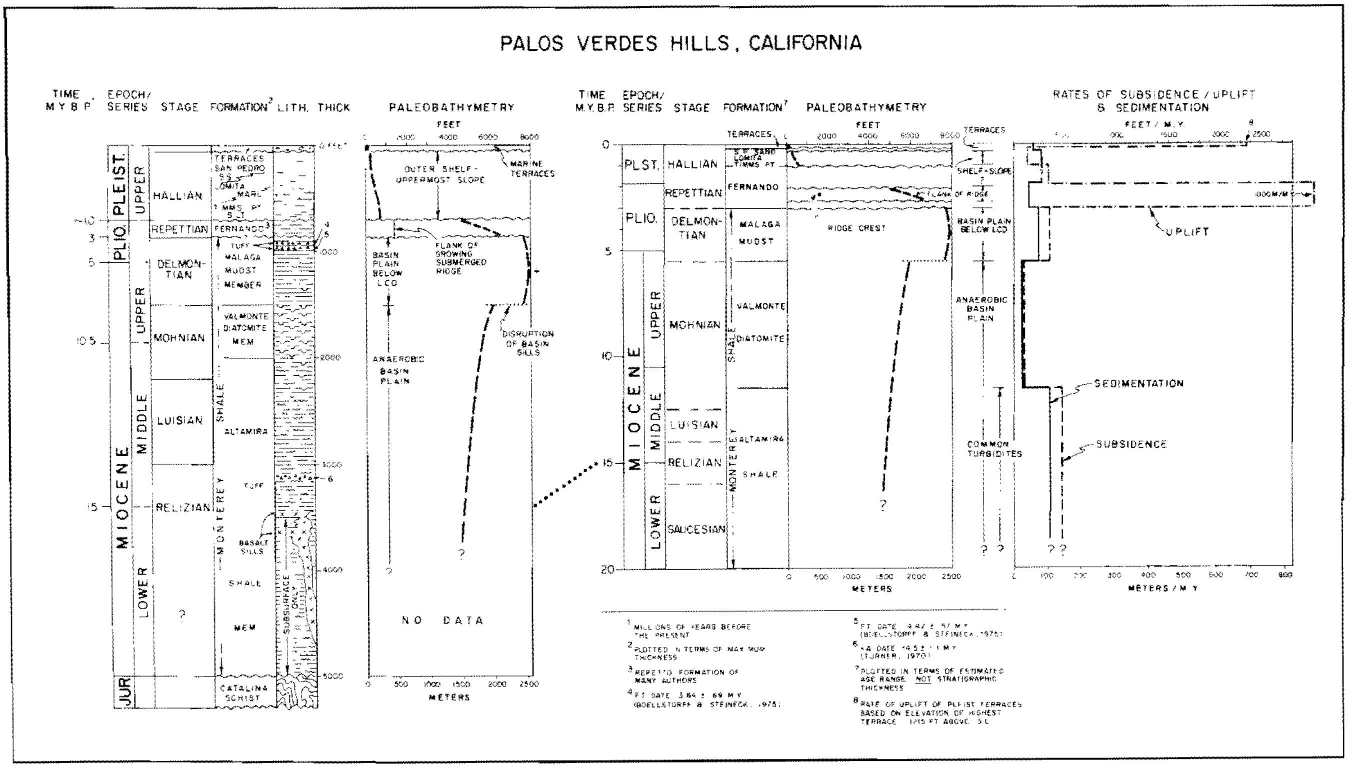


FIGURE 14

Paleobathymetry and marine paleoenvironments within Neogene deposits of the Palos Verdes Hills, California. Note that paleobathymetry is plotted in terms of maximum stratigraphic thickness of each formation and alternately in terms of estimated duration of each unit in time following the time scale and correlations presented on Figure 2 together with the potassium-argon dates of Turner (1970) and the fission-track dates of Boellstorff and Steineck (1975). Estimated paleobathymetry is based on biofacies analysis of foraminiferal and radiolarian assemblages reported from these strata by Woodring, Bramlette, and Kew (1946) and Ingle (1967a). Age assignments include consideration of planktonic foraminiferal and radiolarian data presented by Ingle (1967a), Casey (1972), and Casey and Price (1973).

middle Miocene (Relizian) in the area of Santa Rosa Island (Fig. 12), and 2,000 m or deeper by middle Miocene (Luisian) time along the southern margin of the borderland (Fig. 13). Interestingly, Neogene tectonic and sedimentologic patterns are almost the exact inverse of events terminating Paleogene marine deposition, with the added twist that highest rates of early Neogene sedimentation and subsidence prevailed in areas of former Paleogene stability (e.g., Fig. 13).

All evidence points to a middle Miocene (Luisian) borderland bathymetry consisting of a series of essentially empty basins momentarily deficient in terrigenous debris due to rapid tectonic adjustment of basin margins, formation of intervening sills, and eastward transgression of Miocene strandlines and associated spigots of terrigenous sediment (Fig. 1). The almost simultaneous and ubiquitous appearance of laminated diatomaceous muds (Monterey Formation) at the conclusion of middle Miocene (Relizian-Luisian) subsidence attests to the truly effective nature of basin sills created during this phase of borderland evolution (Figs. 9–14). These dominantly biogenic deposits are the direct analogues of laminated diatomites now forming on basin slopes and floors in the Gulf of California and elsewhere under the influence of well-developed oxygen minimum zones and prolific diatom production in overlying waters (Hulesmann and Emery, 1971; Calvert, 1964; Ingle, 1967a, 1973b; Ingle and Garrison, 1977; Figs. 4, 7).

Benthonic foraminifera characteristic of low oxygen conditions (Table 2) are common in Monterey shales along with displaced members of shelf through middle bathyal biofacies indicative of middle and late Miocene (Relizian to Mohnian) basin sills at 200 to 1,000 m (e.g., Ingle, 1967a, b, 1972; Fig. 9). These latter paleodepths were well within the core of the oxygen minimum layer dictating low oxygen conditions in subsill areas regardless of depth of individual basin floors (Emery, 1960, p. 110) facilitating widespread preservation of seasonal diatomaceous lamina. In fact, relationships documented in the modern low oxygen subsill environment of Santa Barbara Basin (Fig. 1) suggest that (a) laminated Miocene diatomites formed beneath ambient basin waters with dissolved oxygen concentrations of less than 0.1 ml/l; (b) nonlaminated but thin-bedded diatomaceous shales formed beneath waters containing 0.3–0.5 ml/l of oxygen; and (c) more homogeneous diatomaceous muds were deposited under waters containing 0.5–1.0 ml/l of oxygen (Emery and Hulesmann, 1962; Rhodes and Morse, 1971) reflecting progressive and/or alternating exclusion of macrofaunal invertebrates capable of destroying seasonal diatomaceous lamina through bioturbation. Diatomaceous muds and intercalated fine-grained distal turbidites accumulated at rates of 50 to 150 m/m.y.[9] compensated by equally low rates of subsidence. This balance apparently maintained relatively constant depths of basin floors during deposition of the 300 to 900 m of Miocene siliceous shales, diatomites, and diatomaceous shales assigned to the Monterey, lower Sisquoc, and Santa Margarita Formations in the northern borderland and the Monterey, Modelo, Puente, and lower Capistrano formations of the southern borderland (e.g., Figs. 9, 13).

Quiet middle Miocene (Relizian-Luisian) deposition of diatomaceous muds was interrupted in local areas by introduction of coarse terrigenous debris containing large clasts of distinctive glaucophane schist (San Onofre Breccia). This material was shed onto basin slopes and floors from fault scarps and narrow shelves created during rapid early to early middle Miocene basin subsidence in or near areas underlain by Mesozoic Catalina schist basement (Woodford, 1925; Yeats, 1973; Stuart, 1973). Lenses of this unusual lithofacies form portions of early Miocene (Saucesian-Relizian) supra fan base-of-slope deposits in the Santa Rosa Island area (Avila and Weaver, 1969; Fig. 11), and similar breccia occurs interbedded with middle Miocene (Luisian) basinal diatomites in the San Joaquin Hills (Woodford and others, 1954; Fig. 13).

Deteriorating Neogene climate was punctuated by severe global refrigeration in the late Miocene (Ingle, 1967a, 1973a, b; Kennett, 1967; Mayewski, 1973; Kennett and others, 1975; Shackleton and Kennett, 1975a) accompanied by intensification of upwelling and primary productivity in eastern boundary current areas such as southern California. This event is clearly signaled by significant changes in the composition of both benthonic and planktonic foraminiferal biofacies in southern California (Kleinpell, 1938; Ingle, 1967a, 1973b, 1977a, c). Deposition of laminated diatomaceous muds was enhanced under these paleoclimatic conditions and continued unabated in oxygen-deficient borderland basins until latest Miocene (Mohnian-Delmontian) time (e.g., Figs. 9, 11, 13, 14). However, Plio-Pleistocene depositional trends were anticipated by the initial appearance of major submarine fan deposits in the eastern borderland basins in late Miocene (Mohnian) time as represented by the Tarzana fan (Sullwold, 1960) and the Doheny channel-and-fan system (Bartow, 1966; Piper and Normark, 1971) within the Santa Ana Mountains-San Joaquin Hills sequence (Fig. 13). These great wedges of terrigenous clastics moved seaward across basin floors, capping underlying diatomaceous muds and diluting the continuing rain of biogenic debris from the photic zone—a pattern which was to become the dominant theme during later Plio-Pleistocene filling of eastern and northern borderland basins.

PLIOCENE AND PLEISTOCENE EVENTS

Prevailing patterns of Miocene sedimentation were seriously altered as a result of Pliocene flexing and tectonic reorganization of borderland topography (Emery, 1960; Yerkes and others, 1965; Moore, 1969). These processes are reflected by differences in position of late Miocene and middle Pliocene strandlines (Fig. 1) and by rapid Pliocene bathymetric changes induced by increasing rates of subsidence, uplift, and sedimentation throughout the Santa Barbara Embayment area (Figs. 9, 11, 12) and in borderland basins to the south (Figs. 13, 14). Initial late Miocene-early Pliocene uplift along portions of the borderland margin such as that expressed in the eastern Santa Ynez Mountains (e.g., Ingle, 1969) was matched by deepening in major synclinal areas including the Ventura and Los Angeles Basins along with concurrent adjustment of basin sills. This same period saw an increasing flux of terrigenous sediment into these two basins in terms of both fan deposits in northern and eastern base-of-slope areas as noted earlier and widespread appearance of fine-grained material in deep basin plain areas forming a characteristic late Miocene-early Pliocene (Delmontian) lower bathyal lithofacies composed of massive mudstones generally devoid of calcareous foraminifera and containing prolific numbers of radiolarian tests (commonly 500 to 5,000/grams dry sediment; Ingle, 1967a). These latter deposits are

---

[9] Uncorrected for compaction.

typified by the Santa Margarita Formation in the Ventura Basin (Natland, 1957), the Malaga mudstone of the Palos Verdes Hills sequence (Ingle, 1967a), and the lower Capistrano Formation of the Santa Ana Mountains-San Joaquin Hills sequence (Ingle, 1972). All three of these units appear to be analogous to radiolarian-rich muds currently being deposited in the modern Gulf of California at depths in excess of 3,000 m (Van Andel, 1964; Ingle, 1967a). The lack of calcareous foraminifera, common presence of arenaceous foraminifera (Natland, 1957), and abundant radiolarians suggests these mudstones may have been deposited below the local calcium carbonate compensation level (Fig. 7).

Increasing rates of late Miocene-early Pliocene (Delmontian) terrigenous sedimentation, cessation of subsidence, and consequent shoaling along the northwestern margin of the borderland are recorded in the upper Sisquoc Formation (Dibblee, 1950) foreshadowing Plio-Pleistocene uplift of the entire Santa Ynez Mountains area (Fig. 9). Weaver (1969b) also notes probable Pliocene uplift along the present San Miguel Island-Anacapa Island trend south of the Santa Barbara Basin-Ventura Basin trough (Fig. 1), and Emery (1960, p. 94), Moore (1969), and Vedder and others (1974) all conclude that initial growth of major northwest-southeast anticlinal highs such as the Santa Rosa-Cortez ridge (Fig. 1) occurred during early to middle Pliocene time. More specific evidence of the chronology of these compressive and translational events is displayed in the Miocene through Pleistocene sequence of the Palos Verdes Hills (Fig. 14). This readily accessible area constitutes a premier example of Plio-Pleistocene anticlinal growth in the area of a former middle to late Miocene (Relizian-Mohnian) basin plain collecting laminated diatomaceous sediments (Altimira Shale and Valmonte Diatomite). Recent fission-track dates and associated radiolarian faunas (Casey, 1972; Boellstorff and Steineck, 1975) indicate that lower bathyal Malaga Mudstones overlying the diatomaceous units were deposited during latest Miocene and early Pliocene time (about 3 to 6 m.y.B.P.). These beds are in turn disconformably overlain by a thin unit of middle to upper Pliocene glauconitic silts and sands (Fernando Formation)[10] containing lower bathyal through middle bathyal in situ biofacies mixed with high percentages of upper bathyal species displaced down the flank of an adjacent shoal area representing a growing sea-floor structure (Ingle, 1967a). The significant abundances of displaced upper bathyal species and glauconite pellets in this unit indicate the crest of the rising submarine bank or ridge was shallower than 500 m by middle Pliocene time and that initial uplift of the Palos Verdes anticline occurred between 2 and 3 m.y.B.P. at a rate of at least 1,000 m/m.y.[11] (Fig. 14). Continued flexing and growth of this structure took place during Pleistocene time as marked by a significant unconformity separating deep bathyal Pliocene silts from overlying upper bathyal-neritic deposits of Pleistocene age (Lomita Marl, Timms Point Silt, and San Pedro Sand). An additional unconformity is present between these latter deposits and late Pleistocene marine terraces which ring the present hills at elevations of up to 380 m above present sea level (Woodring, Bramlette, and Kew, 1946) indicative of major uplift during latest Pleistocene time (Fig. 14). The episodic middle Pliocene and late Pleistocene history of uplift displayed by the Palos Verdes Hills structure is in all likelihood similar to the pattern of growth experienced by other major northwest-southeast anticlinal ridges separating basins within the present continental borderland of southern California as detailed by Moore (1969).

Equally dynamic uplift of borderland margins paralleled Plio-Pleistocene growth of interbasin ridges resulting in relatively telescoped stratigraphies as illustrated by the Santa Ana Mountains-San Joaquin Hills sequence (Fig. 13). Pliocene and Pleistocene shoaling in this particular area was the combined result of major increase in rate of sedimentation coincident with rapid uplift. The transition from lower bathyal radiolarian-rich mudstones to lower bathyal coarse silt and sands in the upper Capistrano Formation marks the initial appearance of a prograding wedge of slope deposits onto this portion of the basin floor. Lower bathyal, middle bathyal, upper bathyal, and shelf biofacies appear sequentially in the overlying Plio-Pleistocene Fernando Formation and quantitative biofacies analysis of this sequence demonstrates that displaced species constitute well over 75 percent of most lower bathyal assemblages marked by *Melonis pompilioides* (Ingle, 1972), similar to modern trends in the Gulf of California (Fig. 5).

In contrast to the interrupted and/or abbreviated Plio-Pleistocene sequences deposited along the eastern and northern margins of the borderland and on seaward interbasin ridges, the subsiding Los Angeles and Ventura Basins provided receptacles for continuous deposition of enormous volumes of sediment re-

---

[10] "Repetto Formation" of many authors.

[11] Rate based on deepest possible middle Pliocene crest bathymetry of −500 m.

sulting in expanded records of this period. These two depocenters have received an inordinate amount of study due to the prolific accumulations of hydrocarbons present in both areas generated from highly organic Miocene diatomaceous sediments lying beneath basin fill of Plio-Pleistocene terrigenous clastics (Barbat, 1958; Holman, 1958; Mayuga, 1970). Papers by Bandy (1953), Natland (1957), Woodford and others (1954), Conrey (1967), and Yerkes and others (1965) illustrate that more than 6,000 m of terrigenous detritus were deposited in the northwest-southeast-trending central trough of the Los Angeles Basin during Pliocene and Pleistocene time, primarily in the form of turbidites which poured into the subsiding depression from the north and east, filling the basin by latest Pleistocene time. A similar and equally dynamic history of Pliocene and Pleistocene subsidence and turbidite deposition is present in over 6,200 m of basin plain, deep sea fan, slope, and shelf deposits held within the western Ventura Basin as described by Natland (1933, 1957) and Natland and Kuenen (1951).

Paleobathymetric analysis of Plio-Pleistocene sequences in both the Los Angeles and Ventura Basins is facilitated by the fact that the vast majority of foraminifera found as fossils in these sediments are currently living within established bathymetric limits in the Recent northeastern Pacific as discussed and illustrated by Natland (1933, 1957), Natland and Kuenen (1951), and Bandy (1953), Natland and Rothwell (1954), White (1956), Ingle (1967a, 1972, 1976), and Kern and Wicander (1974). However, analysis of planktonic foraminifera from various sections in these same deposits has shown that appearances of depth-diagnostic biofacies (Table 2) vary in time and space both within and between the Los Angeles and Ventura Basins as a function of varying rates of subsidence, uplift, and sedimentation, as might be expected in this dynamic province (Bandy, 1967; Ingle, 1967a, 1976). Despite these differences in timing and duration of discrete paleoenvironmental controlled biofacies and lithofacies in any given area, the fundamental pattern of Plio-Pleistocene basin filling is essentially the same in both basins and closely follows the model of borderland basin sedimentation proposed by Gorsline and Emery (1959). In each instance, the rapid transgression of outer submarine fan debris across early Pliocene basin floors is followed by the sequential appearance of interlobe, mid fan, supra fan, slope, shelf, and, finally, nonmarine alluvial facies exemplified by the western Ventura Basin sequence (Fig. 12). Significantly, recent fission-track dates (Izett and others, 1974; Boellstorff and Steineck, 1975), paleomagnetic signatures (Blackie and Yeats, 1976), and planktonic biostratigraphy (Ingle, 1967a; Bandy and Wilcoxin, 1970; Casey, 1972) suggest that portions of the coarse Plio-Pleistocene basin fill ("Repetto," Pico, Fernando, and Capistrano Formations) are younger than traditionally assumed (Fig. 12), forcing a revaluation of previously estimated rates of sedimentation and subsidence (Bandy, 1953; Yerkes and others, 1965) in terms of both the currently accepted radiometric ages of the Pliocene-Miocene (5 m.y.B.P.) and Pliocene-Pleistocene (1.8 m.y.B.P.) boundaries as well as the estimated positions of these boundaries in local sections (Figs. 2, 12, 13).

Recalibration of the Plio-Pleistocene basin-filling finale in the Ventura area (Fig. 2) demonstrates the very abrupt and dramatically high increases in rates of sediment accumulation and subsidence that were induced as Pliocene submarine fan debris spilled onto the deep basin floor (Fig. 12). The immediately preceding and tectonically induced pulse of late Miocene-early Pliocene subsidence occurred at rates of less than 500 m/m.y. but quickly accelerated to 1,000 m/m.y. about 3 m.y.B.P., when rapid sediment loading occurred due to fan transgression. Plio-Pleistocene rates of sediment accumulation averaging 2,000 m/m.y. outpaced subsidence and rapidly filled the Ventura Basin to capacity by late Pleistocene time, with similar events taking place in the adjacent Los Angeles Basin (Yerkes and others, 1965). Rate of sediment accumulation dropped sharply in the later Pleistocene as sediments began to pass across the brimful Ventura Basin with rates of subsidence almost balanced by rate of sediment accumulation just prior to major late Pleistocene flexing of this area and initiation of the present cycle of basin filling centered in the partially filled basins west and south of the modern strandline (Figs. 1, 12).

ACKNOWLEDGMENTS

It has been my pleasure to discuss the micropaleontology, stratigraphy, and geologic history of southern California with many of the authors appearing in the accompanying list of references along with an equal number of unpublished workers in the area. I readily acknowledge my dependency on the collective efforts of all of these individuals, most especially K. O. Emery of Woods Hole Oceanographic Institution and the late Orville Bandy to whom this volume is dedicated. Nevertheless, I relieve all of these colleagues of any responsibility for my manipulations and interpretations of their hard-won data which appear in this report. I also thank Anne Berry and Marie Phillips for typing and editorial assistance, and Perfecto Mari for

drafting many of the detailed illustrations accompanying this paper.

REFERENCES

Addicott, W. O., 1969, Tertiary climatic change in the marginal northeastern Pacific Ocean: Science, v. 165, p. 583–586.

Akpati, B. N., 1966, Micropaleontology of the Jalama and Anita formations: California Univ., Los Angeles, unpub. M.S. thesis.

Arnold, R., 1909, Environment of the Tertiary faunas of the Pacific Coast of the United States: Jour. Geology, v. 17, p. 509–533.

Atwater, T., 1970, Implications of plate tectonics for the Cenozoic tectonic evolution of western North America: Geol. Soc. America Bull., v. 81, p. 3313–3356.

Avila, F. A., and Weaver, D. W., 1969, Mid-Tertiary stratigraphy, Santa Rosa Island, *in* Weaver, D. W., Doerner, D. P., and Nolf, B., eds., Geology of the northern Channel Islands: Pac. Secs. Am. Assoc. Petroleum Geologists-Soc. Econ. Paleontologists and Mineralogists, Pacific Secs., Spec. Pub., p. 48–67.

Bagg, R. M., 1912, Pliocene and Pleistocene foraminifera from southern California: U.S. Geol. Survey Bull. 513, p. 1–153.

Bailey, T. L., 1952, Geology of southwestern Santa Barbara County, California, by T. W. Dibblee, Jr. (review): Am. Assoc. Petroleum Geologists Bull., v. 36, p. 176–182.

Bailey, T. L., and Jahns, R. H., 1954, Geology of the Transverse Range Province, Southern California, [Pt. 6] *in* Chap. 2 *of* Jahns, R. H., ed., Geology of southern California: California Div. Mines Bull. 170, p. 83–106.

Bandy, O. L., 1953, Ecology and paleoecology of some California foraminifera: Jour. Paleontology, v. 27, p. 161–203.

———, 1960a, The geologic significance of coiling in the foraminifera *Globigerina pachyderma* (Ehrenberg): Jour. Paleontology, v. 34, p. 671–681.

———, 1960b, General correlation of foraminiferal structure with environment. Internat. Geol. Congr., 21st Sess., Norden, pt. 22, p. 7–19.

———, 1961, Distribution of foraminifera, radiolaria and diatoms in sediments of the Gulf of California: Micropaleontology, v. 7, p. 1–26.

———, 1963, Larger living foraminifera of the continental borderland of southern California: Cushman Found. Foram. Research Contr., v. 14, pt. 4, p. 121–126.

———, 1967, Foraminiferal definition of the boundaries of the Pleistocene in southern California, *in* Sears, M., ed., Progress in Oceanography, v. 4: New York, Pergamon Press, p. 27–49.

———, 1968, Cycles in Neogene paleoceanography and eustatic changes: Palaeography, Palaeoclimatology, Palaeoecology, v. 5, p. 63–75.

———, 1971, Neogene planktonic foraminiferal zones, California, and some geologic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 12, p. 131–150.

———, 1972a, Upper Paleogene planktonic correlations, Santa Barbara area, California, *in* Weaver, D. W., ed., Guidebook central Santa Ynez Mountains: Pacific Secs. Am. Assoc. Petroleum Geologists-Soc. Econ. Paleontologists and Mineralogists, Santa Barbara, p. 55–58.

———, 1972b, Late Paleogene-Neogene planktonic biostratigraphy and some geologic implications, California, *in* Steinmeyer, E., ed., Pacific Coast Miocene biostratigraphic symposium. Pacific Sec. Soc. Econ. Paleontologists and Mineralogists, Bakersfield, p. 37–51.

Bandy, O. L., and Arnal, R. E., 1957, Distribution of Recent foraminifera off the West Coast of Central America: Am. Assoc. Petroleum Geologists Bull., v. 41, p. 2037–2053.

———, 1960, Concepts of a foraminiferal paleoecology: Am. Assoc. Petroleum Geologists Bull., v. 44, p. 1921–1932.

———, 1969, Middle Tertiary basin development, San Joaquin Valley, California: Geol. Soc. America Bull., v. 80, p. 783–820.

Bandy, O. L., and Ingle, J. C., Jr., 1970, Neogene planktonic events and radiometric scale, California: Geol. Soc. America Spec. Paper 124, p. 131–172.

Bandy, O. L., Ingle, J. C., Jr., and Resig, J. M., 1964, Facies trends, San Pedro Bay, California: Geol. Soc. America Bull., v. 75, p. 403–424.

Bandy, O. L., and Kolpack, R. J., 1963, Foraminiferal and sedimentological trends in the Tertiary section of Tecolote Tunnel, California: Micropaleontology, v. 9, p. 117–170.

Bandy, O. L., and Rodolfo, K. S., 1964, Distribution of foraminifera and sediments, Peru-Chile Trench area: Deep-Sea Research, v. 11, p. 817–837.

Bandy, O. L., and Wilcoxin, J. A., 1970, The Plio-Pleistocene boundary, Italy and California: Geol. Soc. America Bull., v. 81, p. 2939–2948.

Barbat, W. F., 1958, The Los Angeles Basin area, California, *in* Higgins, J. W., ed., A guide to the geology and oil fields of the Los Angeles and Ventura regions: Los Angeles, Pacific Sec. Am. Assoc. Petroleum Geologists, p. 37–49.

Barron, J. A., 1973, Late Miocene-early Pliocene paleotemperatures for California from marine diatom evidence. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 14, p. 277–291.

———, 1975, Marine diatom biostratigraphy of the upper Miocene-lower Pliocene strata of southern California: Jour. Paleontology, v. 49, p. 619–632.

Bartow, J. A., 1966, Deep submarine channel in upper Miocene, Orange County, California: Jour. Sed. Petrology, v. 36, p. 700–705.

Beckmann, J., 1953, Die Foraminiferen der Oceanic Formation (Eocaen-Oligocenaen) von Barbadoes: Ecologae Geol. Helvetiae, v. 46, p. 301–412.

Berger, W. H., 1970, Planktonic foraminifera: selective solution and the lysocline: Marine Geology, v. 8, p. 111–138.

———, 1974, Deep-sea sedimentation, *in* Burk, C. A., and Drake, C. L., eds., The geology of continental margins: New York, Springer-Verlag, p. 213–241.

Berggren, W. A., 1969, Cenozoic chronostratigraphy, planktonic foraminiferal zonation and the radiometric time scale: Nature, v. 224, p. 1072–1075.

———, 1972, A Cenozoic time-scale—some implications for regional geology and paleobiogeography: Lethaia, v. 5, p. 195–215.

Berggren, W. A., McKenzie, D. P., Sclater, J. G., and Van Hinte, J. E., 1975, World-wide correlation of Mesozoic magnetic anomalies and its implications: discussion and reply: Geol. Soc. America Bull., v. 86, p. 267–272.

Berggren, W. A., and Van Couvering, J. A., 1974, The late Neogene. Biostratigraphy, geochronology, and paleoclimatology of the last 15 million years in marine and continental sequences: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 16, Spec. Issue, p. 1–216.

Blackie, G. W., and Yeats, R. S., 1976, Magnetic reversal stratigraphy of the Plio-Pleistocene producing section of the Saticoy Oil Field, Ventura Basin, California: Am. Assoc. Petroleum Geologists Bull., v. 60, p. 1985–1992.

Blaisdell, R. C., 1953, The stratigraphy and foraminifera of the Matilija, Cozy Dell, and "Coldwater" Formations near Ojai, California: California Univ. Berkeley, unpub. M.S. thesis.

Boellstorff, J. D., and Steineck, P. L., 1975, The stratigraphic significance of fission-track ages on volcanic ashes in the marine late Cenozoic of southern California: Earth and Planetary Sci. Letters, v. 27, p. 143–154.

Bramlette, M. N., and Wilcoxin, J. A., 1967, Middle Tertiary calcareous nannoplankton of the Cipero section, Trinidad, W. I.: Tulane Studies in Geology, v. 5, p. 93–131.

Bukry, D., Brabb, E. E., and Vedder, J. G., 1973, Correlation of Tertiary nannoplankton assemblages from the Coast and Peninsular Ranges of California: Preprint, Congress Latinoamericano de Geologia, Second, Caracas, p. 1–35.

Bukry, D., Brabb, E. E., and Vedder, J. G., 1977, Correlation of Tertiary nannoplankton assemblages from the Coast and Peninsular ranges of California. Congreso Latinoamericano de Geologia, Second, Mem., t. 3, p. 1461–1483.

Calvert, S. E., 1964, Factors affecting distribution of laminated sediments in the Gulf of California, *in* van Andel, T., and Shor, G., eds., Marine geology of the Gulf of California: Am. Assoc. Petroleum Geologists Mem., p. 311–330.

Casey, R. E., 1972, Neogene radiolarian biostratigraphy and paleotemperatures: southern California, the experimental MOHOLE, Antarctic Core 14-8: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 12, p. 115–130.

Casey, R. E., and Price, A. B., 1973, A tentative radiolarian zonation and paleoceanographic interpretation from Newport Bay, California, *in* Fischer, P., and Johnson, D., eds., Miocene sedimentary environments and biofacies, southeastern Los Angeles Basin: Soc. Econ. Paleontologists and Mineralogists, Guidebook Field Trip no. 1, 1973 Ann. Mtg., Los Angeles, p. 67–70.

Conrey, B. L., 1967, Early Pliocene sedimentary history of the Los Angeles Basin, California: California Div. Mines and Geology, Spec. Rept. 93.

Corey, W. H., 1954, Tertiary basins of southern California, [Pt.] 8 *in* Chap. 3 *of* Jahns, R. H., ed., Geology of Southern California: California Div. Mines Bull. 170, p. 73–83.

———, 1965, The paleogeography of the lower Tertiary formations of Santa Barbara County, California, *in* Weaver, D. W., and Dibblee, T., eds., Western Santa Ynez Mountains, Santa Barbara County, California: Coast Geol. Soc. and Pacific Sec. Soc. Econ. Paleontologists and Mineralogists, Guidebook, p. 31–37.

Crowell, J. C., 1974, Origin of late Cenozoic basins in southern California, *in* Dickinson, W. R., ed., Tectonics and sedimentation: Soc. Econ. Paleontologists and Mineralogists, Spec. Pub. 22, p. 190–204.

Devereux, I., 1967, Oxygen isotope paleotemperature measurements on New Zealand Tertiary fossils: New Zealand Jour. Sci., v. 10, p. 988–1011.

Dibblee, T. W. Jr., 1950, Geology of southwestern Santa Barbara County, California: California Div. Mines Bull. 150, p. 1–95.

———, 1966, Geology of the central Santa Ynez Mountains, Santa Barbara County, California: California Div. Mines and Geology Bull. 186, p. 1–99.

Dickinson, W. R., 1969, Geologic problems in the mountains between Ventura and Cuyama, *in* Dickinson, W. R., ed., Geologic setting of upper Miocene gypsum and phosphorite deposits, upper Sespe Creek and Pine Mountain, Ventura County, California: Pacific Sec. Soc. Econ. Paleontologists and Mineralogists, Field Trip Guidebook, p. 1–23.

Dickinson, W. R., and Graham, S. E., 1975, Sedimentary environments, depositional systems, and stratigraphic cycles, *in* Dickinson, W. R., ed., Current concepts of depositional systems with applications for petroleum geology: Bakersfield, San Joaquin Geol. Soc., p. 01–010.

Dickinson, W. R., and Lowe, D. R., 1966, Stratigraphic relations of phosphate and gypsum bearing upper Miocene strata, upper Sespe Creek, Ventura County, California: Am. Assoc. Petroleum Geologists Bull., v. 50, p. 2464–2470.

Doerner, D. P., 1969, Lower Tertiary biostratigraphy of southwestern Santa Cruz Island, *in* Weaver, D. W., Doerner, D. P., and Nolf, B., Geology of the northern Channel Islands: Pacific Secs. Am. Assoc. Petroleum Geologists and Soc. Econ. Paleontologists and Mineralogists, Spec. Pub., p. 17–29.

Dorf, E., 1955, Plants and the geologic time scale, *in* Poldervarrt, A., ed., Crust of the earth: Geol. Soc. America Spec. Paper 62, p. 575–592.

Dorman, F. H., 1966, Australian Tertiary paleotemperatures: Jour. Geology, v. 74, p. 49–61.

———, 1968, some Australian oxygen isotope temperatures and a theory for a 30-million-year world temperature cycle: Jour. Geology, v. 76, p. 297–313.

Dott, R. H., 1969, Circum-Pacific late Cenozoic structural rejuvenations; implications for sea floor spreading: Science, v. 166, p. 874–876.

Dott, R. H., and Shaver, R. H., eds., 1974, Modern and ancient geosynclinal sedimentation: Soc. Econ. Paleontologists and Mineralogists Spec. Pub. 19, p. 1–380.

Douglas, R. G., 1973, Benthonic foraminiferal biostratigraphy in the central North Pacific, Leg 17, Deep Sea Drilling Project: Deep Sea Drilling Proj., Initial Repts., v. 17, p. 607–671.

Durham, J. W., 1950, Cenozoic marine climates of the Pacific Coast: Geol. Soc. America Bull., v. 61, p. 1243–1264.

Edwards, L. N., 1972, Notes on the Vaqueros and Rincon Formations, west-central Santa Ynez Mountains, *in* Weaver, D. W., ed., Guidebook central Santa Ynez Mountains, Pacific Secs. Am. Assoc. Petroleum Geologists and Soc. Econ. Paleontologists and Mineralogists, p. 46–54.

Emery, K. O., 1960, The sea off southern California, a modern habitat of petroleum: New York, John Wiley and Sons, p. 1–366.

———, 1969, Continental rises and oil potential: Oil and Gas Jour., v. 67, p. 231–243.

Emery, K. O., and Hulesmann, J., 1962, The relationships of sediments, life, and water in a marine basin: Deep-sea Research, v. 8, p. 165–180.

Emiliani, C., 1954, Temperatures of Pacific bottom waters and polar superficial waters during the Tertiary: Science, v. 119, p. 853–855.

———, 1956, Oligocene and Miocene temperatures of equatorial and subtropical Atlantic Ocean: Jour. Geology, v. 64, p. 281–288.

Evernden, J. F., Savage, D. E., Curtis, G. H., and James, G. T., 1964, Potassium-argon dates and the Cenozoic mammalian chronology of North America: Am. Jour. Sci., v. 262, p. 145–198.

Garrison, R. E., and Fischer, A. G., 1969, Deep-water limestones and radiolarites of the Alpine Jurassic, *in* Friedmann, G. M., ed., Depositional environments in carbonate rocks: Soc.

Econ. Paleontologists and Mineralogists, Spec. Pub. 14, p. 20–54.

Gibson, J. M., 1973, Foraminiferal biostratigraphy of the Anita Formation, western Santa Ynez Mountains, Santa Barbara County, California: Southern California Univ., Los Angeles, unpub. M.S. thesis, p. 1–319.

———, 1974, Campanian-Maestrichtian foraminifer and nannoplankton biostratigraphy, Jalama Formation, western Santa Ynez Mountains, Santa Barbara County, California: Pacific Sec. Soc. Econ. Paleontologists and Mineralogists, preprint v. 1974 Ann. Mtg., p. 40–48.

Gorsline, D. S., and Emery, K. O., 1959, Turbidity current deposits in San Pedro and Santa Monica basins off southern California: Geol. Soc. America Bull., v. 70, p. 279–290.

Harman, R. A., 1964, Distribution of foraminifera in the Santa Barbara Basin, California: Micropaleontology, v. 10, p. 81–96.

Hedgpeth, J. W., 1957, Classification of marine environments, *in* Hedgpeth, J. W., ed., Treatise on marine ecology and paleoecology: Geol. Soc. America Mem. 67, v. 1, p. 17–28.

Holman, W. H., 1958, Correlation of producing zones of Ventura Basin oil fields, *in* Higgins, J. W., ed., A guide to the geology and oil fields of the Los Angeles and Ventura regions: Los Angeles, Pacific Sec. Am. Assoc. Petroleum Geologists, p. 191–199.

Hornaday, G. R., 1961, Foraminifera from the Sacate Formation south of Refugio Pass, Santa Barbara County, California: California Univ. Pub. Geol. Sci., v. 37, p. 165–232.

———, 1972, Oligocene smaller foraminifera associated with an occurrence of *Miogypsina* in California: Jour. Foram. Research, v. 2, p. 35–46.

Hulesmann, J., and Emery, K. O., 1961, Stratification in Recent sediments of Santa Barbara Basin as controlled by organisms and water characteristics: Jour. Geology, v. 69, p. 279–290.

Ingle, J. C., Jr., 1962, Paleoecologic, sedimentary, and structural history of the late Tertiary Capistrano Embayment, California: Southern California Univ., unpub. M.S. thesis.

———, 1967a, Foraminiferal biofacies and the Miocene-Pliocene boundary in southern California: Bulls. Am. Paleontology, v. 52, p. 1–217.

———, 1967b, Modern biofacies and lithofacies as empirical geological models, *in* Bandy, O. L., ed., Current concepts of paleoecology: Washington: Am. Geol. Inst., Short Course Lec. Notes, p. J1-A-1–J1-A-21.

———, 1969, Foraminiferal trends and paleobathymetry within the Monterey and Santa Margarita Formations, upper Sespe Creek-Pine Mountain area, Ventura County, California, *in* Dickinson, W. R., ed., Geologic setting of upper Miocene gypsum and phosphorite deposits, upper Sespe Creek and Pine Mountain, Ventura County, California: Pacific Sec. Soc. Econ. Paleontologists and Mineralogists, Guidebook, p. 78–92.

———, 1972, Biostratigraphy and paleoecology of early Miocene through early Pleistocene benthonic and planktonic foraminifera, San Joaquin Hills-Newport Bay, Orange County, California: *in* Steinmeyer, E., ed., The Pacific Coast Miocene biostratigraphic symposium: Pacific Sec. Soc. Econ. Paleontologists and Mineralogists, p. 255–283.

———, 1973a, Neogene foraminifera from the northeastern Pacific Ocean, Leg 18, Deep Sea Drilling Project: *in* Deep Sea Drilling Proj. Initial Repts., v. 18, p. 517–567.

———, 1973b, Summary comments on Neogene biostratigraphy, physical stratigraphy, and paleo-oceanography in the marginal northeastern Pacific Ocean: Deep Sea Drilling Proj., Initial Repts., v. 18, p. 949–960.

———, 1975a, Paleoecologic indicators and trace fossils, *in* Dickinson, W. R., ed., Current concepts of depositional systems with applications for petroleum geology: Bakersfield, San Joaquin Geol. Soc., p. 8-1–8-11.

———, 1975b, Paleobathymetric analysis of sedimentary basins, *in* Dickinson, W. R., ed., Current concepts of depositional systems with applications for petroleum geology: Bakersfield, San Joaquin Geol. Soc., p. 11-1–11-12.

———, 1975c, Summary of late Paleogene-Neogene insular stratigraphy, paleobathymetry, and correlations, Philippine Sea and Sea of Japan region: Deep Sea Drilling Proj., Initial Repts., v. 31, p. 837–855.

———, 1976, Late Neogene paleobathymetry and paleoenvironments of the Humboldt Basin, northern California, *in* Fritsche, A. E., Ter Best, H., and Wornardt, W. W., eds., The Neogene symposium: Pacific Sec. Soc. Econ. Paleontologists and Mineralogists, Los Angeles, p. 53–61.

———, 1977a, Late Neogene marine events and the Pliocene-Pleistocene boundary in the marginal North Pacific: Gior. Geologia, Ser. 2a, v. 41, no. I–II, p. 359–374.

———, 1977b, Cenozoic paleoclimatic trends, history of the California Current, and Pacific Coast biostratigraphy: Geol. Soc. America, Abstracts with Programs, v. 9, p. 1032–1033.

———, 1977c, Summary of late Neogene planktic foraminiferal biofacies, biostratigraphy, and paleoceanography of the marginal North Pacific Ocean: Internat. Cong. Pacific Neogene Stratigraphy, First, Tokyo, Proc., p. 177–182.

Ingle, J. C., Jr., and Garrison, R. E., 1977, Origin, distribution, and diagenesis of Neogene diatomites around the North Pacific rim: Internat. Cong. Pacific Neogene Stratigraphy, First, Tokyo, Proc., p. 348–350.

Ingle, J. C., Jr., Graham, S. A., and Dickinson, W. R., 1976, Evidence and implications of worldwide late Paleogene climatic and eustatic events: Geol. Soc. America, Abstracts with Programs, v. 8, p. 934–935.

Izett, G. A., Naeser, C. W., and Obradovich, J. D., 1974, Fission track age of zircon from an ash bed in the Pico Formation (Pliocene and Pleistocene) near Ventura, California: Geol. Soc. America, Abstracts with Programs, v. 6, p. 197.

Jackson, E. D., Silver, E. A., and Dalrymple, G. B., 1972, Hawaiian-Emperor chain and its relation to Cenozoic circum-Pacific tectonics: Geol. Soc. America Bull., v. 83, p. 601–618.

Keller, G., and Ingle, J. C., Jr., 1977, Neogene planktonic foraminiferal biostratigraphy and paleoceanography of the northeastern Pacific: evidence from DSDP sites 173 and 310 at the North Pacific Front: Geol. Soc. America, Abstracts with Programs, v. 9, p. 1046–1047.

Keller, G. and Ingle, J. C., Jr., 1976, Recent benthic foraminiferal biofacies and water mass properties, southern Peru-Chile Trench area: Geol. Soc. America, Abstracts with Programs, v. 8, p. 951.

Kelley, F. R., 1943, Eocene stratigraphy in the western Santa Ynez Mountains, Santa Barbara County, California: Am. Assoc. Petroleum Geologists Bull., v. 27, p. 1–19.

Kennett, J. P., 1967, Recognition and correlation of the Kapitean Stage (Upper Miocene, New Zealand): New Zealand Jour. Geol. Geophysics, v. 10, p. 1051–1063.

———, 1968, Paleo-oceanographic aspects of the foraminiferal zonation in the upper Miocene-lower Pliocene of New Zealand: Gior. Geologia, v. 35, p. 143–156.

———, 1977, Cenozoic evolution of Antarctic glaciation, the Circum-Antarctic Ocean, and their impact on global paleoceanography: Jour. Geophys. Research, v. 82, p. 3843–3860.

Kennett, J. P., Houtz, R. E., Andrews, P. B., Edwards, A. R., Gustin, V. A., Hajos, M., Hampton, M., Jenkins, D. G., Margolis, S. V., Ovenshine, A. T., and Perch-Nielsen, K., 1975, Cenozoic paleoceanography in the southwest Pacific Ocean, Antarctic glaciation, and the development of the circum-Antarctic Current: Deep Sea Drilling Proj., Initial Repts., v. 29, p. 1155–1169.

Kennett, J. P., and Shackleton, N. J., 1976, Oxygen isotopic evidence for the development of the psychrosphere 38 Myr ago: Nature, v. 260, p. 513–515.

Kern, J. P., and Wicander, E. R., 1974, Origin of a bathymetrically displaced marine invertebrate fauna in the upper part of the Capistrano Formation (lower Pliocene), southern California: Jour. Paleontology, v. 48, p. 495–505.

Kleinpell, R. M., 1938, Miocene stratigraphy of California: Tulsa, Okla., Am. Assoc. Petroleum Geologists, p. 1–450.

Kleinpell, R. M., and Weaver, D. W., 1963, Oligocene biostratigraphy of the Santa Barbara Embayment, California. I. Foraminiferal faunas from the Gaviota and Alegria Formations: California Univ. Pubs. Geol. Sci., v. 43, p. 1–77.

Link, M., 1975, Matilija sandstone: a transition from deepwater turbidite to shallow-marine deposition in the Eocene of California: Jour. Sed. Petrology, v. 45, p. 63–78.

Lipps, J. H., 1967, Planktonic foraminifera, intercontinental correlation and age of the California mid-Cenozoic microfaunal stages: Jour. Paleontology, v. 41, p. 994–999.

———, 1972, Plankton biostratigraphy and paleoecology of the eastern North Pacific Ocean: introduction: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 12, p. 3–14.

Lipps, J. H., and Kalisky, M., 1972, Calcareous nannoplankton biostratigraphy and paleoecology, *in* Steinmeyer, E., ed., Proc. Pacific Coast Miocene biostratigraphic symposium: Pacific Sec. Soc. Econ. Paleontologists and Mineralogists, Bakersfield, p. 239–254.

Loel, W., and Corey, W. H., 1932, The Vaqueros Formation, lower Miocene of California. I. Paleontology. California Univ. Pubs., Dept. Geol. Sci. Bull., v. 22, p. 31–410.

Mallory, V. S., 1959, Lower Tertiary biostratigraphy of the California Coast Ranges: Tulsa, Okla., Am. Assoc. Petroleum Geologists, p. 1–417.

Margolis, S. V., and Kennett, J. P., 1971, Cenozoic paleoglacial history of Antarctica recorded in subantarctic deep-sea cores: Am. Jour. Sci., v. 271, p. 1–36.

Mayewski, P. A., 1973, Glacial geology and late Cenozoic history of the Transantarctic Mountains: Ohio State Univ., unpub. Thesis, 215 p.

Mayuga, M. N., 1970, Geology and development of California's giant—Wilmington Field, *in* Halbouty, M. T., ed., Geology of giant petroleum fields: Am. Assoc. Petroleum Geologists Mem. 14, p. 158–184.

McCracken, W. A., 1969, Sedimentary structures and paleocurrent analysis of the Sespe Formation, Ventura Basin, California: Am. Assoc. Petroleum Geologists Bull., v. 53, p. 463.

McKeel, D. R. and Lipps, J. H., 1975, Eocene and Oligocene planktonic foraminifera from the central and southern Oregon Coast Range: Jour. Foram. Research, v. 5, no. 4, p. 249–269.

Middleton, G. V., 1973, Johannes Walther's law of the correlation of facies: Geol. Soc. America Bull., v. 84, p. 979–988.

Moore, D. G., 1969, Reflection profiling studies of the California Continental Borderland—structure and Quaternary turbidite basins: Geol. Soc. America Spec. Paper 107, p. 1–142.

Murray, J., 1973, Distribution and ecology of living benthic foraminiferids: London, Crane, Russak, p. 1–274.

Natland, M. L., 1933, Temperature and depth classification of some Recent and fossil foraminifera in the southern California region: California Univ., Scripps Inst. Oceanography Bull., Tech. Ser., p. 225–230.

———, 1952, Pleistocene and Pliocene stratigraphy of southern California: California Univ., Los Angeles, unpub. Ph.D. dissert.

———, 1957, Paleoecology of West Coast Tertiary sediments, *in* Ladd, H. S., ed., Treatise on marine ecology and paleoecology: Geol. Soc. America Mem. 57, v. 2, p. 543–571.

Natland, M. N., and Keunen, P. H., 1951, Sedimentary history of the Los Angeles and Ventura regions, *in* Hough, J. L., ed., Turbidity currents and the transportation of coarse sediment into deep water: Soc. Econ. Paleontologists and Mineralogists Spec. Pub. 2, p. 76–107.

Natland, M. N., and Rothwell, W. T., 1954, Fossil foraminifera of the Los Angeles and Ventura regions, California, [Pt.] 5 *in* Chap. 3 *of* Jahns, R. H., ed., Geology of southern California: California Div. Mines Bull. 170, p. 33–42.

Nelson, C. H., 1975, Turbidite fans and other base-of-slope deposits, *in* Dickinson, W. R., ed., Current concepts of depositional systems with applications for petroleum geology: Bakersfield, San Joaquin Geol. Soc., p. 6-1-6-5.

Neumann, G., and Pierson, W. J., Jr., 1966, Principles of physical oceanography: Englewood Cliffs, N.J., Prentice-Hall, 545 p.

Nilsen, T. H., and Clarke, S. H., 1975, Sedimentation and tectonics in the early Tertiary continental borderland of central California: U.S. Geol. Survey Prof. Paper 925, p. 1–64.

Normark, W. R., 1974, Submarine canyons and fan valleys: factors affecting growth patterns of deep-sea fans *in* Dott, R. H., and Shaver, R. H., eds., Modern and ancient geosynclinal sedimentation: Soc. Econ. Paleontologists and Mineralogists Spec. Pub. 19, p. 56–68.

Normark, W. R., and Piper, D. J. W., 1969, Deep-sea fan valleys, past and present: Geol. Soc. America, Bull., v. 80, p. 1859–1866.

Obrien, J. M., 1972, Narizian-Refugian (Eocene-Oligocene) marine and marginal marine sedimentation, western Santa Ynez Mountains, Santa Barbara County, California, *in* Weaver, D. W., ed., Guidebook central Santa Ynez Mountains, Santa Barbara County, California: Pacific Sec. Soc. Econ. Paleontologists and Mineralogists, p. 37–43.

Packham, G. H., and Falvey, D. A., 1971, An hypothesis for the formation of marginal seas in the western Pacific: Tectonophysics, v. 11, p. 79–107.

Phillips, F. J., 1972, Age correlation of the Eocene Ulatisian and Narizian stages, California: discussion: Geol. Soc. America Bull., v. 83, p. 2217–2224.

Phleger, F. B., 1951, Ecology of foraminifera, northwest Gulf of Mexico. Part 1. Foraminiferal distribution: Geol. Soc. America Mem. 46, p. 1–88.

———, 1960, Ecology and distribution of Recent foraminifera: Baltimore, Johns Hopkins Press, p. 1–297.

———, 1964, Pattern of living foraminifera, *in* van Andel, T. H., and Shor, G. G., eds., Marine geology of the Gulf of California: Am. Assoc. Petroleum Geologists Mem. 3, p. 377–394.

Phleger, F. B., and Soutar, A., 1973, Production of benthic foraminifera in three east Pacific oxygen minima. Micropaleontology, v. 19, p. 110–115.

Pierce, R. L., 1972, Revaluation of the late Miocene biostratigraphy of California: summary of evidence, *in* Steinmeyer, E., ed., The Pacific Coast Miocene biostratigraphic symposium:

Pacific Sec., Soc. Econ. Paleontologists and Mineralogists, Bakersfield, p. 334–340.

Piper, D., and Normark, W. R., 1971, Re-examination of a Miocene deep-sea fan and fan-valley, southern California: Geol. Soc. America Bull., v. 82, p. 1823–1830.

Poore, R. Z., and Brabb, E. E., 1977, Eocene and Oligocene planktonic foraminifera from the upper Butano Sandstone and type San Lorenzo Formation, Santa Cruz Mountains, California: Jour. Foram. Research, v. 7, p. 249–272.

Reed, R. D., 1933, Geology of California: Tulsa, Okla., Am. Assoc. Petroleum Geologists, p. 1–355.

Reed, R. D., and Hollister, J. S., 1936, Structural evolution of southern California: Tulsa, Okla., Am. Assoc. Petroleum Geologists, p. 1–157.

Renz, H. H., 1948, Stratigraphy and fauna of the Agua Salada Group, State of Falcon, Venezuela: Geol. Soc. America, Mem. 32, 219 p.

Rhodes, D. C., and Morse, J. W., 1971, Evolutionary and ecologic significance of oxygen-deficient marine basins: Lethaia, v. 4, p. 413–428.

Richards, F. A., 1957, Oxygen in the ocean, in, Hedgpeth, J. W. (ed.), Treatise on marine ecology and paleoecology: Geol. Soc. America, Mem. 67, v. 1, p. 185–238.

Ricci-Lucchi, F., 1975, Depositional cycles in two turbidite formations of northern Apennines (Italy): Jour. Sed. Petrology, v. 45, p. 3–43.

Saito, T., and Van Donk, J., 1974, Oxygen and carbon isotope measurements of late Cretaceous and early Tertiary foraminifera: Micropaleontology, v. 20, p. 152–177.

Savin, S. M., 1977, The history of the earth's surface temperature during the past 100 million years: Earth and Planetary Sci. Ann. Rev., v. 5, p. 319–355.

Savin, S. M., Douglas, R. G., and Stehli, F. G., 1975, Tertiary marine paleotemperatures: Geol. Soc. America Bull., v. 86, p. 1499–1510.

Schenck, H. G., 1929, Discocyclina in California: San Diego Soc. Nat. History Trans., v. 5, p. 211–240.

Schmidt, R., 1970, Planktonic foraminifera from the lower Tertiary of California: California Univ., Los Angeles, unpub. Ph.D. dissert., p. 1–339.

———, 1971, Planktonic foraminiferal zonation from the lower Tertiary of California: paleogeographic and paleoclimatic implications: Geol. Soc. America, Abstracts with Programs, v. 3, p. 190.

Schnitker, D., 1974, West Atlantic abyssal circulation during the past 120,000 years: Nature, v. 248, p. 385–387.

Schrader, H. J., 1973, Cenozoic diatoms from the northeast Pacific, Leg 18: Deep Sea Drilling Proj. Initial Repts., v. 18, p. 673–797.

———, 1974, Revised diatom stratigraphy of experimental Mohole, Guadalupe Site: California Acad. Sci. Proc., ser. 4, no. 23, p. 517–562.

Selley, R. C., 1970, Ancient sedimentary environments: Ithaca, Cornell Univ. Press, p. 1–237.

Shackleton, N. J., and Kennett, J. P., 1975a, Paleotemperature history of the Cenozoic and initiation of Antarctic glaciation: oxygen and carbon isotope analysis in DSDP sites 277, 279, and 281: *in* Deep Sea Drilling Proj. Initial Repts., v. 29, p. 743–755.

———, J. P., 1975b, Late Cenozoic oxygen and carbon isotopic changes at DSDP Site 284: implications for glacial history of the northern hemisphere and Antarctica: Deep Sea Drilling Proj. Initial Repts., v. 29, p. 801–807.

Silver, E. A., 1974, Basin development along translational continental margins, *in* Dickinson, W. R., ed., Geologic interpretations from global tectonics with applications for California geology and petroleum exploration: Bakersfield, San Joaquin Geol. Soc., p. 6-1–6-5.

Sliter, W. V., 1972, Cretaceous foraminifers—depth habitats and their origin: Nature, v. 239, p. 514–515.

———, 1975, Foraminiferal life and residue assemblages from Cretaceous slope deposits: Geol. Soc. America Bull., v. 86, p. 897–906.

Sliter, W. V., and Baker, R. A., 1972, Cretaceous bathymetric distribution of benthic foraminifers: Jour. Foram. Research, v. 2, p. 167–183.

Smith, P. B., 1960, Foraminifera of the Monterey Shale and Puente Formations, Santa Ana Mountains and San Juan Capistrano area, California: U.S. Geol. Survey Prof. Paper 294-M, p. 463–495.

———, 1964, Ecology of benthonic species: U.S. Geol. Survey Prof. Paper 429-B, p. B1-B55.

Snyder, W., Dickinson, W. R., and Silberman, M. L., 1976, Tectonic implications of space-time patterns of Cenozoic magmatism in the western United States: Earth and Planetary Sci. Letters, v. 32, p. 91–106.

Stauffer, P. H., 1967a, Sedimentologic evidence on Eocene correlations, Santa Ynez Mountains, California: Am. Assoc. Petroleum Geologists Bull., v. 51, p. 607–611.

———, 1967b, Grain-flow deposits and their implications, Santa Ynez Mountains, California: Jour. Sed. Petrology, v. 37, p. 487–508.

Steineck, P. L., 1971, Middle Eocene refrigeration—new evidence from California planktonic foraminiferal assemblages: Lethaia, v. 4, p. 125–129.

Steineck, P. L., and Gibson, J. M., 1971, Age and correlation of the Eocene Ulatisian and Narizian stages, California: Geol. Soc. America Bull., v. 82, p. 477–480.

———, 1972, Age and correlation of the Eocene Ulatisian and Narizian stages, California reply: Geol. Soc. America, Bull., v. 83, p. 535–536.

Streeter, S. S., 1973, Bottom water and benthonic foraminifera in the North Atlantic: glacial-interglacial contrasts: Quaternary Research, v. 3, p. 131–141.

Stuart, C. J., 1973, Lithofacies in the San Onofre Breccia, Laguna to Dana Point, Orange County, California: a preliminary report, in, Fisher, P. and Johnson, D. (eds.), Miocene sedimentary environments and biofacies, southeastern Los Angeles Basin: Soc. Econ. Paleontologists and Mineralogists, Guidebook Field Trip no. 1, Amer. Assoc. Petrol. Geologists Ann. Mtg. 1973, p. 55–58.

Sullwold, H. H., Jr., 1960, Tarzana fan, deep submarine fan of late Miocene age, Los Angeles County, California: Am. Assoc. Petroleum Geologists Bull., v. 44, p. 433–457.

Sverdrup, H. U., Johnson, M. W., and Fleming, R. H., 1942, The oceans, their physics, chemistry, and general biology: Englewood Cliffs, N.J., Prentice-Hall, p. 1–1087.

Theyer, F., 1971, Size-depth variation in *Cyclammina cancellata* Brady, Peru-Chile Trench area, in, Reid, J. L. (ed.), Antarctic oceanology I: Amer. Geophysical Union, Antarctic Research Series, v. 15, p. 309–313.

Turner, D. L., 1970, Potassium-argon dating of Pacific Coast Miocene foraminiferal stages, *in* Bandy, O. L., ed., Radiometric dating and paleontologic zonation: Geol. Soc. America Spec. Paper 124, p. 131–172.

van Andel, T. H., 1964, Recent marine sediments of Gulf of

California, *in* van Andel, T. H., and Shor, G. G., eds., Marine geology of the Gulf of California: Am. Assoc. Petroleum Geologists Mem. 3, p. 216–310.

———, 1975, Mesozoic/Cenozoic calcite compensation depth and global distribution of calcareous sediments: Earth and Planetary Sci. Letters, v. 26, p. 187–194.

VAN ANDEL, T. H., and SHOR, G., eds., 1964, Marine geology of the Gulf of California: Am. Assoc. Petroleum Geologists Mem. 3, p. 1–408.

VAN KAMP, P. C., HARPER, J. D., CONNIFF, J. J., and MORRIS, D. A., 1974, Facies relations in the Eocene-Oligocene in the Santa Ynez Mountains, California: Geol. Soc. London Jour., v. 130, p. 545–565.

VEDDER, J. G., 1972, Revision of stratigraphic nomenclature for some Eocene formations in Santa Barbara and Ventura counties, California: U.S. Geol. Survey Bull., 1354-D, 12 p.

VEDDER, J. G., BEYER, L. A., JUNGER, A., MOORE, G. W., ROBERTS, A. E., TAYLOR, J. C., and WAGNER, H. C., 1974, Preliminary report on the geology of the continental borderland of southern California: U.S. Geol. Survey Misc. Field Studies Map, MF-644, p. 1–34.

WALKER, R., 1975, Upper Cretaceous resedimented conglomerates at Wheeler Gorge, California: description and field guide: Jour. Sed. Petrology, v. 45, p. 105–112.

WALKER, R. G., and MUTTI, E., 1973, Turbidite facies and facies associations, *in* Middleton, G. V., and Bouma, A. H., eds., Turbidites and deep-water sedimentation: Pacific Sec., Soc. Econ. Paleontologists and Mineralogists, Short Course Syllabus, p. 119–158.

WEAVER, D. W., 1962, Eocene foraminifera from west of the Refugio Pass, California: California Univ. Pubs. Geol. Sci., v. 37, p. 353–420.

———, 1969a, The Cretaceous rocks, *in* Weaver, D. W., Doerner, D. P., and Nolf, B., Geology of the northern Channel Islands: Pacific Secs. Am. Assoc. Petroleum Geologists and Soc. Econ. Paleontologists and Mineralogists, Spec. Pub., p. 14–16.

———, 1969b, Paleogeographic implications and geologic history, *in* Weaver, D. W., Doerner, D. P., and Nolf, B., Geology of the northern Channel Islands: Pacific Secs. Am. Assoc. Petroleum Geologists and Soc. Econ. Paleontologists and Mineralogists, Spec. Pub., p. 115–131.

WEAVER, D. W., DOERNER, D. P., and NOLF, B., 1969, Geology of the northern Channel Islands: Pacific Secs. Am. Assoc. Petroleum Geologists and Soc. Econ. Paleontologists and Mineralogists, Spec. Pub., p. 1–200.

WEAVER, D. W., and MOLANDER, G. E., 1964, The Eocene faunal sequence in the eastern Santa Rosa Hills, Santa Barbara County, California: California Univ. Pubs. Geol. Sci., v. 41, p. 161–248.

WEAVER, D. W., and WEAVER, D. W., 1962, Upper Eocene foraminifera from the southwestern Santa Ynez Mountains, California: California Univ. Pubs. Geol. Sci., v. 41, p. 1–96.

WHITE, W. R., 1956, Pliocene and Miocene foraminifera from the Capistrano Formation, Orange County, California: Jour. Paleontology, v. 30, p. 237–260.

WILCOXIN, J. A., 1969, Tropical planktonic zones and calcareous nannoplankton correlations in part of the California Miocene: Nature, v. 221, p. 950–951.

WILSON, E. J., 1954, Foraminifera from the Gaviota Formation east of Gaviota Creek, California: California Univ. Pubs. Geol. Sci., v. 30, p. 103–170.

WOODFORD, A. O., 1925, the San Onofre Breccia: Univ. California Publ., Dept. Geological Sci., v. 15, p. 159–280.

WOODFORD, A. O., SCHOELLHAMER, J. E., VEDDER, J. G., and YERKES, R. F., 1954, Geology of the Los Angeles Basin, [Pt.] 5 *in* Chap. 2 of Jahns, R. H., ed., Geology of Southern California: California Div. Mines, Bull. 170, p. 65–81.

WOODRING, W. P., and BRAMLETTE, M. N., 1950, Geology and paleontology of the Santa Maria district, California: U.S. Geol. Survey Prof. Paper 222, 185 p.

WOODRING, W. P., BRAMLETTE, M. N., and KEW, W. S. W., 1946, Geology and paleontology of Palos Verdes Hills, California: U.S. Geol. Survey Prof. Paper 207, p. 1–145.

YEATS, R. S., 1968, California structure, sea floor spreading, and history of the Pacific Basin: Geol. Soc. America Bull., v. 79, p. 1698–1702.

———, 1977, High vertical rates of crustal movement near Ventura, California: Science, v. 196, p. 295–298.

———, 1973, San Onofre Breccia as evidence for the western boundary of the Peninsula Ranges block, in, Fisher, P. and Johnson, D. (eds.), Miocene sedimentary environments and biofacies, southeastern Los Angeles Basin: Soc. Econ. Paleontologists and Mineralogists Guidebook Field Trip no. 1, Amer. Assoc. Petrol. Geologists Ann. Mtg. 1973, p. 53–54.

YERKES, R. F., MCCULLOCH, T. H., SCHOELLHAMER, J. E., and VEDDER, J. G., 1965, Geology of the Los Angeles Basin—an introduction: U.S. Geol. Survey Prof. Paper 420-A, p. 1–57.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 196–201, pl. 1, 1980

PALEOCEANOGRAPHIC CONTROL OF PLANKTONIC FORAMINIFERAL DISTRIBUTIONS IN THE LATE CRETACEOUS NIOBRARA FORMATION OF THE WESTERN INTERIOR, NORTH AMERICA

WILLIAM E. FRERICHS
Department of Geology, University of Wyoming, Laramie, Wyoming 82071

ABSTRACT

Planktonic foraminiferal assemblages from the Late Cretaceous Niobrara Formation of the Western Interior, U.S.A., can be divided into a lower temperate fauna, a middle subtropical fauna and an upper temperate fauna. The subtropical fauna is marked by conspicuous keeled planktonic foraminifera. The presence of *Marginotruncana concavata* indicates that the subtropical fauna is of late Coniacian to early Santonian age. Faunal studies of formations correlative with the Niobrara Formation indicate that the subtropical fauna is an easily traced assemblage which has been noted as far north as Montana.

INTRODUCTION

In recent years it has been shown that migrations of species of planktonic foraminifera reflect changes in the surface-water temperature of the oceans (Bandy, 1960; Ericson, Ewing, and Wollin, 1964; Climap, 1976; and many others). Most of these studies have concentrated on Pleistocene faunas, but a few authors have studied older migrations in the late Miocene and Pliocene (Bandy, 1960; Bandy, 1968; Bandy, Butler, and Wright, 1969; Jenkins, 1967). Studies of paleoceanographically controlled migrations of species of planktonic foraminifera in older rocks are essentially nonexistent.

Bandy (1960), however, did establish criteria for paleotemperature interpretations in rocks older than the late Miocene. Bandy pointed out that planktonic foraminifera having a keel have a subtropical and tropical distribution in today's oceans and that geologic evidence suggests that this has always been the case. The "keeled line," as he defined it, represented the northernmost occurrence of keeled planktonic foraminifera in the northern hemisphere through time. In subsequent publications, Bandy (1964, 1967) illustrated variations in the keeled line which he attributed to major changes in surface-water temperature.

The present paper is part of an ongoing project to study the planktonic foraminiferal faunas of the Niobrara Formation (early Coniacian to late Campanian) and equivalent formations in the Western Interior. As part of this project Niobrara sections at Pueblo, Colorado, and Centennial Valley, Wyoming, were sampled at intervals ranging from one to five feet. These samples were then washed through a screen with 63 μm openings, randomly split until two to three hundred specimens of planktonic foraminifera were counted from each sample, and the number of keeled specimens counted. Samples from two sections of the equivalent Hilliard Formation in western Wyoming were treated in the same manner, although the sampling interval was greater.

The purpose of this study is to illustrate the presence of a paleoceanographic controlled migration of planktonic foraminifera in sediments of the Niobrara Formation and correlative units in the Western Interior, and to demonstrate its use in correlation. The Niobrara Formation ranges in age from Coniacian to

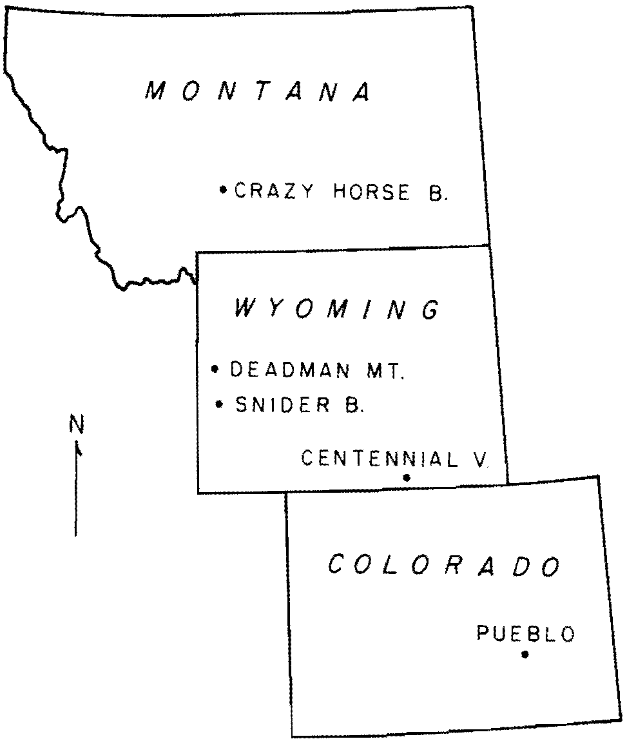


FIGURE 1

Index map showing the locations of Western Interior sections discussed in this paper.

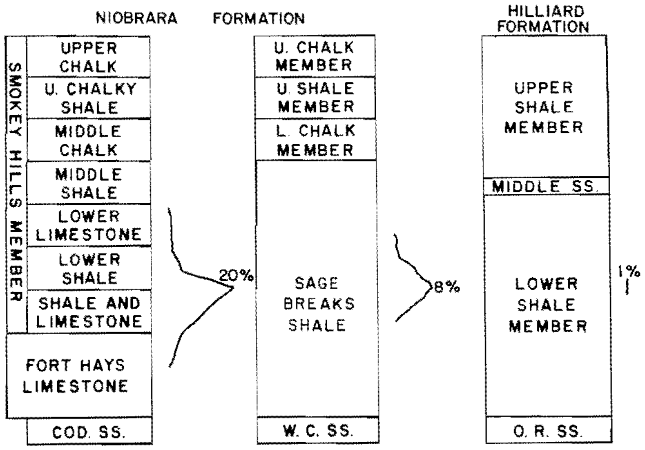


FIGURE 2

Correlation of sections of the Niobrara Formation near Pueblo, Colorado (left), and Centennial Valley, Wyoming (center), with the Hilliard Formation of southwestern Wyoming (right). The lines to the right of each generalized section indicate the relative abundance of keeled planktonic foraminifera at each locality. The correlation between sections is based on the peak abundance.

late Campanian (Frerichs and others, 1975; unpub. data) and crops out from northern New Mexico in the south to Montana in the north and from Wyoming in the west to the Missouri River in the east. Planktonic foraminiferal assemblages from the formation are mainly temperate (Frerichs and Adams, 1973; Frerichs and others, 1975 and 1977). Keeled planktonic foraminifera or species apparently adapted to warmer waters are abundant in only a thin portion of the Niobrara Formation.

RESULTS AND DISCUSSION

I believe that this interval of keeled planktonic foraminiferal occurrence marks a major temperature-controlled migration of subtropical to tropical foraminifera into the Western Interior. As such, the occurrence of abundant keeled planktonic foraminifera represents a correlative horizon which may be used throughout the Western Interior in rocks of the Niobrara and correlative formations. If this is correct, the migration of keeled planktonic foraminifera into the Western Interior should be traceable from south to north, and keeled planktonic foraminifera should be more abundant in the southern part of the Western Interior and decrease to a featheredge of abundance to the north.

This distributional pattern can in fact be found in the Western Interior. The southernmost section of the Niobrara Formation used in this study is at Pueblo, Colorado (Fig. 1). This section has become a standard section for the Niobrara Formation in the Western Interior. Keeled planktonic foraminifera first form a percentage of the planktonic population in the upper few feet of the Fort Hays Member, and are a common element of the planktonic assemblage for 130 feet of section and then disappear in the lower few feet of the middle shale unit of the Smoky Hill Member (Fig. 2). The peak of the keeled planktonic foraminiferal interval with a relative abundance of 20 percent is at the top of the shale and limestone unit of the Smoky Hill Member. A total of eight keeled planktonic foraminiferal species have been identified from this interval, of which *Marginotruncana concavata* is the most important.

Marginotruncana concavata is an index fossil for the late Coniacian and early Santonian epochs of the Late Cretaceous and it or synonymous species have been reported from Austria (Tollman, 1960), Germany (de Klasz, 1953), the Isle of Wight (Barr, 1962), Russia (Subbotina, 1953), Switzerland (Mornod, 1950), Israel (Brotzen, 1934), Algeria (Sigal, 1952), Gabon (de Klasz, 1961), Madagascar (Collignon, 1959), Libya (Barr, 1972), Tunisia (Dalbiez, 1955), Mexico (Pessag-


1

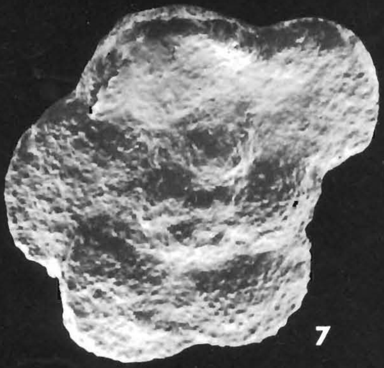

2


3


4


5

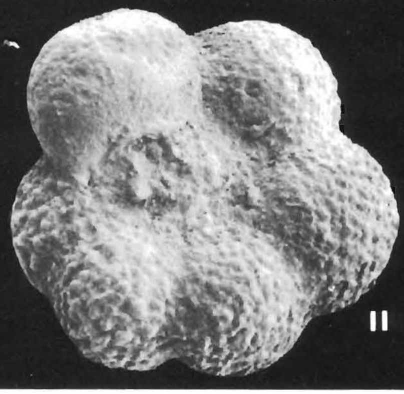

6


7


8


9


10


11

no, 1967), Trinidad (Bolli, 1957), and the United States (Takayanagi, 1965; Pessagno, 1967). Santonian occurrences are more common and Coniacian occurrences have only been reported from Texas (Pessagno, 1967), the Isle of Wight (Barr, 1962), Libya (Barr, 1972), and Gabon (Collignon, 1959).

In the Western Interior *Marginotruncana concavata* has been found in a sample from bed 36 of the shale and limestone unit of the Smoky Hill Member of the Niobrara Formation at Pueblo, Colorado (Scott and Cobban, 1964). This is the first reported occurrence of *M. concavata* in the Western Interior and it is from a horizon directly below bed 37 of the shale and limestone unit which contains *Inoceramus deformis* Meek and *Inoceramus* (*Volviceramus*) *involutus* Sowerby, and one foot above bed 34 which contains *Inoceramus deformis* Meek.

Four specimens of *Marginotruncana concavata* have been identified from this sample which contains, in addition to *Marginotruncana concavata,* the following planktonic foraminiferal species: *Marginotruncana angusticarenata, Marginotruncana coronata, Marginotruncana indica, Marginotruncana pseudolinneana, Archaeoglobigerina bosquensis,* and *Heterohelix reussi.* All of the above species have been reported from the late Coniacian to early Santonian interval and are consistent with the occurrence of *Marginotruncana concavata* (Pl. 1).

According to Scott and Cobban (1964), and based upon the stratigraphic occurrence of *Inoceramus deformis* and *Inoceramus involutus,* the uppermost bed 37 of the shale and limestone unit is middle Coniacian in age and the remainder of the unit is early Coniacian (Fig. 1). The occurrence of *Marginotruncana concavata* in bed 36, however, raises a question as to the age of this unit and suggests a late Coniacian to early Santonian age for the upper portion of the shale and limestone unit.

Further north in Centennial Valley, near Laramie, Wyoming (Fig. 1), the keeled planktonic foraminiferal interval is found in the center of the Sage Breaks Shale (Fig. 2). The keeled zone is less than 75 feet thick in Centennial Valley, and peak values are 8 percent, appreciably less than at Pueblo. *Marginotruncana concavata* is not present at this more northern locality and the number of keeled planktonic foraminifera decreases to six species. The two most abundant species are *Marginotruncana marginata* and *Marginotruncana pseudolinneana* which have ranges extending into the early Santonian, with *M. pseudolinneana* becoming extinct at the end of the early Santonian (Pessagno, 1967). *Archaeoglobigerina bosquensis,* a nonkeeled species which is rare in the late Coniacian but common in Santonian rocks of Texas (Pessagno, 1967), is found in the keeled interval and limits the age of the interval to late Coniacian to early Santonian. The time interval defined is very similar to the keeled interval at Pueblo, Colorado, and the hypothesis concerning the migration of a keeled planktonic foraminiferal assemblage in the Western Interior seems to be substantiated. Consequently, a late Coniacian to early Santonian age is assigned to the peak abundance of the keeled zone in Centennial Valley.

Further north and to the west in the Hilliard Formation of Snider Basin, Wyoming (Fig. 1), keeled planktonic foraminifera have been noted in a 50-foot zone 500 feet above the top of the Frontier Formation. At this locality keeled planktonic foraminifera are not abundant enough to form an appreciable percent of the fauna, but the two keeled species noted, *M. marginata* and *M. pseudolinneana,* are the two most abundant species found in Centennial Valley. Apparently, Snider Basin is near the northern limit of keeled planktonic foraminifera. The limit does extend further north, however, as this author has noted keeled planktonic foraminifera (*M. pseudolinneana* and *M. marginata*) in the Hilliard Formation at Deadman Mountain, Wyoming (Fig. 1), and *M. marginata* has been reported as far north as the Kevin Shale in west-central Montana (Fig. 1) by Strong (1972).

The horizon defined by the peak of this keeled abundance zone approximates a late Coniacian to early Santonian time line which can be used as a correlation tool in the thick shale sequences of western Wyoming.

←

PLATE 1

1–3 *Marginotruncana coronata* Bolli. Specimen from the Sage Breaks Shale, Centennial Valley, Wyoming. ×115.

4–6 *Marginotruncana angusticarenata* (Gandolfi). Specimen from the Sage Breaks Shale, Centennial Valley, Wyoming. ×130.

7–9 *Marginotruncana concavata* (Brotzen). Specimen from the Smokey Hill Member, Niobrara Formation, Pueblo, Colorado. ×55.

10, 11 *Archaeoglobigerina bosquensis* Pessagno. Specimen from the Sage Breaks Shale, Centennial Valley, Wyoming. ×160.

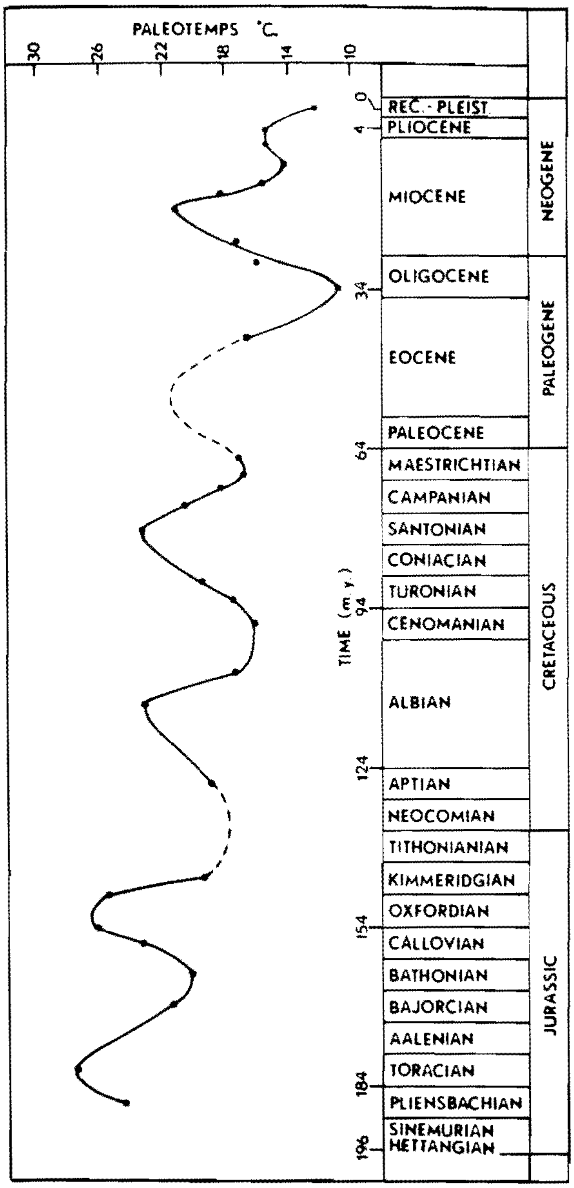


FIGURE 3

O^{18}/O^{16} paleotemperature curve for temperate surface water temperatures (composite of many authors). Note that the late Coniacian-early Santonian is a warm interval. This part of the curve is based upon the work of Lowenstam and Epstein (1954).

CONCLUSION

An environmentally induced migration of warm-water keeled planktonic foraminifera into the Western Interior sea during Late Cretaceous time forms a recognizable biostratigraphic horizon throughout the Western Interior. The diversity of keeled planktonic foraminifera decreases from the south to north and no additional species occur in the more northerly assemblages. These two factors seem to indicate a southern dispersal point. Care must be taken when correlating the keeled intervals as it is the peaks which are synchronous, while the first and last appearances of keeled species in different sections are probably diachronous. The age of the peaks has been dated as late Coniacian to early Santonian in the Pueblo, Colorado, section where *Marginotruncana concavata* occurs in the sample with the peak abundance.

That water mass oscillations are the controlling factor for a migration of tropical and subtropical faunas northward in the late Coniacian to early Santonian is strongly suggested from an examination of the oxygen-isotopic paleotemperature curve for temperate areas. A major warming of temperate waters is indicated for the Coniacian and Santonian epochs (Fig. 3) (Lowenstam and Epstein, 1954). A late Coniacian to early Santonian age for the peak abundance of tropical keeled species in the Western Interior agrees well with this curve.

REFERENCES

BANDY, O. L., 1960, The geologic significance of coiling ratios in the foraminifer *Globigerina pachyderma* (Ehrenberg), Jour. Paleontology, v. 34, p. 671–681.

———, 1964, Cenozoic planktonic foraminiferal zonation: Micropaleontology, v. 10, p. 1–17.

———, 1967, Cretaceous planktonic foraminiferal zonation: Micropaleontology, v. 13, p. 1–31.

———, 1968, Paleoclimatology and Neogene planktonic foraminiferal zonation, Gior. Geologia, ser. 2, v. 35, p. 277–290.

BANDY, O. L., BUTLER, E. A., and WRIGHT, R. C., 1969, Alaskan upper Miocene marine glacial deposits and the *Turboratalia pachyderma* datum plane, Science, v. 166, p. 607–609.

BARR, F. T., 1962, Upper Cretaceous planktonic foraminifera from the Isle of Wight, England: Palaeontology, v. 4, p. 552–580.

———, 1972, Cretaceous biostratigraphy and planktonic foraminifera of Libya: Micropaleontology, v. 18, p. 1–46.

BOLLI, H. M., 1957, The genera *Praeglobotruncana, Rotalipora, Globotruncana,* and *Abathomphalus* in the Upper Cretaceous of Trinidad, B. W. I.: U.S. Natl. Mus. Bull. 215, p. 51–60.

BROTZEN, F., 1934, Foraminiferen aus dem Senon Palastinas: Deutsch. Pälastinas Ver., Zeitschr., v. 57, p. 28–72.

CLIMAP PROJECT MEMBERS, 1976, The surface of the ice-age earth: Science, v. 191, p. 1131–1137.

COLLIGNON, M., 1959, Correlations sommaires entre les despots du Cretace Supérieur de Madagascar et ceux de l'Europe Occidentale en particulier de la France, *in* Colloque sur le Cretace Supérieur Français: Soc. Savantes de Paris Cong. Compte Rendu, p. 41–52.

DALBIEZ, F., 1955, The genus *Globotruncana* in Tunisia: Micropaleontology, v. 1, p. 49–72.

ERICSON, D. B., EWING, M., and WOLLIN, G., 1964, The Pleistocene epoch in deep-sea sediments: Science, v. 146, p. 723–732.

FRERICHS, W. E., and ADAMS, P. R., 1973, Correlation of the Hilliard Formation with the Niobrara Formation: Wyoming Geol. Assoc., Guidebook, 25th Field Conf., p. 193–200.

FRERICHS, W. E., ATHERTON, C. C., and SHIVE, P. N., 1975, Planktonic foraminifera from the chalky members of the Niobrara Formation: Jour. Foram. Research, v. 5, no. 3, p. 122–152.

FRERICHS, W. E., POKRAS, E. M., and EVETTS, M. J., 1977, The genus *Hastigerinoides* and its significance in the biostratigraphy of the western interior: Jour. Foram. Research, v. 7, p. 149–156.

JENKINS, D. G., 1967, Recent distribution, origin, and coiling ration changes in *Globoratalia pachyderma* (Ehrenberg): Micropaleontology, v. 13, p. 195–203.

KLASZ, I. DE, 1953, Einige neue oder wenig bekannte Foraminiferen aus der helvetischen O erkreide der bayerischen Alpen sudlich Traunstein (Oberbayern): Geol. Bavarica, no. 17, p. 223–244.

———, 1961, Presence de *Globotruncana concavata* (Brotzen) et *Gl. concavata carinata* Dalbiez (Foraminifères) dans le Coniacian de Gabon (Afrique equatoriale): Soc. Géol. France Compte Rendu, p. 123–124.

LOWENSTAM, H. A., and EPSTEIN, S., 1954, Paleotemperatures of the post-Aptian Cretaceous as determined by the oxygen isotope method: Jour. Geology, v. 62, p. 207–248.

MORNOD, L., 1950, Les Globorotalides du Cretace superieur du Montsalvens, (Prealpes fribourgeoises): Eclogae Geol. Helvetiae, v. 42, no. 2, p. 573–596.

PESSAGNO, E. A., JR., 1967, Upper Cretaceous planktonic foraminifera from the Western Gulf Coastal Plain: Paleontographica Americana, v. 5, p. 249–445.

SCOTT, G. R., and COBBAN, W. A., 1964, Stratigraphy of the Niobrara Formation at Pueblo, Colorado: U.S. Geol. Survey Prof. Paper 454-L, p. 1–30.

SIGAL, J., 1952, Aperçu stratigraphique sur la micropaleontologie due Cretace: Internat. Geol. Congr., 19th, Algeria, Mon., Ser. 1, no. 26, p. 1–47.

STRONG, C. P., JR., 1972, Foraminifera from the Colorado Group in west-central Montana: Montana Geol. Soc., 21st Ann. Field Conf., p. 85–90.

SUBBOTINA, N. H., 1953, Fossil foraminifera from the U.S.S.R.: Globigerinidae, Hantkeninidae and Globorotaliidae: Vses. Neft. Nauchno-Issled. Geol.-Razved. Inst. Trudy, n. ser., no. 76, p. 1–296.

TAKAYANAGI, Y., 1965, Upper Cretaceous planktonic foraminifera from the Putah Creek subsurface section along the Yolo-Solano county line, California: Tohoku Univ. Sci. Rept., 2nd ser. (Geol.), v. 36, no. 2, p. 161–237.

TOLLMAN, A., VON, 1960, Die foraminiferen fauna des Oberconiac aus der Gosau des Ausseer. Weissenbachtales in Steiermark: Geol. Jahrb., Bd. 103, p. 133–203.

TAXONOMIC STUDIES

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 205–214, pls. 1–3, 1980

AN EXTANT OPALINE FORAMINIFER: TEST ULTRASTRUCTURE, MINERALOGY, AND TAXONOMY

JOHANNA M. RESIG[1], HEINZ A. LOWENSTAM[2], RONALD J. ECHOLS[3], AND STEPHEN WEINER[2]

ABSTRACT

Fabric and mineralogical studies of the test of a modern benthic foraminiferal species, recovered from several widely speparated locations in the Pacific and off Antarctica, have shown it to be constructed of opal precipitated by the foraminifer. Although microarchitecture and gross morphology of the siliceous test is similar to that in miliolid foraminifera, its mineralogy and structural details preclude assignment to any of the available taxa within the Order Foraminiferida. A new suite of taxa of suborder and lesser rank is proposed to accommodate this new form, which has been designated *Silicoloculina profunda*, n. gen, n. sp.

INTRODUCTION

Increased attention is being directed toward determining the physical and chemical properties, structures, and functions of bioinorganic materials in marine organisms, where they occur as strengthening agents of skeletal hard parts. Recent studies, utilizing modern techniques, have shown that the biosynthesis of X-ray amorphous, hydrous silica (opal) in the sea is accomplished by diatoms, silicoflagellates, radiolarians, sponges, the patellacean gastropods (Lowenstam, 1971), holothurians of the Family Molpadiidae (Lowenstam and Rossman, 1975), and some Arthropoda, namely the copepods. This indicates that the taxonomic diversity of opal-precipitating marine biota is far greater than has been realized in the past and stresses the fact that our knowledge of the chemical composition and structure of the bioinorganic constituents of hard parts is as yet very limited. Hence, a distinct possibility exists that there are still other taxa which may be involved in opal fixation.

The extensive literature on the anatomy and histology of marine organisms, published prior to and shortly after the turn of this century, contains a number of references to "siliceous" hard parts, cements, or inclusions (Vinogradov, 1953). The "siliceous" nature of the material was commonly deduced from wet chemical analyses in which silica was found to be the major elemental constituent, or from the fact that it was acid-resistant. Only a few of the earlier reported "siliceous" precipitates have been re-examined in recent decades. In the case of the onchidellid gastropods, the siliceous deposits were found to consist of detrital quartz (Lowenstam, 1974). The "siliceous" cement in agglutinated tests of some members of the foraminiferal Family Rzehakinidae was shown to be an acid-resistant, organic membrane, stated to consist of acid mucopolysaccharide (Lipps, 1971, 1973).

We report here the occurrence of an opaline test in a modern foraminiferal species recovered in surface sediment and cores from the Scotia Sea (Echols, 1971), the Peru-Chile Trench area, the Central Pacific Basin (Lineberger, 1975), and the Bering Sea (see appendix 1 for sampling data not previously published). The origin of the opal is discussed and the species is described.

MORPHOLOGY

Attention was initially drawn to the new foraminifer, which has the gross morphology of a miliolid (Pl. 1),

---

[1] Department of Geology and Geophysics and Hawaii Institute of Geophysics, University of Hawaii.

[2] Department of Geological and Planetary Sciences, California Institute of Technology, Pasadena, California.

[3] Mobil Oil Corporation, Dallas, Texas.

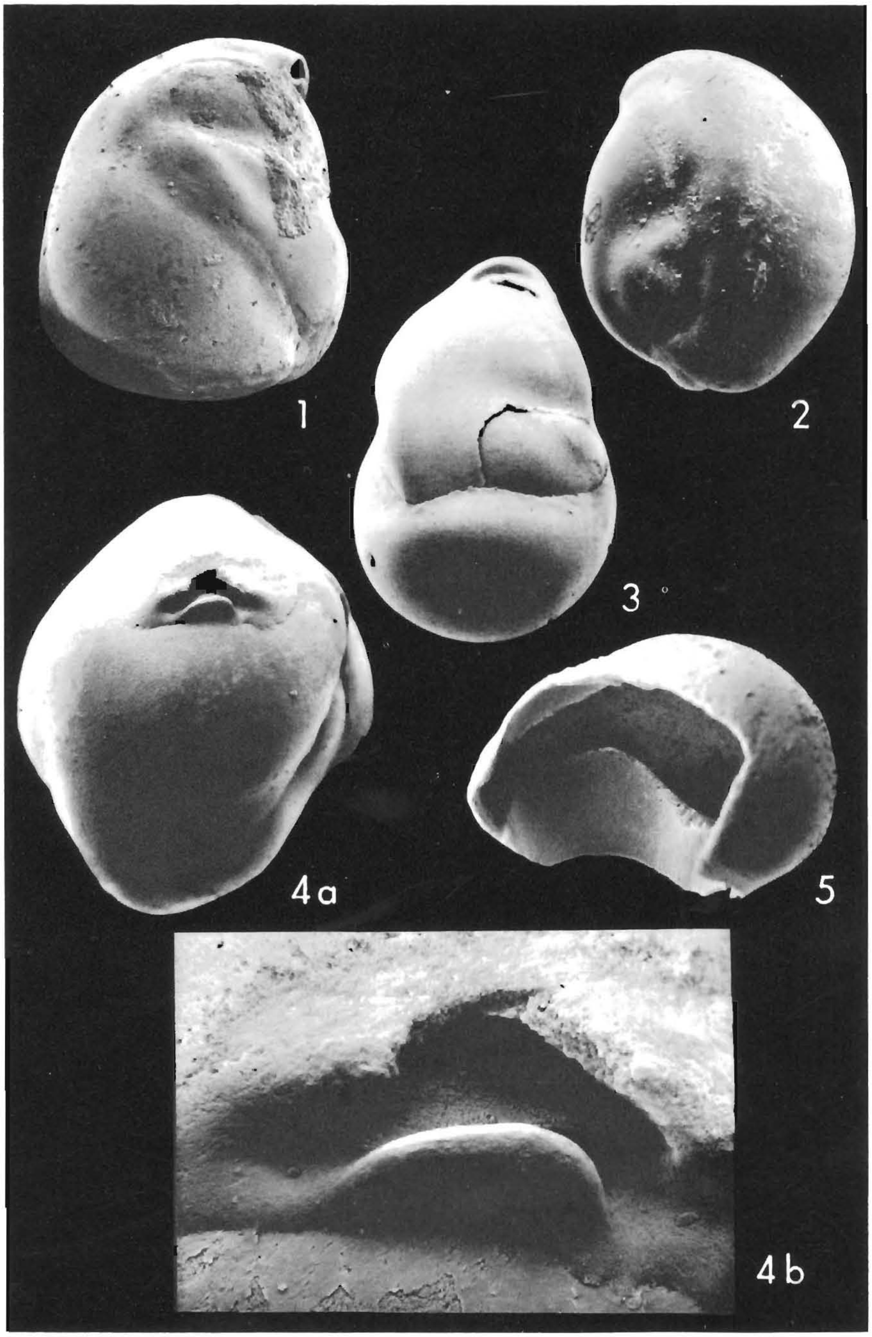


PLATE 1

Various views of *Silicoloculina profunda*, n. gen., n. sp.

1 Lateral view of holotype (USNM 272501) showing chamber neck; ×179, Y71-8-70MG3 (0–3 cm).

2 Lateral view of paratype (USNM 272502) showing side opposite that in Figure 1; ×154, DSDP 320, 1–3 (114–116 cm).

3 Inferior view of paratype (USNM 272503) showing intersection of axial planes of succeeding chambers; ×132, DSDP 320 (120–122 cm).

4 a. Apertural view of paratype (USNM 272504); ×158, DSDP 320A, 1–2 (139–141 cm). b. Enlargement of apertural tooth showing attachment to apertural rim; ×788.

5 Interior of detached chamber showing lagenoid chamber shape and lateral chamber extensions; ×150, DSDP 320, 1–2 (120–122 cm).

because of its unusual occurrence in otherwise totally agglutinated assemblages below the CCD in the Scotia Sea and the Peru-Chile Trench. Each volution of the test consists of two chambers, added so that the broad posterior portion of each chamber covers the preceding aperture and the long axes of the chambers cross. The chamber narrows to a neck toward the aperture, which contains a broad tooth. The test has an opalescent-porcelaneous appearance when dry and is transparent and hyaline when wet. Specimens range from about 0.25 to 0.50 mm in length.

ULTRASTRUCTURE

Tests of the new form obtained from off Antarctica, the Peru-Chile Trench, and from the Central Pacific Basin were mechanically cleaned and then fragmented to study their ultrastructure with the aid of a scanning electron microscope. One of these specimens from the Scotia Sea (Eltanin 712) had been stained with rose Bengal, indicating that it had been alive at the time of collection. The basic features of the microarchitecture were found to be the same for all specimens examined from the three widely distant sampling sites and hence the following description applies to them all.

SEM micrographs show the test wall to consist of an outer organic membrane, a median layer of mineralized tubular rods, and an inner organic membrane (Pl. 2, Fig. A). The thickness of the outer layer is approximately 0.1 μm, the median layer is 19 μm, and the inner layer is 0.1 μm. The mineralized median layer, which is the major component of the test wall, can be subdivided into three microarchitectural units based on orientation and packing density of the rods. The outer and inner subunits are only 0.2 μm thick. They consist of one to two layers of a two-dimensional array of tightly packed rods parallel to the inner and outer surfaces of the test and chamber walls (Pl. 3, Figs. A, B, D). The rods are arranged in parallel to subparallel sheets, which are occasionally crossed by discordant rods. Clusters of parallel-aligned rods are commonly bordered by others with a different axial orientation (Pl. 2, Figs. B, C, D). Angular openings which sometimes occur between the clusters (Pl. 3, Figs. A, B, D) are the result of loose packing and are not comparable to the perforations in some calcareous and agglutinated foraminifera. The central subunit has a thickness of about 18 μm, and is therefore the main component of the median layer. It is characterized by a three-dimensional, random array of tubular rods which are firmly joined wherever they come in contact, thus forming an open mesh, rigid framework. Individual rods predominate; however, couplings of two parallel-aligned rods are not uncommon. Arrays in excess of two aligned rods are occasionally present. The interstitial spaces and the central cavity of the rods are, in the specimens examined by us, devoid of any infilling material. Even the specimen stained with rose Bengal did not show any additional organic material between the rods or in the rod lumens. According to the orientation of the rods, the contact relations of the three subunits are unconformable, hence sharply defined (Pl. 3, Figs. A, D).

The hollow rods are the principal constituents of the test and account for the rigidity of its wall. Their morphologic features and the nature of their contacts were determined from high resolution SEM micrographs, obtained from vertical fracture surfaces of the test wall and from the test surfaces where the organic veneer had been exfoliated. The rods are invariably rectilinear over their length (Pl. 3, Figs. A and D). Their surface geometry is variable. In the central subunit, some rods are hexagonal to circular in cross section, but most are quadrangular to circular. In the inner subunit of the middle layer, the similarly shaped rods appear to be largely truncated at the side which is in contact with the bounding organic membrane. All rods are hollow centrally, the space always being large in proportion to the thickness of the wall, giving the rods a tubular appearance. In rods laterally joined or in angular contact, the lumens of the individual rods generally remain separated by an intervening wall (Pl. 3, Figs. B and D). However, the wall separating the lumens can be incomplete or absent (Pl. 3, Figs. A, B, and C). Even when they lie adjacent, the lumens, as seen in cross section, usually maintain their individual identity in diameter and shape (Pl. 3, Fig. B). The cross-sectional outlines of the lumens are the same as those of the rods, namely quadrangularly shaped rods have quadrangular lumens and rounded rods have round lumens. In rods located at or near the border of the outer organic membrane, the diameter of the lumens tends to approximate the thickness of the rod wall. However, with increasing distance from the outer surface, the diameter of the lumens increases markedly compared to the thickness of the rod wall (Pl. 3, Figs. A and D). Uniform wall thickness is maintained in each adjoining rod which is even in minimal contact with others. Where the contact area is extensive, the common wall of adjoining rods usually has the same thickness as the unattached wall segments (Pl. 3, Figs. A and B). The common wall shows no evidence of lateral fusion of originally discrete wall segments.

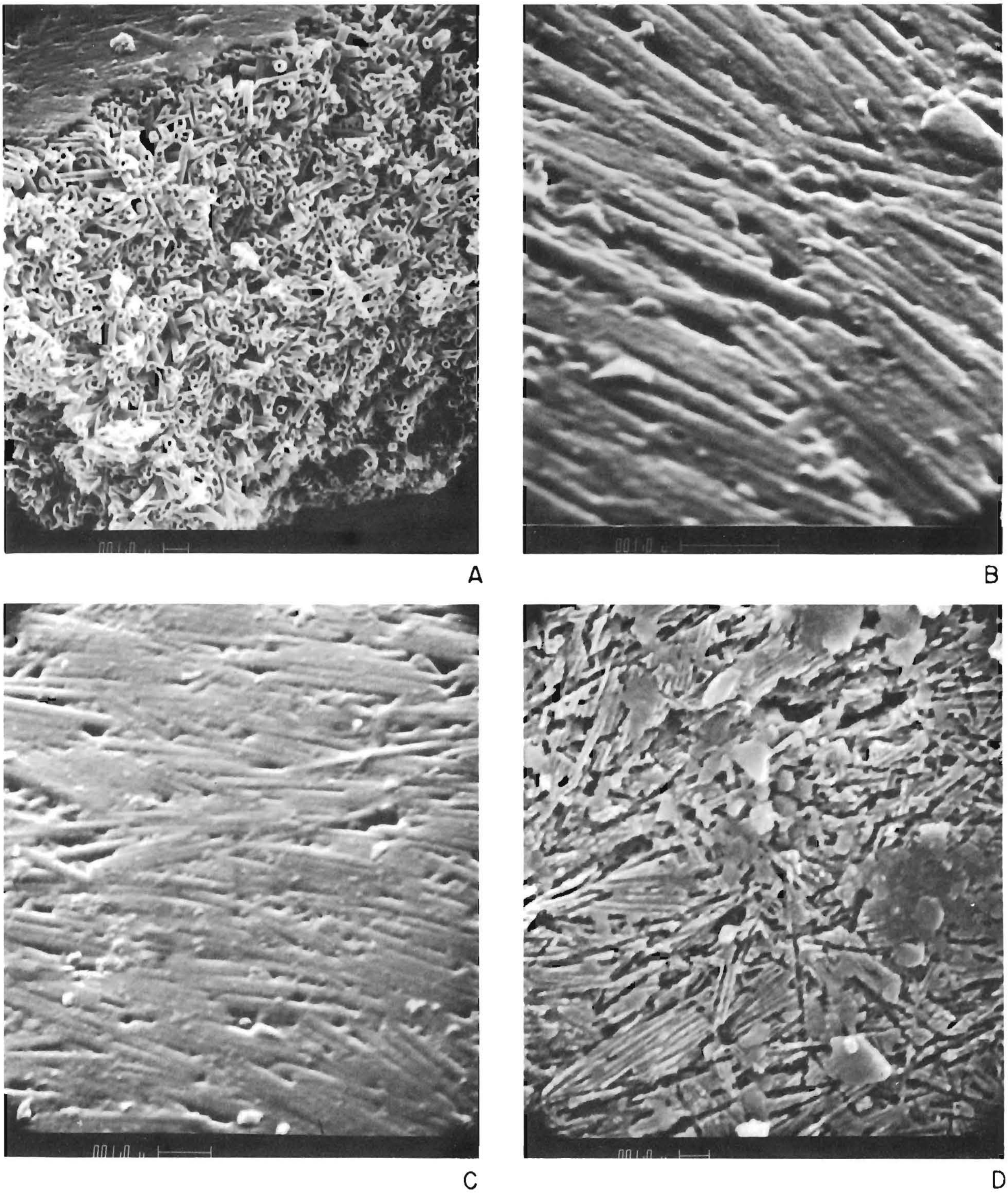


PLATE 2

Wall ultrastructure.
(Scale bar = 1 μm)

A Cross section of outer chamber wall.

B, C Exterior surface of test, showing the outer organic membrane covering the outermost subunit of the middle layer.

D Innermost subunit of middle layer partly covered by the inner organic membrane.

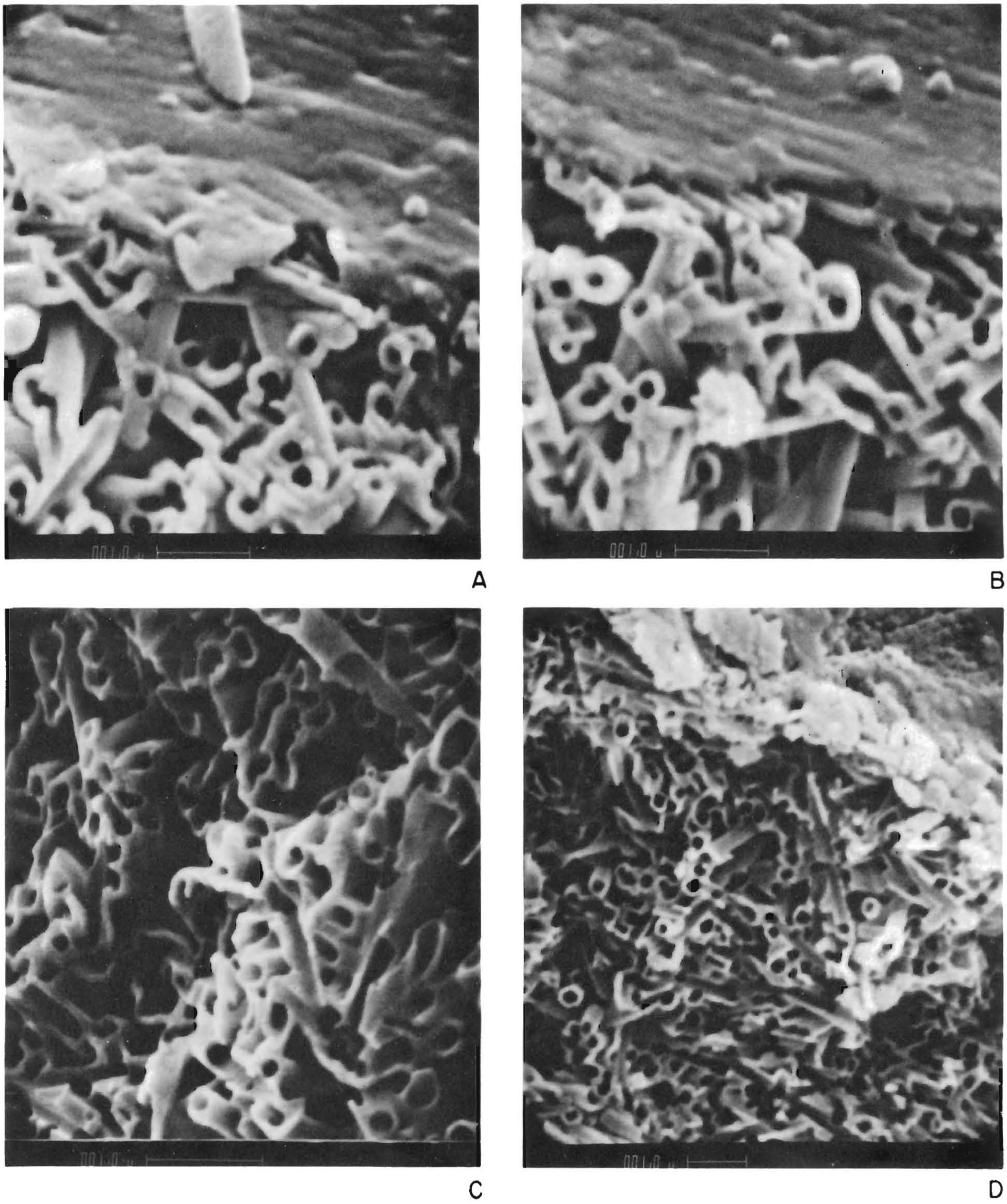


PLATE 3

Morphology and fabric of tubular rods.
(Scale bar = 1 μm)

A, B Cross section of outer organic membrane, the outermost subunit and the middle layer.

C Cross section of central part of middle layer showing exceptional concentration of fused rods.

D Cross section of inner organic membrane, innermost subunit and the middle layer.

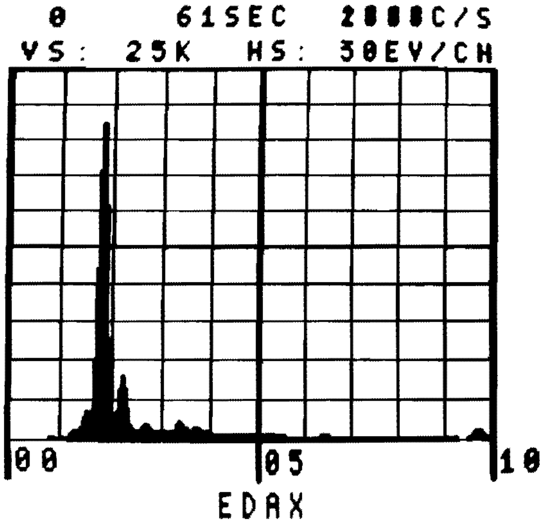


FIGURE 1

Graphic presentation of the counts versus energy produced during energy dispersive analysis of X-rays (EDAX) emitted by the test of the new form. Analysis carried out under accelerating voltage of 20 kV, with 200,000 counts total on all channels. The 1.8 keV peak was produced by silicon; gold coating the specimen produced the 2.2 keV peak.

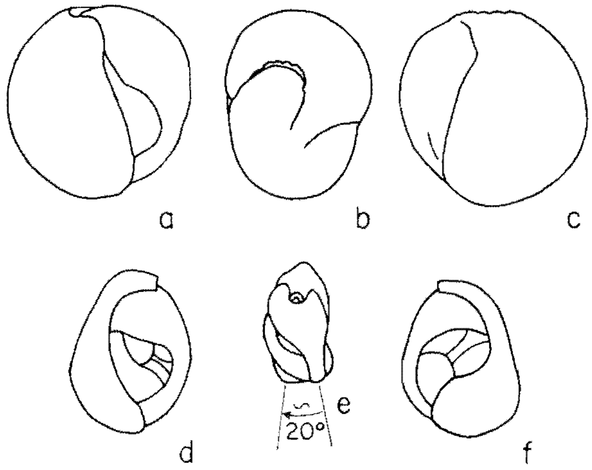


FIGURE 2

Some aspects of coiling in *Silicoloculina profunda*, n. gen., n. sp. a–c. Camera lucida drawings of lateral and apertural views of large test that appears triloculine due to extensive concealment of early volutions by lateral extensions of chambers, length 0.49 mm, chamber neck and aperture broken. d–f. Sketches showing disposition of chambers in lateral and apertural views of *Silicoloculina*.

MINERALOGY

Hydrochloric acid does not dissolve the test, nor does it disintegrate in a 30 percent solution of hydrogen peroxide. Energy dispersive X-ray analysis (EDAX) of a section of the test wall produced only one pronounced peak, at 1.8 keV (Fig. 1), which is the counts versus energy signature of silicon. The infrared absorption spectrum, obtained on a cleaned and cloroxed sample of one entire test, matches the spectrum of our opal standard (Lowenstam, 1971). Hence, the inorganic fraction of the test consists entirely of amorphous, hydrous silica (opal).

DISCUSSION

Some agglutinated foraminifera are highly selective in the construction of their tests and are known to incorporate solely or largely opaline sponge spicules (summarized in Loeblich and Tappan, 1964). As the spicules usually are visible on the outer surface of the test wall and have a characteristic shape, there is no doubt that they are derived from silica-precipitating sponges. In the case of the new foraminifer described here, there are several lines of evidence which preclude a derived origin for the opaline test and support opal precipitation by the protist itself. The rods of the foraminiferal test have the following characteristics: their lumens vary somewhat in shape but duplicate the surface geometry of the rods, occasionally the lumens of several adjoining rods coalesce, the lumens and walls of the rods are of uniform dimensions throughout the length of a single rod, and lumen diameter generally increases toward the base of the test wall. Opaline spicules which are formed by species among the demosponges and hexactinellid sponges as well as the spines of certain radiolarians and silicoflagellates (R. Casey, pers. comm.) do not possess all of these features. When considering them individually, one could argue that at least those rods which have a quadrangular cross section might be derived from hexactinellid sponges, which have a similarly shaped axial canal (Reiswig, 1971). However, the diameter of the hexactinellid axial canals and the lumens of the foraminiferal rods relative to their wall thicknesses are significantly different. Moreover, the sponge spicules have a circular cross section, whereas the rods have a quadrangular one. Epi- and diagenetic alterations of sponge spicules commonly result in major enlargement of their axial canals. However, the canal diameter of altered spicules varies greatly along the spicular axis, whereas the lumens of the rods are invariably uniform. Hence, the hexactinellid sponge spicules cannot be the source of even a portion of the rods in the foraminiferal wall.

Particles for an agglutinated test, however rare, are to be found in the sediment. Therefore, fine fraction smears of two surface samples (Y71-8-70MG3 and KK74-FFC48) from the Peru-Chile Trench area were mounted on 30-mm-diameter plugs and carefully examined under the scanning electron microscope. No siliceous hard parts resembling the rods of the siliceous foraminiferal test were noted. Only some broken sponge spicules were observed, which were different in size and morphology from the foraminiferal rods.

On the other hand, the ultrastructure of the mineralized wall of the new form bears a striking resemblance to that of miliolid foraminifera, which are known to secrete their tests. The miliolid wall consists of a three-dimensional random array of calcite needles veneered by a two-dimensional array of needles parallel to the outer surface of the test; the mineralized wall occurs between two organic membranes (Hay and others, 1963; Towe and Cifelli, 1967; Lynts and Pfister, 1967; Hemleben, 1969; Haake, 1971). However, in the miliolids, the structural units are not hollow, suggesting differences in the process of mineral precipitation in these two groups. The dimensions of the structural units of the two groups also appear to differ. The siliceous rods on the exterior and interior surfaces of the wall are about 4 μm to 5 μm long and about ⅓ μm in diameter, whereas calcite crystals and rods in the miliolids thus far studied are reported to be about ½ μm to 2 μm long and about ⅛ μm to ½ μm in diameter (Hay and others, 1963; Lynts and Pfister, 1967).

As in the case of microarchitecture of the wall, the test morphology of the new siliceous form is similar to that of some members of the Family Miliolidae, but the two types of foraminifera differ in the orientation of the longitudinal axes of their chambers. In the siliceous foraminifera, the planes of bilateral symmetry of the successive chambers cross one another, whereas in the Family Miliolidae they radiate out from the longitudinal axis of the test. Thus, in contrast to the miliolids in which the longitudinal axes of the chambers normally lie parallel, lateral aspects of the test of the siliceous form reveal early chambers with their longitudinal axes oblique to those of the latest volution as a result of the continual shift in chamber orientation (Fig. 2, d–f). In advanced growth stages, this difference is obscured due to extensive overlap of lateral extensions of the chambers on earlier volutions of the test (Fig. 2, a–c). These lateral extensions also tend to obscure the distinctive lagenoid shape of the chambers, clearly visible in young specimens.

It may be concluded that the new foraminifer precipitates opal for its test. Microarchitectural similarities suggest that it may have developed from a miliolid stock. Indeed, Ponder (1974) included Echols' (1971) siliceous specimens in his redescription of the Genus *Miliolinella*. But the siliceous form is distinct in its chamber shape and addition as well as in mineral composition, so that his definition appears to us to be too broad. The siliceous form is sufficiently differentiated to warrant wide taxonomic separation from the miliolids.

TAXONOMY

TAXONOMIC ASSIGNMENT OF THE NEW FORM

The modern subdivision of the Foraminiferida into suborders on the basis of test mineralogy and structure (Loeblich and Tappan, 1964) has historical precedent going back to about the middle of the 19th century (Carpenter, and others, 1862; Reuss, 1862). In this classification, construction of the wall is regarded as reflective of the nature of the secreting protoplasm, whereas isomorphic test configurations are considered adaptive products unrelated to phylogeny. The classification recognizes 5 suborders as follows: Allogromiina (membranous and tectinous tests), Textulariina (agglutinated tests), Fusulinina (calcareous microgranular tests), Miliolina (calcitic imperforate tests), and Rotaliina (calcareous perforate tests). The only provision made for tests of siliceous composition is among the Textulariina where forms with milioline chamber arrangement and "siliceous or agglutinated" walls are grouped together in the Family Rzehakinidae (Cushman, 1933; Loeblich and Tappan, 1964, p. 220). The microstructure of the siliceous wall in this family must be taken as agglutinated according to the suborder under which it is classified, and indeed Cushman precisely defined the wall structure of members of this group as "arenaceous, usually siliceous."

The species with a secreted, opaline test described in this report may not be assigned to any of the available taxa within the Order Foraminiferida. Therefore, a new suite of taxa of suborder and lesser rank is proposed to accommodate this distinctive form.

SYSTEMATICS

Order FORAMINIFERIDA Eichwald, 1830
Suborder Silicoloculinina, n. subord.

Test of secreted opaline silica, imperforate.

Family Silicoloculinidae, n. fam.

Test free, proloculus followed directly by chambers with two to a volution, arranged in intersecting planes; aperture terminal, with a tooth modification.

Genus **Silicoloculina**, n. gen.
Plate 1, Figures 1–4, Plate 2, Figures A–D

Chambers two to a volution, alternating so that the posterior of each new chamber covers the preceding aperture and rotated so that the planes of bilateral symmetry of succeeding chambers intersect at an angle of about 20° to the right or to the left, dependent upon coiling direction. Chambers lagenoid, developing broad lateral extensions which progressively obscure the preceding chambers, producing an external triloculine appearance in large specimens. Wall siliceous with an organic covering, imperforate, porcelaneous to opaline in appearance; aperture a terminal arch, with a tooth arising from the lower rim.

Type species: *Silicoloculina profunda*, n. sp.

The generic name was selected to indicate similarity in gross morphology to certain miliolid foraminifera and is derived from the Latin, *silex* (flint) plus *loculina* (cell, dim. of locus); gender feminine.

Silicoloculina profunda n. sp.
Plate 1, Figures 1–4

Miliolina labiosa (d'Orbigny)—Earland, 1934, Discovery Repts., v. 10, p. 50, pl. 1, figs. 5–7.
'*Miliolinella*' sp.—Echols, 1971, Antarctic Research Ser., v. 15, p. 157, pl. 12, fig. 1.
Miliolinella cf. *circularis* (Bornemann)—Fillon, 1974, Micropaleontology, v. 20, p. 144, pl. 3, fig. 13.

Test ovate in outline, somewhat flattened; chambers lagenoid in shape with lateral extensions, two to a volution, with the ultimate chamber occupying about ⅔ of the perimeter of the test and rotated with each chamber addition so that planes of bilateral symmetry of successive chambers intersect at an angle of about 20°; wall of secreted opaline silica in the form of hollow rods, imperforate with an organic covering, the surface smoothly finished and procelaneous to opalescent when dry, transparent when wet; aperture a terminal low arch with a simple broad tooth.

Length of holotype 0.33 mm; paratypes range from 0.23 to 0.49 mm in length; proloculus diameter 0.06 mm.

Types and occurrence. Holotype (USNM 272501) from Recent surface sediment at lat 8°41.9′S, long 82°13.3′W, water depth 4,378 m (Y71-8-70MG3, 0–3 cm) on the western margin of the Peru-Chile Trench. Figured paratypes (USNM 272502) from DSDP 320, 1-3 (114–116 cm), Quaternary; (USNM 272503) from DSDP 320, 1-2 (120–122 cm), Quaternary; (USNM 272504) from DSDP 320A, 1-2 (139–141 cm), Quaternary. In the type area off the coast of Peru, the species has been recovered between lat 7°35′S and 21°12′S, in water depths of 4,237 to 6,505 m, with one occurrence in a calcareous sample from a water depth of 2,734 m. It also occurs in 993 to 4,644 m water depths in the Scotia Sea (Echols, 1971), in the Ross Sea (Fillon, 1974), in DSDP cores in the Bering Sea, and in water depths of 3,960 to 5,339 m in the Central Pacific Basin (Lineberger, 1975), indicating that it is widely distributed. Echols (1971) found specimens that stained with rose Bengal from about 2,300 and 3,100 m water depth in the Scotia Sea.

Specimens of *Silicoloculina profunda* were noted at subsurface depths as great as 25 m in strata dated as early Quaternary (Scientific Staff, 1974) at the Deep Sea Drilling Project Sites 320 and 321 on the Nazca Plate. They occur down to the *Denticulina kamtschatica* diatom zone of late Miocene or early Pliocene age in the DSDP borings in the Bering Sea and have been found in the *Dorcadospyris alata* radiolarian zone of middle Miocene age in the Central Pacific Basin (Lineberger, 1975). The cored sediment as well as the surface sediment containing the new form is generally rich in radiolarian and diatom skeletons, but in spite of the concentration of siliceous remains, the new form is always rare.

The specific name is derived from the Latin *profundus* (deep), emphasizing the general deep-sea habitat of the species.

REMARKS

In the course of a literature survey to determine other possible members of the new suborder, it became apparent that in the Family Rzehakinidae, only the nominal genus, *Rzehakina*, having a homogeneous fine-grained siliceous test, might belong in this suborder. The other included genera (*Ammoflintina*, *Miliammina*, *Silicosigmoilina*, *Spirolocammina*, *Spirosigmoilinella*, *Trilocularena*, and *Psamminopelta*) have agglutinated type species. The Rzehakinidae resemble the Nubeculariidae among the porcelaneous foraminifera in having a primary planispiral stage, in contrast to the primary milioline-like coiling of the Silicoloculinidae. Thus, the possible reassignment of the Rzehakinidae to the new suborder would not affect the validity of the new family. Hansen and Hanzlikova (1974), however, determined that the type species of *Rzehakina*, *Silicina epigona* Rzehak, is agglutinated of very fine particles and diagenetically altered. In addition, one of the writers examined a paratype of *Rzehakina venezuelana* Hedberg (Stanford University 6873) which has a semi-transparent finely granular siliceous wall. Under 5,000× magnification, the surface of the wall appeared as an irregular surface of polygons, unlike the rods seen in the modern siliceous form. As the genus is confined to Upper Cretaceous and Lower Tertiary strata, alteration of the original test material may be the rule.

Determination of the wall structure of contemporary foraminifera is an easier task. Numerous investigators have reported Recent milioline morphotypes from deep or cold waters where biogenic precipitation of calcite must be difficult. Some of those foraminifera may belong in the taxa described in this paper.

ACKNOWLEDGMENTS

RV YAQUINA samples on the Nazca Plate were taken by the staff of the School of Oceanography, Oregon State University, in the course of a National Science Foundation IDOE cooperative project, which also funded this research (Grant GX-28675). The National Science Foundation-sponsored Deep Sea Drilling Project, managed by the Scripps Institution of Oceanography, generously allowed examination of the cores from the sites on the Nazca Plate and in the Bering Sea. James Ingle permitted reference to the Stanford University paratype. Photomicrographs on Plate 1 were produced by Walter Dudley and Karen Margolis in the Hawaii Institute of Geophysics Cambridge S4-10 Scanning Electron Microscope laboratory that was partly financed through a National Science Foundation Grant (GD-34270). Plates 2 and 3 were photographed on an ETEC Autoscan in J. P. Revel's laboratory at California Institute of Technology. Funding was provided by National Science Foundation Grant DES75-08659. We are indebted to these individuals and organizations for their considerable contribution to this study.

This is Hawaii Institute of Geophysics Contribution 764, and Contribution No. 2689, Division of Geological and Planetary Sciences, California Institute of Technology, Pasadena, California.

REFERENCES

CARPENTER, W. B., PARKER, W. K., and JONES, T. R., 1862, Introduction to the study of the foraminifera: London: Robert Hardwicke for the Ray Society, p. 1–319.

CUSHMAN, J. A., 1933, Foraminifera their classification and economic use: Cushman Lab. Foram. Research Spec. Pub. 4, p. 1–349.

EARLAND, A., 1934, Foraminifera 3, the Falklands sector of the Antarctic (excluding South Georgia): Discovery Rept., v. 10, p. 1–208.

ECHOLS, R. J., 1971, Distribution of foraminifera in sediments of the Scotia Sea area, Antarctic waters: Antarctic Research Ser., v. 15, p. 93–168.

EICHWALD, E. VON, 1830, Lethaea Rosica ou Paléontologie de la Russie, Prémier section de l'ancienne période: Stuttgart: E. Schweizerbart, v. 1, p. 1–681.

FILLON, R. H., 1974, Late Cenozoic foraminiferal paleoecology of the Ross Sea, Antarctica: Micropaleontology, v. 20, p. 129–151.

HAAKE, F. -W., 1971, Ultrastructures of miliolid walls: Jour. Foram. Research, v. 1, p. 187–189.

HANSEN, H. J., and HANZLIKOVA, E., 1974, Ultrastructure of some siliceous Foraminiferida: Rev. Española Micropaleontologia, v. 6, p. 447–466.

HAY, W. W., TOWE, K. M., and WRIGHT, R. C., 1963, Ultramicrostructure of some selected foraminiferal tests: Micropaleontology, v. 9, p. 171–195.

HEMLEBEN, C., 1969, Ultrastrukturen bei kalkschaligen Foraminiferen: Naturwissenschaften, v. 56, p. 534–538.

LINEBERGER, P., 1975, Sedimentary processes and pelagic turbidites in the eastern Central Pacific Basin: Hawaii Univ., M.S. Thesis, p. 1–116.

LIPPS, J. H., 1971, Siliceous cement in agglutinated foraminifera?: Jour. Protozoology, v. 18 (suppl.), p. 30.

———, 1973, Test structure in foraminifera: Ann. Rev. Microbiology, v. 27, p. 471–488.

LOEBLICH, A. R., JR., and TAPPAN, HELEN, 1964, Sarcodina, chiefly "thecamoebians" and Foraminiferida, *in* Moore, R. C., ed., Treatise on invertebrate paleontology, Protista 2, part C: Kansas Univ. Press [New York: Geol. Soc. Amer., pt. C, Protista 2], v. 1–2, p. C1-C900.

LOWENSTAM, H. A., 1971, Opal precipitation of marine gastropods (Mollusca): Science, v. 171, p. 487–490.

———, 1974, Impact of life on chemical and physical processes: New York, John Wiley and Sons, The Sea, v. 5, p. 715–796.

LOWENSTAM, H. A., and ROSSMAN, G., 1975, Amorphous, hydrous, ferric phosphatic dermal granules in Molpadia (Holothuroidea): Physical and chemical characterization and ecologic implications of the bioinorganic fraction: Chem. Geology, v. 15, p. 15–51.

LYNTS, G. W., and PFISTER, R. M., 1967, Surface ultrastructure of some tests of Recent Foraminiferida from the Dry Tortugas, Florida: Jour. Protozool., v. 14, p. 387–399.

PONDER, R. W., 1974, The foraminiferal genus *Miliolinella* Wiesner, 1931 and its synonyms: Micropaleontology, v. 20, p. 197–208.

REISWIG, H. M., 1971, The axial symmetry of sponge spicules and its phylogenetic significance: Cahiers Biol. Marine, v. 12, p. 505–514.

REUSS, A. E., 1862, Entwurf einer systematischen Zusammenstellung der Foraminiferen: K. Akad. Wiss. Wien, Math.-Naturw. Cl., Sitzungsber., v. 44 (1861), p. 355–396.

SCIENTIFIC STAFF, 1974, Oceanic basalt and the Nazca Plate: Geotimes, v. 19, p. 20–24.

TOWE, K. M., and CIFELLI, R., 1967, Wall ultrastructure in the calcareous foraminifera: crystallographic aspects and a model for calicification: Jour. Paleontology, v. 41, p. 742–762.

VINOGRADOV, A. P., 1953, The elementary chemical composition of marine organisms: Yale Univ., Sears Found. Marine Research, Mem. 2, p. 1–647.

APPENDIX I

Log of Samples Containing *Silicoloculina*

PERU—CHILE TRENCH AREA

Core*	Location	Water depth (m)	Number of Silicoloculina
Y71-8-71MG1**	7°35.3'S 81°40.0'W	5,535	fragments
Y71-8-75MG3	7°40.4'S 81°20.3'W	5,670	1
Y71-8-76MG3	8°07.0'S 81°36.0'W	5,122	fragments
Y71-8-70MG3	8°41.9'S 82°13.3'W	4,378	4
Y71-8-59MG5	9°21.8'S 80°41.1'W	5,304	1
Y71-7-30MG4	10°03.1'S 88°40.6'W	4,237	2
Y71-7-27MG1	10°14.6'S 82°05.2'W	4,569	5
Y71-6-24MG2	15°16.0'S 76°18.8'W	4,899	1
Y71-6-12MG3	16°26.6'S 77°33.8'W	2,734	1
Y71-6-22MG4	16°48.6'S 74°03.4'W	5,301	fragments
Y71-6-21MG2	16°50.8'S 74°21.7'W	6,505	fragments
Y71-6-19MG3	17°03.0'S 74°24.5'W	5,791	1
Y71-6-14MG3	17°40.2'S 75°47.3'W	4,625	fragments
KK74-FFC48***	21°12.0'S 71°40.1'W	4,540	1

DSDP—NAZCA PLATE

Site	Location	Water depth (m)	Sample	Age	Number of Sili-coloculina
320A	9°00.40'S 83°31.80'W	4,487	1-1 (14–16)	Quat.	1
			1-2 (139–141)	Quat.	2
			1-4 (52–54)	Quat.	2
320	9°00.40'S 83°31.80'W	4,487	1-1 (99–101)	Quat.	1
			1-2 (120–122)	Quat.	1
			1-3 (114–116)	Quat.	2
321	12°01.29'S 81°54.24'W	4,827	4-2 (64–66)	Quat.	1

DSDP—BERING SEA, N. PACIFIC

Site	Location	Water depth (m)	Sample	Age	Number of Sili-coloculina
184	53°42.64'N 170°55.39'W	1,910	7-3 (80–82)	L. Plio.	1
			10-3 (80–82)	L. Plio.	1
189	54°02.14'N 170°13.38'E	3,437	5-1 (76–78)	E. Pleist.	2
			5-4 (76–78)	E. Pleist.	2
190	55°33.55'N 171°38.42'E	3,875	4 cc	M. Pleist.	1
			14 cc	L. Mio.	1
191	56°56.70'N 168°10.72'E	3,854	2 cc	L. Pleist.	2
192	53°00.57'N 164°42.81'E	3,012	1 cc	L. Pleist.	2
			4-2 (43–45)	M. Pleist.	1
			4 cc	M. Pleist.	5
			7 cc	L. Plio.	2
			8-3 (130–132)	L. Plio.	1
			8 cc	L. Plio.	1
			10 cc	E. Plio.	1
			11 cc	E. Plio.	1
			18 cc	L. Plio.	1
			19 cc	L. Plio.	1
			20 cc	L. Plio.	1

* Sample depth 0–3 cm, ¼ core area.

** Y = R. V. YAQUINA, Oregon State University; MG = multiple gravity core.

*** KK = R. V. KANA KEOKI, University of Hawaii; FFC = free-fall core.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 215–224, pls. 1–3, 1980

REGARDING THE GENUS *HEMISPHAERAMMINA* LOEBLICH AND TAPPAN (FORAMINIFERA)

Y. Le Calvez[1] and D. Cesana[2]

ABSTRACT

The genus *Hemisphaerammina* is a senior synonym of *Daitrona*. A detailed scanning electron microscopic and transmission electron microscopic study was conducted on the test, the cytoplasm (ectoplasm and endoplasm), and the nucleus of the species *H. bradyi*.

The arenaceous test has a calcareous cement. Both sides of the test show a very different composition. The differentiation between the outer side, with coarse particles and little cement, and the attached side, with fine particles and abundant cement, results from the selective choice of agglutinated particles. This selection probably occurs at the ectoplasm level.

In contrast to the simple and rather primitive organization of the test, the endoplasm and nucleus show a complex ultrastructure, which is as complex as that of advanced calcareous foraminifera.

On trouve dans les herbiers marins de Banyuls-sur-Mer, fixés sur les feuilles de Posidonies, des Foraminifères à test arénacé, de forme hémisphérique et de couleur blanchâtre (Pl. I, Fig. 1) dont la position systématique resta pendant longtemps très mal définie.

SYSTEMATIQUE

Ces formes furent décrites en 1866 par Jones, Parker et Brady dans le Pliocène inférieur d'Angleterre (Crag of Sutton) sous le nom de *Trochammina* (*Webbina*) *irregularis* (D'Orbigny) var. *hemisphaerica*, avec la diagnose suivante:

"Small, circular, subconical, monothalamous like a low bell-tent, parasitic, recognisable only by its smooth but sandy shell, and general resemblance to the common forms of *Webbina irregularis*. Diam. $^1/_{50}$ inch."

Puis, quelques années plus tard, en 1884, Brady les élevant au rang d'espèce (*Webbina hemisphaerica*) les refigura dans son travail (Challenger, Pl. XI, Fig. 11). Heron-Allen et Earland (1908–1909) en étudiant le matériel de Selsey Bill retrouvèrent ces Foraminifères et furent amenés, tout en faisant des réserves, à les rapporter à *Thurammina papillata* (Brady). Cependant en 1914, dans leur mémoire relatif aux Foraminifères du "Kerimba Archipelago," ils reconnurent (p. 372) qu'il s'agissait de différents stades du développement de *Webbina hemisphaerica*.

En 1904, Rhumbler constatait que certains Foraminifères placés parmi les *Webbina* possédaient un test arénacé alors qu'au sens de D'Orbigny, ce genre ne comprenait que des individus pourvus d'une coquille calcaire; il établit donc pour eux le genre *Webbinella* qui réunissait les espèces *W. clavata* et *W. hemisphaerica*. Ce nouveau genre devait être émendé par Cushman en 1918, qui en sortit les *W. clavata* pour lesquels il créa le genre *Ammolagena* et désigna *Webinella hemisphaerica* comme espèce-type du genre *Webbinella*.

Jusqu'en 1957, ce genre fut maintenu et signalé par de nombreux auteurs et des espèces nouvelles, tant actuelles que fossiles, vinrent s'ajouter à l'espèce-type.

---

[1] Laboratoire de Micropaléontologie, Ecole Pratique des Hautes Etudes, 8 rue de Buffon, 75005 Paris (France).

[2] Laboratoire d'Evolution des Etres Organisés, 105 Bld Raspail, 75006 Paris (France).

A cette époque, A. Loeblich et H. Tappan venus à Londres pour examiner les collections du British Museum, constatèrent que l'holotype de *Webbinella hemisphaerica* était en réalité un Polymorphinidé fixé, voisin de *Bullopora* Quenstedt. Dans ces conditions, les *Webbinella* prenaient tout naturellement place dans la sous-famille des Webbinellinae et la famille des Polymorphinidae; les Foraminifères à test arénacé, préalablement considérés comme des *Webbinella*, ne pouvaient plus être maintenus ni dans ce genre, ni dans cette espèce. Loeblich et Tappan (1964) en firent des *Hemisphaerammina*, avec pour espèce-type *H. bradyi* dont l'holotype était la forme figurée par Brady dans le Challenger (1884; Pl. 41, Fig. 11).

Hemisphaerammina bradyi, puisque tel est désormais le nom de ce Foraminifère, est très caractéristique mais aussi très polymorphe, comme d'ailleurs la plupart des formes arénacées fixées. Cette variabilité du test tient très certainement à sa nature même, mais aussi à la place dont il dispose sur son support. Les feuilles de Posidonies sont très souvent recouvertes de Bryozoaires, d'Algues encroûtantes, de Serpulides, etc., qui gênent son développement. De sorte qu'à côté d'individus parfaitement hémisphériques dont le test est généralement bordé d'une étroite bande déprimée ayant l'aspect d'une petite frange (Cushman, 1918, p. 62), on en trouve d'autres moins réguliers ou légèrement aplatis et parfois dépourvus de frange. L'animal est fortement fixé sur son support et il est malaisé de l'en détacher sans le briser. Pour cette raison, les auteurs n'ont en général examiné que la face supérieure du test. La face inférieure ou face de fixation est plus complexe et montre un dispositif de septa rayonnants qui font partie du test et le divisent en lobes étroits (Pl. I, Figs. 2, 3). Aucune ouverture n'est visible. Les caractères de cette face de fixation ont été remarqués en 1948 par Cushman chez *Webbinella artica*; n'ayant jamais vu la face inférieure de *Hemisphaerammina bradyi*, il a cru se trouver en présence d'une nouvelle espèce. Or il est à peu près certain que ces deux formes sont synonymes; on trouve en effet des *H. bradyi* dont certains lobes sont arrondis et ressemblent tout à fait à ceux figurés par Cushman. Il se pourrait aussi que *Webbinella depressa* H.-A. et E. et *W. limosa* Earland soient conspécifiques de *H. bradyi*; les figures qu'ils en donnent ne représentent que la face supérieure du test mais elles correspondent bien à certains individus de *H. bradyi*.

→

PLANCHE I

Hemisphaerammina bradyi

1 Photographie de l'animal vivant encore fixé sur son support. On observe le test arénacé en forme de dôme, le pourtour déprimé formant une sorte de couronne. ×40.

2 Photographie de la face de fixation de l'animal vivant. Elle montre les septa rayonnants subdivisant la cellule en lobes étroits plus ou moins réguliers occupés par le cytoplasme et l'orifice central (o). ×30.

3 Electromicrographie de la face de fixation d'un test vide. ×50.

4 Electromicrographie de la face supérieure du test, constituée par des éléments grossiers dont des frustules de Diatomées (D) des spicules d'éponges (SP) et un ciment peu abondant. ×100.

5 Photographie d'un animal détaché de son support. On constate le début de la transformation. La cellule prend une forme sphérique et la bordure déprimée disparait. ×30.

6 Electromicrographie de la partie adhérente au support. Les matériaux qui la composent sont très fins et noyés dans une grande quantité de ciment. ×2,000.

Photographies: Lecompte, Laboratoire Arago, Banyuls-sur-Mer; Pl. I.

PLATE I

1 Photograph of the living animal still attached to its substrate. The arenaceous test is dome-shaped, with a ring-like depression near the outer edge. ×40.

2 Photograph of the attached side of the living animal. The radiating septa subdivide the cell into narrow, rather regular lobes which are occupied by the cytoplasm and the central opening (o). ×30.

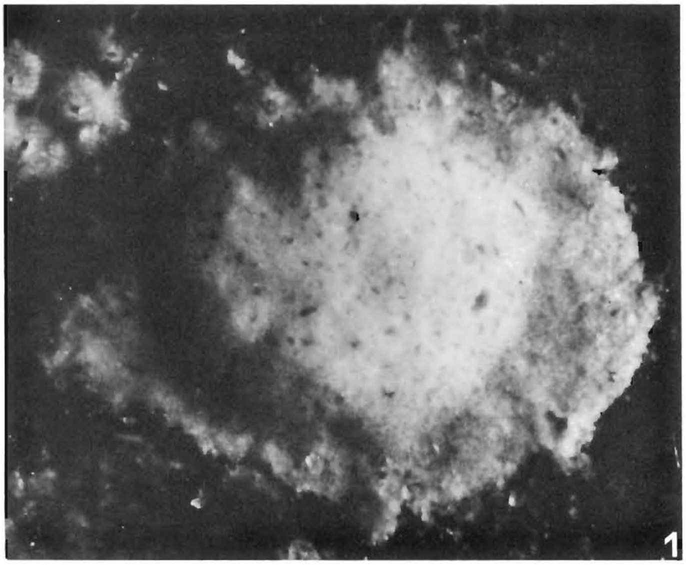
3 Electron micrograph of the attached side of an empty test. ×50.

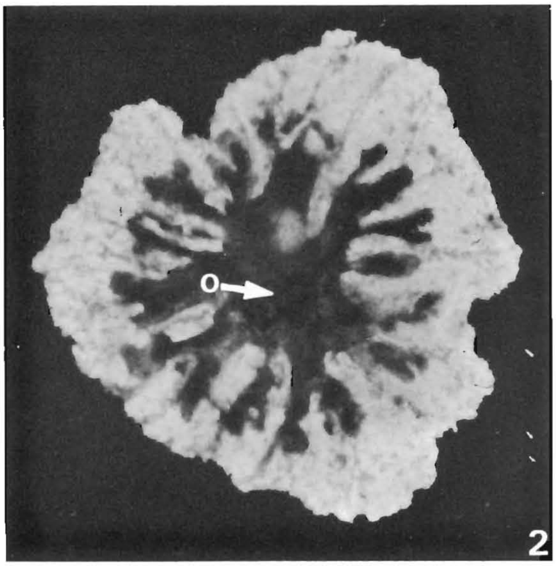
4 Electron micrograph of the upper side of the test composed of coarse particles including diatom frustules (D), sponge spiculae (SP) and a sparse cement. ×100.

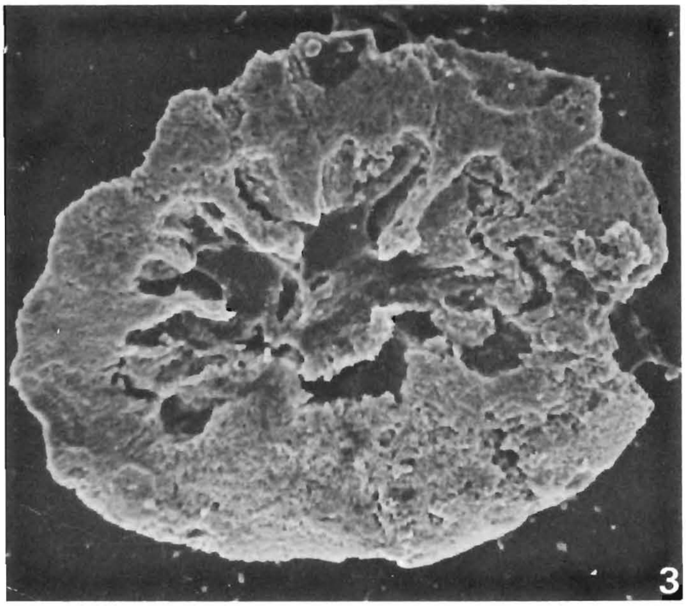
5 Photograph of an animal detached from its substrate. The cell has a more spherical shape and the outer depressed ring disappears. ×30.

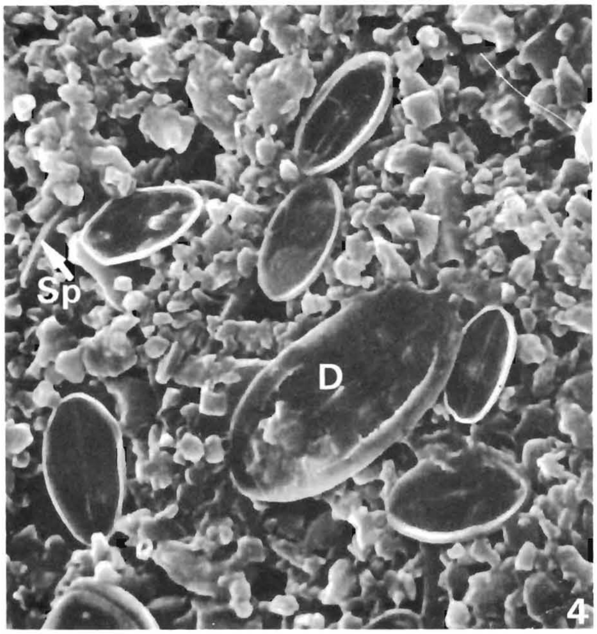
6 Electron micrograph of the part adhering to the substrate. The particles are very fine and are embedded in a large quantity of cement. ×2,000.

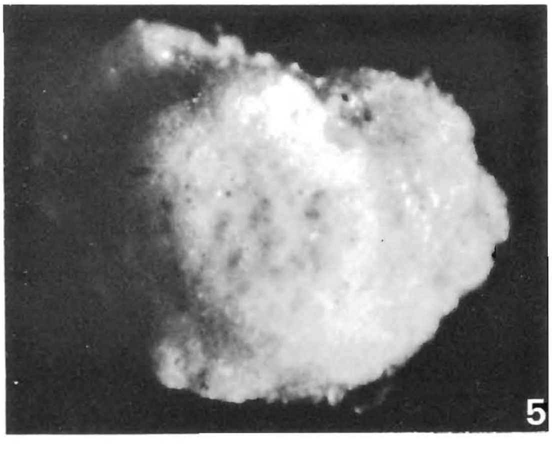
Photographs of Plate I are by Lecompte, Laboratoire Arago, Banyuls-sur-Mer.

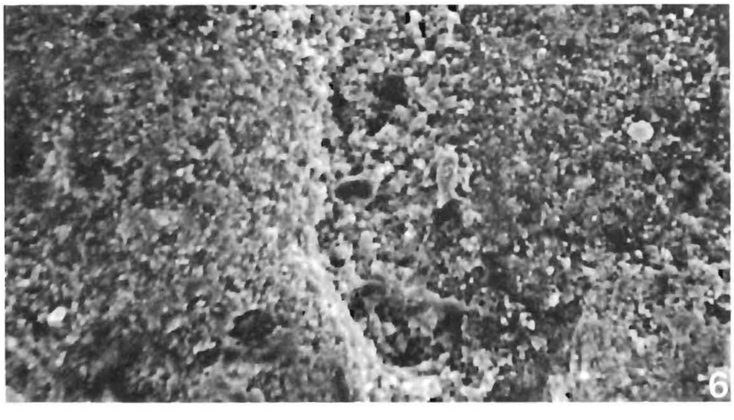

1

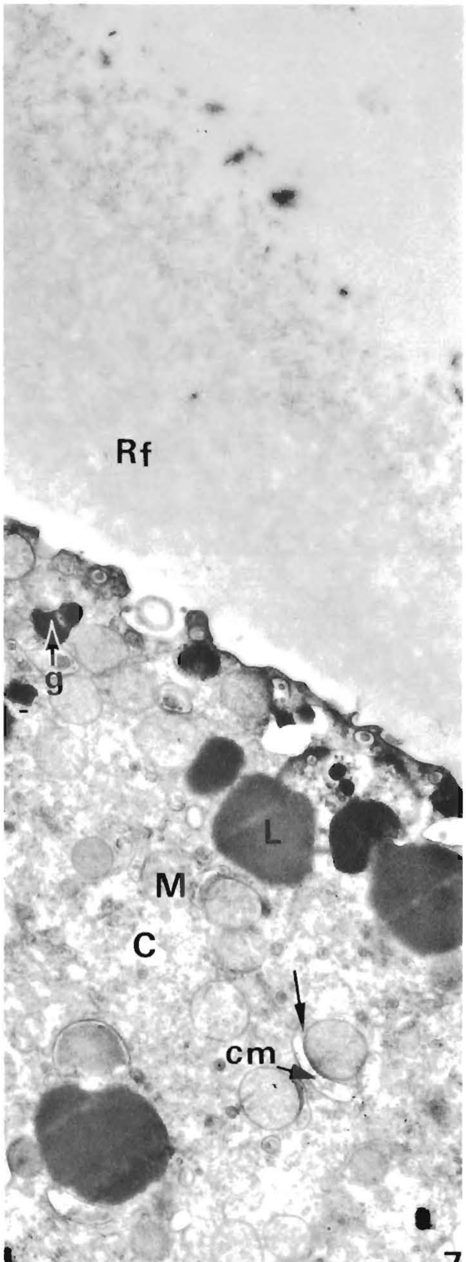

o
2


3

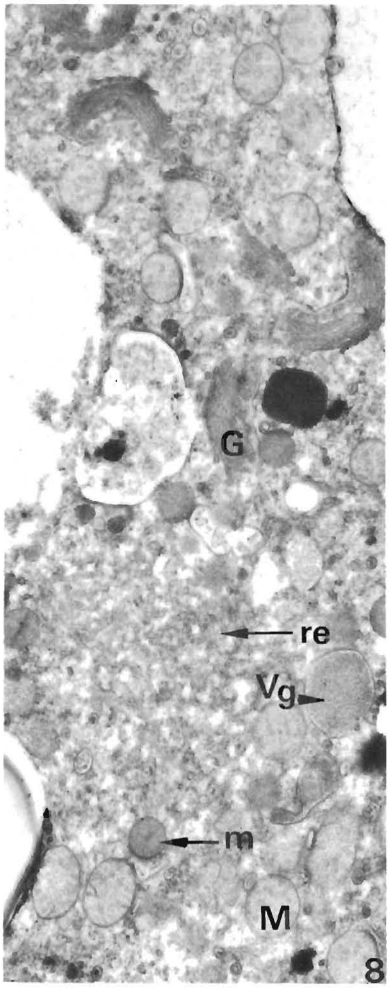

Sp
D
4


5

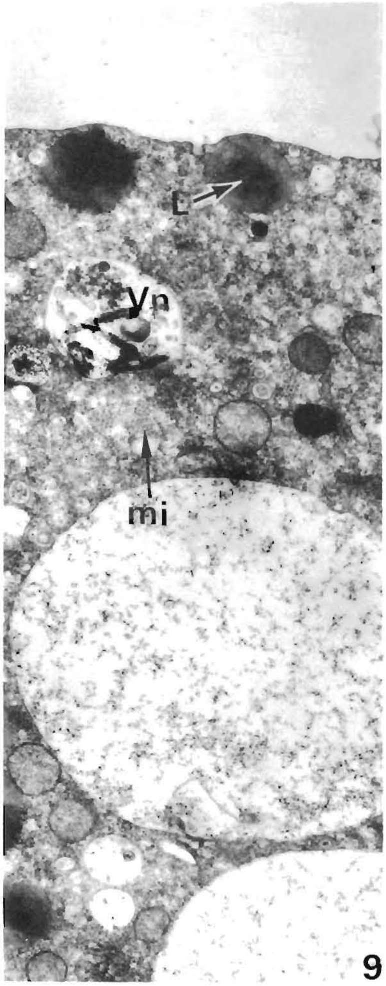

6



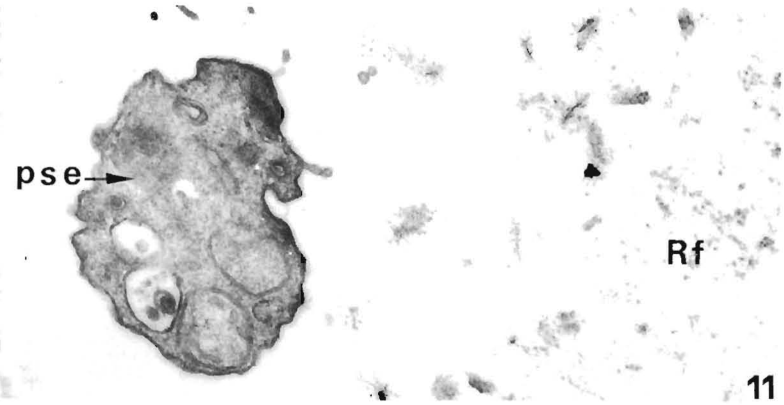
7



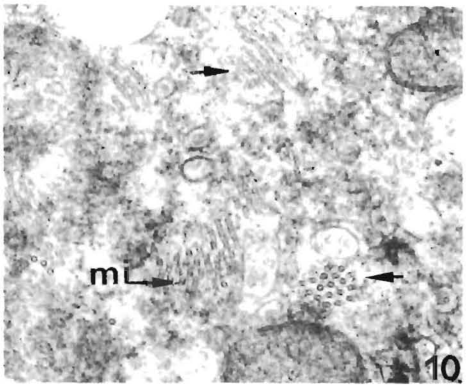
8



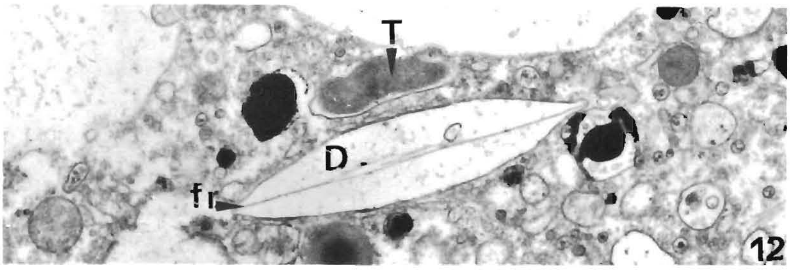
9



11



10



12

Quant à *Webbinella facta* Earland (1934), les figures données par l'auteur ne laissent aucun doute sur son identité avec *H. bradyi.*

Sur l'animal vivant, les pseudopodes sont difficilement observables; ils sont très fins et apparaissent au bord marginal du test.

Lorsqu'on détache de son support *Hemisphaerammina bradyi* et qu'on le place dans un petit récipient rempli d'eau de mer, on constate au bout de quelques heures que le test se recroqueville et se referme sur lui-même, masquant ainsi complètement le protoplasme qui se trouve à l'intérieur d'un test grossièrement globuleux (Pl. I, Fig. 5). Quelques pseudopodes très ténus apparaissent et fixent l'animal à la paroi du récipient.

Une section dans ce test globuleux fait apparaître les septa divisant en lobes l'unique chambre qui le compose, septa n'atteignant pas la région centrale qui est plus ou moins grande suivant les individus. En d'autres termes, on se trouve en face d'un animal qui correspond à la diagnose donné par Loeblich et Tappan en 1961 pour le genre *Daitrona,* nouveau nom donné aux Foraminifères décrits en 1896 par Goës sous le nom de *Crithionina lens.* Nous sommes donc en droit de penser que les *Daitrona lens* sont en réalité des *Hemisphaerammina bradyi* qui se sont détachés de leur support et ont pris la forme globuleuse, isolant ainsi le protoplasme du milieu extérieur. Il s'agirait en fait d'un phénomène de protection de la matière vivante qui permettrait à l'animal de continuer à vivre et d'assurer la pérennité de l'espèce.

Hemisphaerammina et *Daitrona* deviennent congénériques et le premier étant le plus ancien, il doit être maintenu.

Par ailleurs, les particularités de la face inférieure d'*H. bradyi* doivent être considérées comme un caractère spécifique et non comme un critère générique, car il existe des *Hemisphaerammina* qui en sont dépourvues. *H. crassa* décrite par J. Le Calvez en 1935 possède une face supérieure rappelant celle de *H. bradyi,* avec toutefois cette différence que le test, toujours peu compact, est plus épais et hérissé de nombreux brins végétaux qui sont des fibres provenant des rhizomes de Posidonies. La face inférieure, celle de la fixation, montre une cavité centrale arrondie, sans septa rayonnants.

J. Le Calvez (p. 90) qui a étudié les aspects protoplasmiques et nucléaires de *H. bradyi* et *H. crassa* constate qu'ils "sont si semblables qu'ils indiquent une parenté certaine" et que par conséquent, il est impossible d'établir un genre pour les formes pourvues de septa rayonnants et un autre genre pour celles qui en sont dépourvues. Ajoutons à cela que ces deux espèces sont des formes d'herbiers et qu'elles co-

←

PLANCHE II

7 La coupe passe par le cytoplasme (C) et le revêtement microfibrillaire (Rf) d'*Hemisphaerammina*. Des corps multivésiculaires (cm) sont en contact avec des mitochondries (M) (flèche). Des gouttelettes lipidiques (L) et des granules osmiophiles (g) sont alignés à la périphérie de la cellule. ×13,600.

8 Une portion de cytoplasme montrant le réticulum endoplasmique granulaire (re), des appareils de Golgi (G), des corps denses ou microbodies (m), des mitochondries (M) et des vésicules avec contenu granulaire (Vg). ×13,600.

9 Une portion d'un lobe cytoplasmique montrant de nombreux microtubules (mi) groupés en faisceaux, des vacuoles nutritives (Vn) et des gouttelettes lipidiques (L). ×13,600.

10 A fort grossissement, des microtubules (mi) groupés en faisceaux diversement orientés (flèche). ×32,000.

11 La coupe passe par un pseudopode (pse) situé à l'extérieur du revêtement microfibrillaire (Rf). ×32,000.

12 Une portion du cytoplasme avec une frustule (fr) de Diatomée (D) et un trichocyste (T). ×13,600.

PLATE II

7 The section cuts through the cytoplasm (C) and the microfibrillar coat (Rf) of *Hemisphaerammina*. The close relation between mitochondria (M) and multivesicular bodies (cm) is visible (arrow) as well as the lipidic droplets (L) and osmiophilic granules (g) along the periphery of the cell. ×13,600.

8 A portion of the cytoplasm showing endoplasmic reticulum (re), Golgi apparatus (G), microbodies (m), mitochondria (M) and vesicles with a granular content (Vg). ×13,600.

9 A portion of a branch of an adult cell showing many microtubules (mi) grouped in bundles, food vacuoles (Vn) and the lipidic droplets (L). ×13,600.

10 A high magnification of microtubules (mi) grouped in diversely orientated bundles (arrows). ×32,000.

11 A pseudopodium (pse) near the outside of the microfibrillar coat (Rf). ×32,000.

12 A portion of cytoplasm with a frustule (fr) of Diatom (D) and a trichocyst (T). ×13,600.

existent à Banyuls-sur-Mer. *H. bradyi* y est toutefois plus abondante et sa répartition bathymétrique plus grande; on la trouve entre 5 et 20 mètres de profondeur alors que *H. crassa* est restreinte à une zone comprise entre 0,50 et mètres.

ULTRASTRUCTURE

J. Le Calvez le premier décrivit la morphologie du test ainsi que la structure cytoplasmique et nucléaire de *Hemisphaerammina bradyi* Loeblich et Tappan sous le nom de *Webbinella hemispherica* (J.P.B.).

Nous avons repris en microscopie électronique l'étude de cette espèce dont le cycle biologique est encore mal connu.

METHODES EMPLOYEES

Les tests desséchés ont été observés et photographiés au microscope électronique à balayage (type CAMEBAX, CAMECA) après métallisation par vaporisation d'or pur.

Pour les observations au microscope électronique à transmission, les *Hemisphaerammina* ont été fixées au glutaraldéhyde à 2,5% dans un tampon phosphate 0,4 M une heure à température ambiante, puis postfixées à l'acide osmique à 2% dans le même tampon une heure à 0°C. Les cellules débarassées de leur test ont été incluses dans l'Epon. Les coupes ultrafines effectuées au microtome Richert OMU 2 ont été contrastées à l'acétate d'uranyle aqueux puis au citrate de plomb. Elles ont été observées et photographiées au microscope électronique Philips EM 300 du "Laboratoire de microscopie électronique appliquée à la Biologie, C.N.R.S."

MORPHOLOGIE DU TEST

Nous avons déjà décrit l'aspect extérieur du test et sa conformation dans la partie de ce travail consacré à la systématique.

Le microscope électronique à balayage confirme la structure arénacée du test. Les différents éléments qui le composent sont agglomérés par un ciment calcaire. Les deux faces montrent une texture très différente.

La face supérieure, bombée, est constituée de matériaux assez grossiers. Les grains de quartz, de calcaire, les spicules d'Eponge et les très nombreuses frustules de Diatomées sont réunis par un ciment peu abondant donnant à cette face un aspect lâche et grossier (Pl. I, Fig. 4).

La face de fixation est composée de matériaux beaucoup plus fins, uniquement d'origine sédimentaire. Ils

→

PLANCHE III

13, 14 Les deux sections traversent le noyau (N). L'enveloppe nucléaire (en) a un coutour irrégulier et dessine des sillons qui s'enfoncent plus ou moins profondément dans le noyau (flèche). Elle est extérieurement recouverte d'une fine couche de cytoplasme (C). Un réseau de larges citernes (ci) sépare le noyau du cytoplasme (C). La membrane interne de l'enveloppe nucléaire est tapissée d'une lame de matériel microfibrillaire (lf) qui par place s'organise en un réseau alvéolaire (flèches). Dans le nucléoplasme (np), on observe de nombreux nucléoles (n) de forme irrégulière. Figure 13, ×11,200: Figure 14, ×20,000.

15 Une Diatomée (D) entourée par une frustule caractéristique (fr). ×14,000.

16 La section coupe tangentiellement le noyau (N) montré dans les Figures 13, 14. A certaines places et contre l'enveloppe nucléaire, la lame fibreuse (lf) s'organise en une mince couche alvéolaire (al) (flèche). Le réseau de larges citernes (ci) sépare le noyau (N) du cytoplasme (C). ×20,000.

17 Une Zooxanthelle dans l'endoplasme. Elle possède des chloroplastes (Cl), un noyau avec un nucléole central (n) et des chromosomes caractéristiques (Chr). ×14,000.

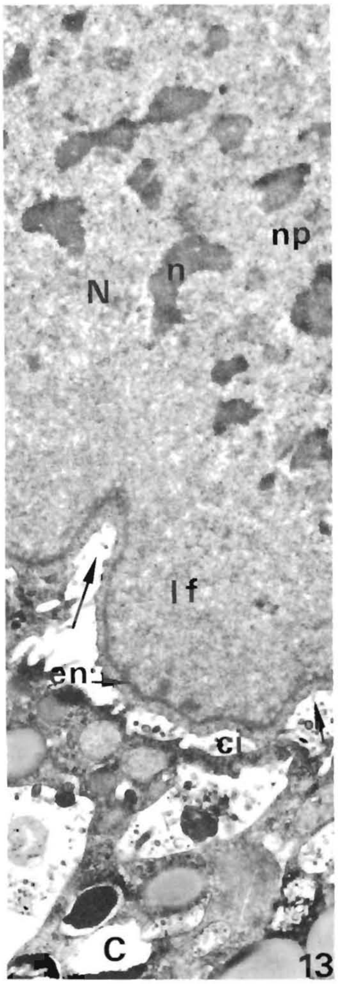
PLATE III

13, 14 Two sections through the nucleus (N). The nuclear envelope (en) shows an irregular outline with invaginations (arrows). It is covered externally with a fine cytoplasmic layer (C) and a network of large cisternae (ci). The inner membrane of the nuclear envelope is lined with a fibrous lamina (lf). In the nucleoplasm (np), the irregularly shaped compact nucleoli (n) are present. Figure 13, ×11,200; Figure 14, ×20,000.

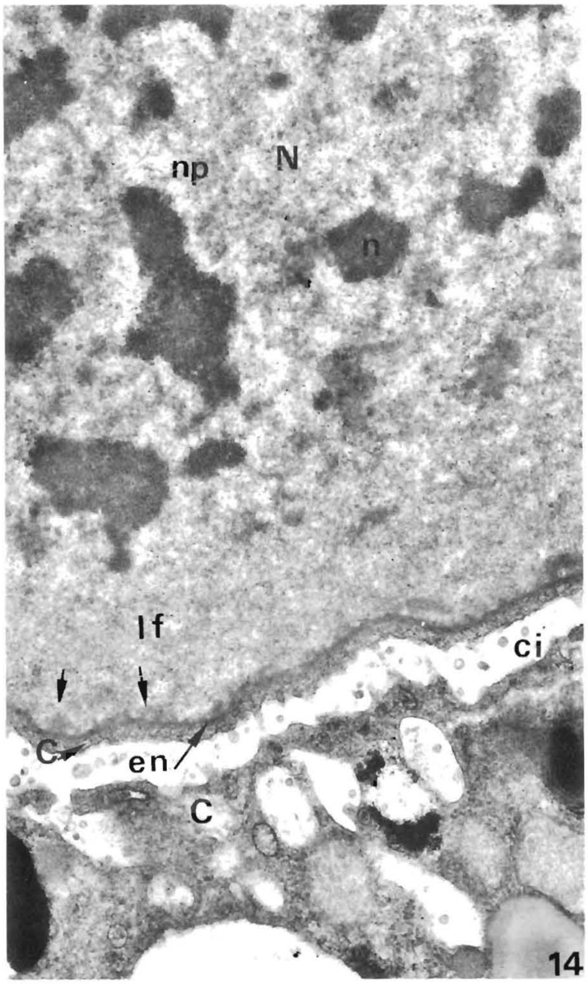
15 A Diatom (D) surrounded by the characteristic frustule (fr). ×14,000.

16 A tangential section through the same nucleus (N) as the one shown in Figures 13 and 14. In certain areas in contact with the inner nuclear membrane, the organization into an alveolar layer (al) of the fibrous lamina (lf) is clearly visible (arrows). A network of large disternae (ci) is between the nucleus (N) and the cytoplasm (C). ×20,000.

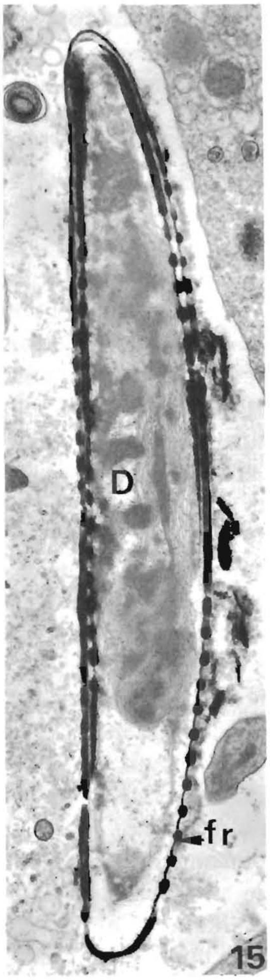
17 A Zooxanthel in the endoplasm. It possesses chloroplasts (Cl) and a nucleus with a central nucleolus (n) and the characteristic chromosomes (Chr). ×14,000.



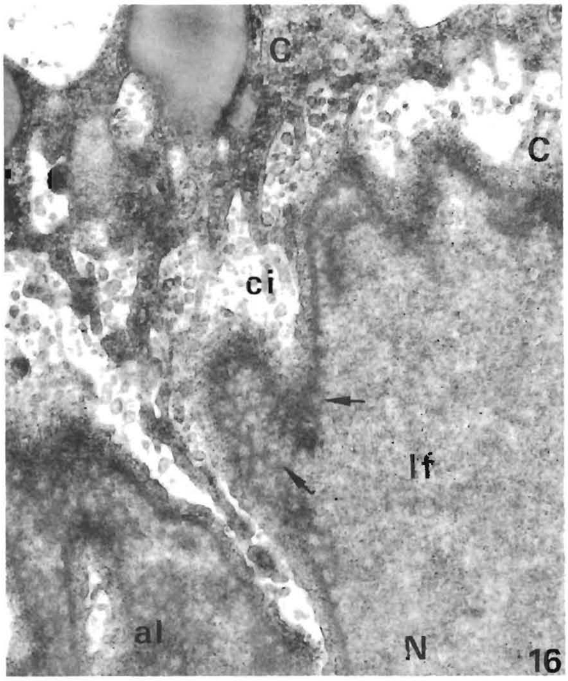
13



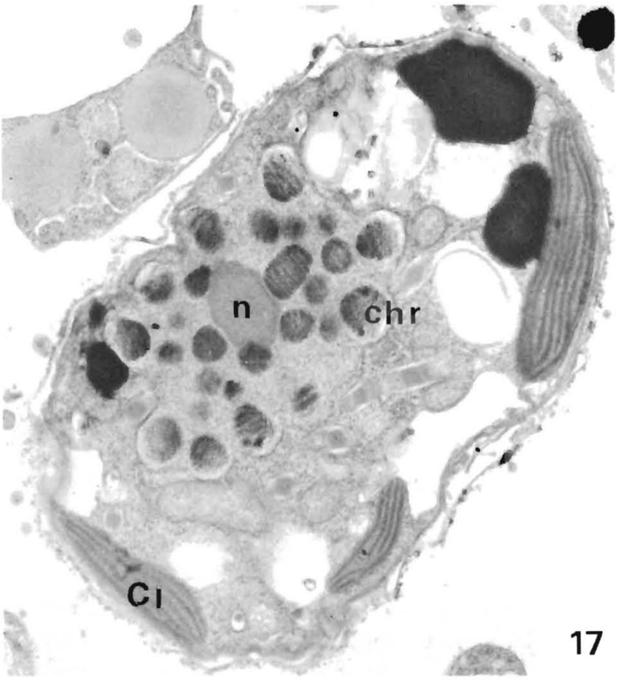
14



15



16



17

sont complètement noyés dans une grande quantité de ciment. De ce fait, cette partie du test apparaît beaucoup plus fine et régulière (Pl. I, Fig. 6).

CYTOPLASME

Comme chez la plupart des Foraminifères, le cytoplasme se compose d'un endoplasme et d'un ectoplasme.

L'endoplasme, de couleur jaune vif à orangé, occupe toute la loge du test et constitue un dôme bordé de lobes rayonnants, étroits et irréguliers. Il épouse parfaitement les contours du test. Sa face plane, en contact direct avec le support, comporte une petite ouverture centrale circulaire (Pl. I, Fig. 2). Cette dernière, vue en section polaire, se présente sous la forme d'un cylindre de faible profondeur. Elle est chez le Protiste vivant le point de départ des pseudopodes, et le passage de l'endoplasme à l'ectoplasme se fait à son niveau. L'endoplasme est dense, sauf dans la région centrale de la cellule et dans les environs immédiats de l'ouverture où il tend à se vacuoliser.

L'ectoplasme est généralement enlevé avec le test au cours de la préparation du matériel. Toutefois nous avons pu obtenir quelques électromicrographies de pseudopodes (Pl. II, Fig. 11) dans lesquels l'ectoplasme apparaît pauvre en organites.

Le plasmalemme de l'endoplasme est recouvert sur toute la surface de la cellule d'un revêtement sur lequel d'ailleurs s'appuie le test. Ce revêtement de structure homogène dans les cellules observées au microscope photonique paraît au microscope électronique constitué de deux couches.

La couche interne, de 2,5 μm d'épaisseur en moyenne, est formé de microfilaments si ténus et si serrés que cette couche semble constituée par un matériel compact et homogène.

La couche externe, plus mince (1 μm), de texture lâche, filamenteuse, est bordée de flocons denses aux électrons (Pl. II, Fig. 7).

L'endoplasme homogène comprend un réticulum endoplasmique granulaire bien développé à proximité duquel se trouvent de nombreux corps denses analogues à des "microbodies," une multitude de petites mitochondries et d'abondants dictyosomes de structure classique (Pl. II, Fig. 8).

L'endoplasme renferme également un grand nombre de vacuoles nutritives et de vésicules. Tantôt les vésicules possèdent un contenu finement granuleux qui s'accompagne parfois d'un nodule compact dense aux électrons (Pl. II, Figs. 7, 8), tantôt elles comprennent un matériel faiblement osmiophile d'aspect spumeux auquel s'adjoignent de minuscules ampoules plus contrastées.

Des formations analogues à des corps multivésiculaires sont également très abondantes et un grand nombre d'entre elles sont fréquemment en contact ou au voisinage immédiat des mitochondries (Pl. II, Fig. 7).

Des granules de matériel très osmiophile et des gouttelettes lipidiques se répartissent dans tout le volume cellulaire. Plusieurs d'entre eux se disposent le long du plasmalemme et forment une barrière continue en bordure de la cellule (Pl. II, Figs. 7, 9).

Les lobes endoplasmiques qui rayonnent entre les septas à partir du disque cellulaire central contiennent de nombreux et courts microtubules réunis en faisceaux diversement orientés (Pl. II, Figs. 9, 10).

Par ailleurs, des éléments analogues à des trichocystes s'observent vers la périphérie de la cellule (Pl. II, Fig. 12). Des Algues du genre Diatomée et du genre Zooxanthelle se reconnaissent aisément dans l'endoplasme (Pl. III, Figs. 15, 17).

LE NOYAU

Placé à l'extrémité d'un lobe protoplasmique, le noyau, de taille gigantesque, se présente sous la forme d'une vésicule quelquefois fortement aplatie d'environ 60 à 80 μm de diamètre moyen.

L'enveloppe nucléaire, très mince, est percée de pores nombreux, rapprochés et régulièrement espacés. Elle est recouverte par une mince couche de cytoplasme d'environ, 0,1 μm d'épaisseur, séparée du reste de la cellule par un réseau de larges citernes et canaux (Pl. III, Figs. 13, 14, 16).

Par ailleurs, l'enveloppe nucléaire montre un contour irrégulier et dessine des sillons qui pénètrent plus ou moins profondément dans le noyau (Pl. III, Figs. 13, 16).

La membrane interne de l'enveloppe nucléaire est bordée d'une épaisse couche de matériel fibrillaire. Cette couche, de 2,5 à 3 μm d'épaisseur, n'offre aucune organisation particulière. Toutefois, contre la membrane et par endroit, le matériel microfibrillaire s'ordonne en un mince réseau alvéolaire (Pl. III, Figs. 13, 14, 16).

Le noyau contient un nombre important de nucléoles groupés à sa périphérie. Ces nucléoles sont de forme irrégulière et de structure compacte (Pl. III, Figs. 13, 14).

DISCUSSION ET CONCLUSION

Cette étude montre que les genres *Daitrona* et *Hemisphaerammina* sont analogues et doivent être mis en synonymie.

Le microscope électronique à balayage révèle que chez cet organisme primitif, en ce qui concerne l'organisation du test, il existe malgré tout une différenciation entre la face supérieure et la face de fixation. Cette différenciation provient d'une sélection dans le choix des matériaux de construction du test, sélection qui se fait vraisemblablement au niveau de l'ectoplasme.

L'étude au microscope électronique de l'endoplasme d'*Hemisphaerammina* permet de constater que celui-ci possède des caractères particuliers. Ce sont d'une part l'alignement des gouttelettes lipidiques et des granules de matériel osmiophile à la périphérie de la cellule, le long du plasmalemme, et d'autre part la présence de nombreux et courts faisceaux de microtubules disposés les uns à côté des autres avec des orientations différentes. L'existence de faisceaux microtubulaires a été montrée chez d'autres Foraminifères (Hedley et coll., 1967; Marszalek, 1969; Febvre-Chevalier, 1971; Leutenegger, 1977) mais généralement, ces faisceaux sont orientés dans le sens d'écoulement de l'endoplasme (par exemple entre deux loges), ou du déplacement des pseudopodes. Ils sont alors répartis parallèlement les uns par rapport aux autres et non dans des directions opposées comme chez *Hemisphaerammina*.

Par ailleurs, l'apparente relation entre les mitochondries et des formations analogues à des corps multivésiculaires constitue un fait singulier que nous avons d'ailleurs observé chez un autre Foraminifère; *Iridia lucida* (Cesana, travail non publié).

Enfin, le revêtement qui recouvre extérieurement le plasmalemme d'*Hemisphaerammina bradyi* serait analogue à la couverture organique rencontrée chez la plupart des Foraminifères agglutinés et appelée "basale chitinoïde" par Lacroix (1931) et J. Le Calvez (1938), "chitinous inner lining" par Christiansen (1958), ou "chitinous lining" par Hedley (1962).

L'ultrastructure du noyau montre que l'enveloppe nucléaire est bordée intérieurement par une couche de matériel fibrillaire. Cette organisation n'est pas exceptionnelle. Elle a été trouvée chez de nombreux Foraminifères ayant fait l'objet d'une étude au microscope électronique (voir les travaux de Dahlgren, 1967a, b; Febvre-Chevalier, 1971; Cesana, 1975; Leutenegger, 1977). Cependant, l'absence d'une structure régulière dans toute l'épaisseur de la lame fibreuse intranucléaire distingue le noyau d'*Hemisphaerammina* de ceux des autres Foraminifères chez lesquels la structure alvéolaire s'étend à l'ensemble de la couche fibrillaire.

Les gros noyaux de plusieurs Foraminifères sont séparés de l'endoplasme par une couronne de larges vésicules; elle a été signalée par plusieurs auteurs (Schwab, 1969; Leutenegger, 1977). Toutefois, chez *Hemisphaerammina*, c'est un réseau de citernes et de canaux qui entoure le noyau et une organisation similaire ne semble avoir été observée que par Dahlgren (1976a) chez *Ovamina*.

Si cette étude a permis de mettre en évidence que le test d'*Hemisphaerammina* possède une organisation simple, voire primitive, il n'en est rien de l'endoplasme ni du noyau. Ceux-ci montrent une structure aussi complexe que celle observée chez des Foraminifères à test calcaire évolué et plusieurs de leurs formations dont nous avons signalé la singularité posent des problèmes tant fonctionnels que biologiques.

REFERENCES

Brady, H. B., 1884, Report on the Foraminifera dredged by H. M. S. Challenger: Zoology, v. 9, p. 1–814.

Cesana, D., 1975, Les stades initiaux de la gamogonie chez *Iridia lucida* Le Calvez (Foraminifère Lagynidae): Acad. Sci. Comptes Rendus, t. 281, p. 263–266.

Christiansen, B., 1958, The foraminifer fauna in the Dröbak Sound in the Osla Fjord (Norway): Nytt Magasin Zool., v. 6, p. 5–91.

Cushman, J. A., 1918, The Foraminifera of the Atlantic Ocean: U.S. Natl. Mus. Bull. 104, pt. 1, p. 1–111.

———, 1948, Arctic Foraminifera: Cushman Found. Foram. Res. Contr., Spec. Pub. no. 23, p. 1–79.

Dahlgren, L., 1967a, On the ultrastructure of the gamontic nucleus and the adjacent cytoplasm of the monothalamous Foraminifer *Ovamina opaca* Dahlgren: Zoologiska Bidrag Från Uppsala, Bd. 37, p. 77–112.

———, 1967b, On the nuclear distribution of RNA and DNA and on the ultrastructure of nuclei and adjacent cytoplasm of the Foraminifers *Hippocrepinella alba* Heron-Allen & Earland and *Globulimina turgida* (Bailey): Zoologiska Bidrag Från Uppsala, Bd. 37, p. 114–136.

Earland, A., 1934, Foraminifera. Part III. The Falklands sector of the Antarctic: Discovery Repts., v. 10, p. 1–208.

Febvre-Chevalier, C., 1971, Constitution ultrastructurale de *Globigerina bulloides* D'Orbigny (Rhizopoda—Foraminifera): Protistologia, t. 7, fasc. 3, p. 311–324.

Goës, A., 1896, The Foraminifera, in Reports on the dredging operations . . . by the U.S. Fish Commission Steamer "Albatros": Harvard Univ. Mus. Comp. Zool. Bull., v. 29, p. 1–103.

Hedley, R. H., 1962, The significance of an "inner chitinous lining" in saccamminid organisation, with especial reference to a new species of *Saccammina* (Foraminifera) from New Zealand: N. Z. Jour. Sci., v. 5, p. 375–389.

Hedley, R. H., Parry D. M., and Wakefield, J. St. J., 1967, Fine structure of *Shepheardella taeniformis* (Foraminifera: Protozoa): Jour. of Roy. Micr. Soc., v. 87, p. 445–456.

Heron-Allen, E., and Earland, A., 1908, On *Cycloloculina*, a new generic type of the Foraminifera with a preliminary study of the Foraminiferous deposits and shore-sand of Selsey Bill: Jour. Roy. Micro. Soc. London, v. 15, p. 529–543.

———, 1914, The Foraminifera of the Kerimba Archipelago: Zool. Soc. London, Trans., pt. 12, p. 363–390.

Jones, T. R., Parker, W. K., and Brady, H. B., 1866, A monograph of the Foraminifera of the Crag. Pt. 1: Palaeont. Soc. London, v. 19, p. 1–72.

Lacroix, E., 1931, Microtexture du test des Textulariidae: Inst. Océanogr. Monaco, Bull. no. 582, p. 1–18.

Le Calvez, J., 1935, Sur quelques Foraminifères de Villefranche et de Banyuls: Archives Zool. Expér. et Générale, v. 77, p. 79–98.

———, 1938, Recherches sur les Foraminifères. I. Développement et reproduction: Archives Zool. Expér. et Générale, v. 80, p. 12–333.

———, 1953, Ordre des Foraminifères: *in* Traité de Zoologie, I, fasc. 2, p. 149–265. Masson et Cie Ed. Direction: P. P. Grassé.

Leutenegger, S., 1977, Ultrastructure de Foraminifères perforés et imperforés ainsi que de leurs symbiotes: Cahiers de Micropal., no. 3, p. 5–52.

Loeblich, A. R., and Tappan, H., 1961, Remarks on the systematics of the Sarcodina (Protozoa) renamed homonyms and new and validated genera: Biol. Soc. Washington, Proc., v. 74, p. 213–234.

———, 1964, Sarcodina, chiefly "Thecamoebians" and Foraminiferida, *in* Moore, R. C., ed., Treatise on Invertebrate Paleontology, Protista 2, Pt. C, v. 1.

Marszalek, D. S., 1969, Observations on Iridia diaphana, a marine Foraminifera: Jour. Protozool., v. 16, p. 599–611.

Rhumbler, L., 1904, Systematische Zusammenstellung der recenten Reticulosa: Archiv. Protistenkunde, v. 3, p. 181–294.

Schwab, D., 1969, Elektronenmikroskopische Untersuchung an der Foraminifere Myxotheca arenilega Schaudinn: Z. Zellforsch. Mikrosk. Anat., v. 96, p. 295–324.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 225–229, pl. 1, 1980

LYCHNOCANOMA BANDYCA N.SP., A NEW, STRATIGRAPHICALLY IMPORTANT, LATE EOCENE RADIOLARIAN

C. Y. MATO AND F. THEYER
Hawaii Institute of Geophysics, 2525 Correa Road, Honolulu, Hawaii 96822

ABSTRACT

Lychnocanoma bandyca n.sp., a radiolarian found in upper Eocene sediments of two deep-sea cores collected in the central equatorial Pacific, is an excellent index of the lower two-thirds of the *Thyrsocyrtis bromia* Zone of the tropical radiolarian zonation. This species is distinguished from other species of *Lychnocanoma* by the circular pores, encased within hexagonal frames, that ornament its campanulate thorax, and by its three prominent cylindrical to conical feet.

INTRODUCTION

Research seeking to extend the Tertiary paleomagnetic time-scale by means of chronologically overlapping Tertiary piston cores (Theyer and Hammond, 1974a, b), requires precise biostratigraphic control to establish the chronology of the magnetic polarity sequence in the cores. Because the piston cores employed in these studies originate from the deep central equatorial Pacific, they are essentially carbonate free, and the only abundant microfossils represented in the sediments are radiolarians. Thus, to enhance the precision of this biostratigraphic-paleomagnetic work, a search is being made for radiolarians of short stratigraphic ranges.

One such radiolarian, undescribed as yet, was found in upper Eocene sections of two Hawaii Institute of Geophysics (HIG) piston cores (Fig. 1). This species is restricted to the lower two-thirds of the *Thyrsocyrtis bromia* Zone of the tropical radiolarian zonation (Riedel and Sanfilippo, 1971). The first appearance of this form seems to occur in core M70-39 at 1,980 cm (Fig. 2), between the extinction horizons of *Calocyclas hispida* and *Artophormis dominasinensis*. Its extinction apparently takes place in core S68-24 at 2,040 cm, between the extinction levels of *Eusyringium fistuligerum* and *Calocyclas turris*. The first appearance and the extinction consequently define a relatively short stratigraphic range for this species which, combined with its striking morphology and general abundance, makes it a useful biostratigraphic index.

SYSTEMATICS

Subclass RADIOLARIA Müller, 1858
Order NASSELLARIA Ehrenberg, 1875
Family THEOPERIDAE Haeckel, 1881, emend. Riedel, 1967
Genus **LYCHNOCANOMA** Haeckel, 1887
Lychnocanoma bandyca n.sp.
Plate 1, Figures 1–6

Lychnocanoma sp., RIEDEL and SANFILIPPO, 1977, p. 889, pl. 10, fig. 8.

Description of the species. Cephalis subhemispherical with a few, randomly arranged, small, irregular pores; apical spine lacking. Thorax campanulate with relatively large, longitudinally arranged, circular pores, embedded in longitudinally arranged hexagonal frames. Irregular, laminar lattice extends from distal thorax on well-preserved specimens. Very fine, randomly arranged distal pores. Three sturdy, prominent,

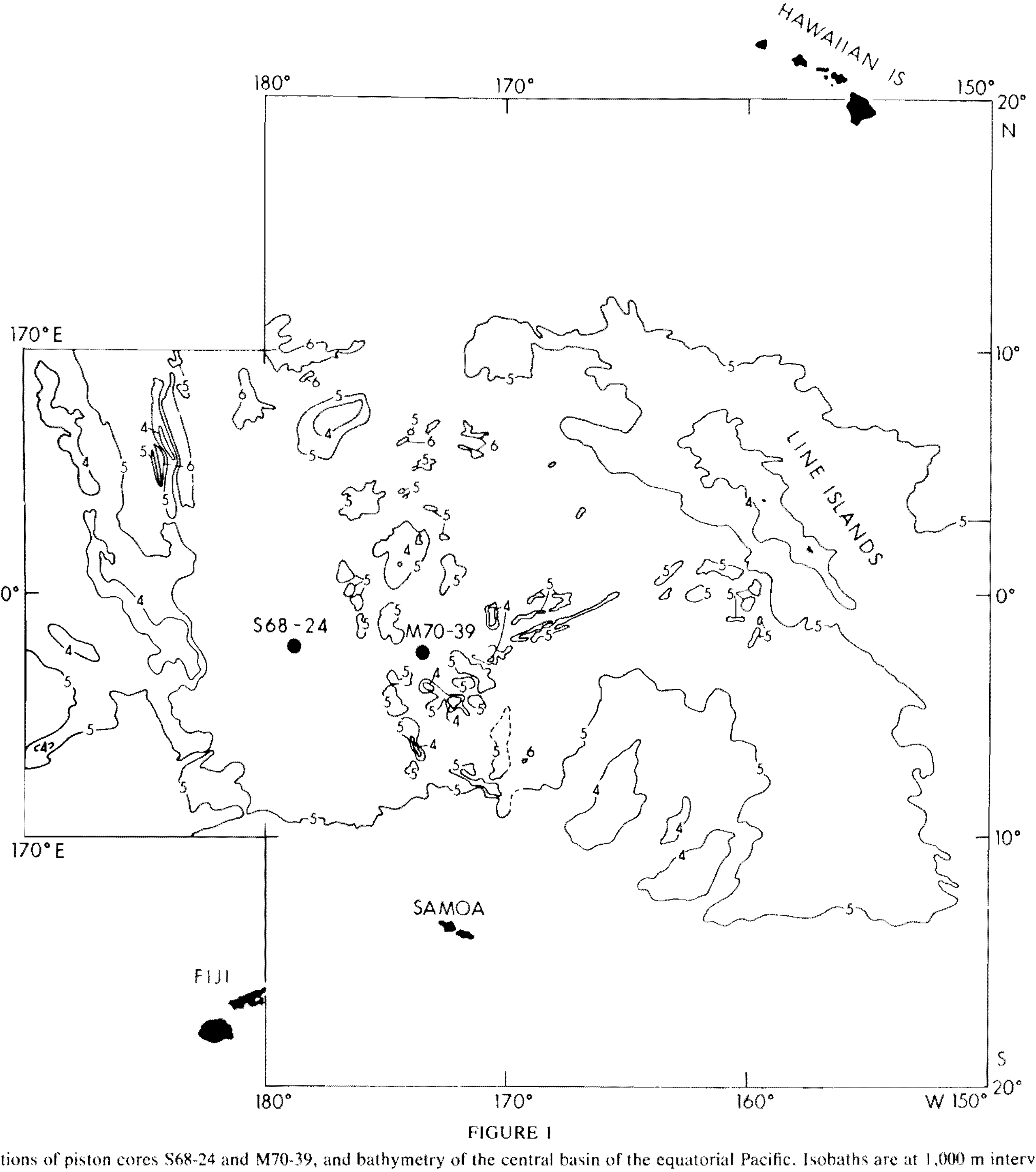


FIGURE 1

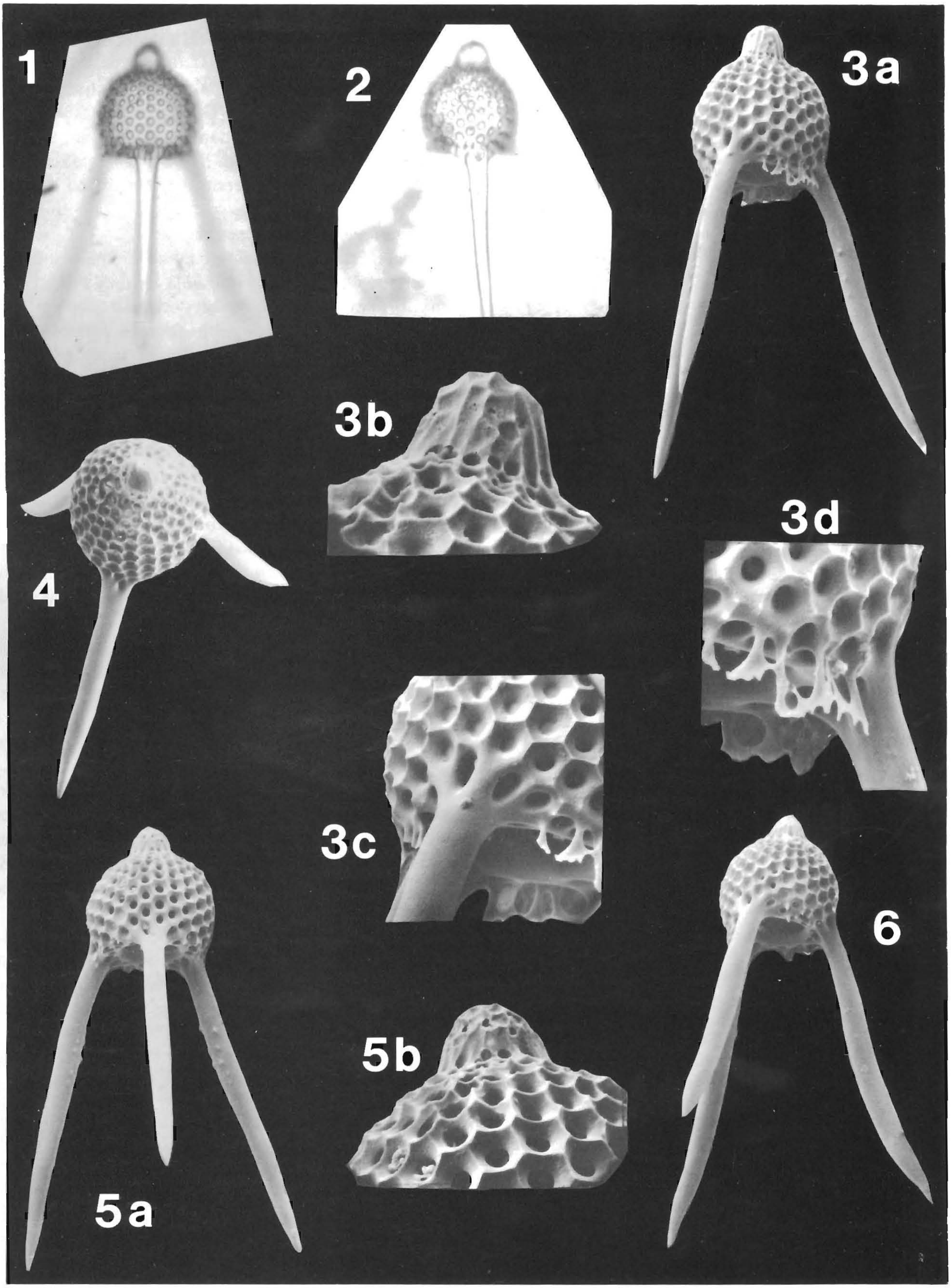
Locations of piston cores S68-24 and M70-39, and bathymetry of the central basin of the equatorial Pacific. Isobaths are at 1,000 m intervals.

PLATE 1

→

1 *Lychnocanoma bandyca* n.sp. Holotype. Core S68-24, 2,143 cm, complete specimen view, 200×. Stored at Hawaii Institute of Geophysics microfossil collection under HIG-MC number 001.

2–6 *Lychnocanoma bandyca* n.sp. Paratypes. 2. Core S68-24, 2,143 cm, complete specimen view, 200×. 3–6. Core M70-39, 1,885 cm; 3A, 5A. 6. Complete specimen views, 216×, 3B (cephalis), 3C, 3D (distal thorax and proximal feet views), enlargements of 3A, 1,350×. 4. Apical view of complete specimen, 216×, 5B. Cephalis, enlargement of 5A, 1,350×. Numbers 1, 2. Transmitting-light-microscope photographs. Numbers 3–6. Scanning-electron-microscope photographs. Paratypes stored at Hawaii Institute of Geophysics microfossil collection under HIG-MC numbers 002–006.


1
2
3a
3b
4
3d
3c
6
5b
5a

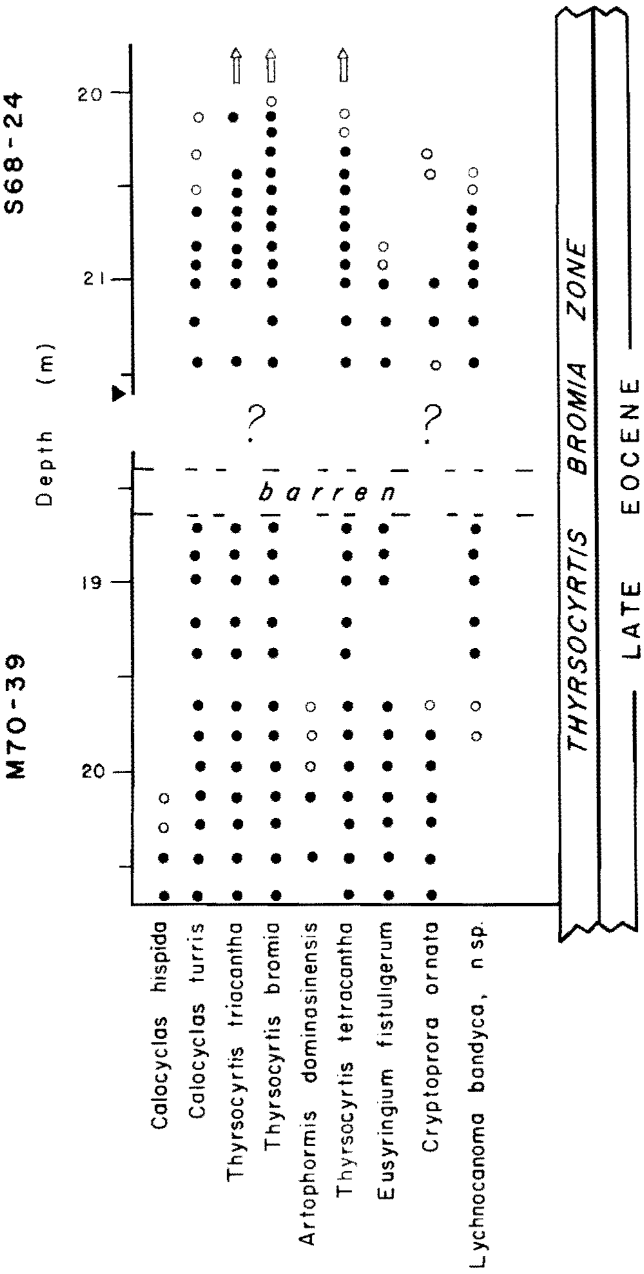


FIGURE 2

Stratigraphic range of *Lychnocanoma bandyca* n.sp., composed from cores S68-24 and M70-39. Question marks reflect possible interval of non-overlap of sediments. Solid triangle indicates bottom of piston core. Arrows mark the continuous range of *Thyrsocyrtis triacantha*, *T. bromia*, and *T. tetracantha* beyond the depicted sampling interval in core S68-24. Black dots show abundant occurrences of specimens, white circles indicate rare occurrences.

cylindrical to conical, straight to slightly curved feet extend from thorax.

Measurements. Overall length, 310–470 μm; of cephalis, 20–30 μm, of thorax, 100–120 μm, of feet, 190–340 μm; greatest width of cephalis, 20–40 μm; of thorax, 120–140 μm (based on 15 specimens from HIG core M70-39, 1,880 cm).

Type locality. Holotype and 18 paratypes from 1,880–1,885 cm within HIG core M70-39, collected at 2°27′S, 173°20′W, at a depth of 5,449 m; and from 2,143 cm within HIG core S68-24, collected at 2°03′S, 178°45′E, at 5,291 m (central basin of the equatorial Pacific; Fig. 1).

Type level. Upper Eocene.

Remarks. This species can be distinguished from other species of *Lychnocanoma* by its distinctive thorax, ornamented by circular pores that are embedded in longitudinally arranged hexagonal frames, and by its three prominent cylindrical to conical feet. Another, apparently undescribed *Lychnocanoma* sp., cited in a Deep Sea Drilling Project (DSDP) report (Ling, 1973, Pl. 2, Figs. 10–11) has a longer stratigraphic range (part of which extends throughout the Eocene) and is distinguished from *Lychnocanoma bandyca* n.sp. by its long conical, apical horn and its three, bladed feet. *Lychnocanoma grande* (Kling, 1973; Pl. 10, Figs. 10–14), which is also similar to *Lychnocanoma bandyca* n.sp., lacks hexagonal frames around the pores of the thorax and has bladed feet.

Within the species' stratigraphic range, the later forms tend to have shorter, and slightly outward-flared feet. *Lychnocanoma bandyca* n.sp. has been previously illustrated by Riedel and Sanfilippo (1977; Pl. 10, Fig. 8). A. Sanfilippo (pers. comm., 1973), in agreement with our data, also found *L. bandyca* n.sp. to range in the lower two-thirds of the *Thyrsocyrtis bromia* Zone. It also occurs in upper Eocene sediments of the Gulf of Mexico, where Foreman (pers. comm., 1974) reports that some specimens from Site 94 (cores 9-15, 9-16) of DSDP Leg 10 have an apical horn or apical thorns.

On the basis of correlations in Site 94 of DSDP Leg 10, it appears that the range of *L. bandyca* n.sp. spans the late Eocene *Globigerapsis semiinvoluta* planktonic foraminiferal Zone, as interpreted by McNeely (1973).

The species is named after the late Professor Orville L. Bandy to honor his numerous contributions to biostratigraphy.

ACKNOWLEDGMENTS

We thank A. Sanfilippo for examining some of our specimens and for giving us her comments. We are also grateful to H. Foreman for comparative material from DSDP Leg 10, and to both colleagues and W.

Riedel for reviewing our manuscript and suggesting improvements. Supported by the National Science Foundation under grant DES 74-19504 and by the Office of Naval Research. Hawaii Institute of Geophysics contribution No. 942.

REFERENCES

KLING, S. A., 1973, Radiolaria from the Eastern North Pacific, Deep Sea Drilling Project, Leg 18: Deep Sea Drilling Proj. Initial Repts., v. 18, p. 617–671.

LING, H. Y., 1973, Radiolaria: Leg 19 of the Deep Sea Drilling Project: Deep Sea Drilling Proj. Initial Repts., v. 19, p. 777–797.

MCNEELY, B. W., 1973, Biostratigraphy of the Mesozoic and Paleogene pelagic sediments of the Campeche Embankment area: Deep Sea Drilling Proj. Initial Repts., v. 10, p. 679–695.

RIEDEL, W. R., and SANFILIPPO, A., 1971, Cenozoic radiolaria from the western tropical Pacific, Leg 7: Deep Sea Drilling Proj. Initial Repts., v. 7, p. 1529–1672.

———, 1977, Cainozoic Radiolaria: *in* Ramsay, A. T. S., ed., Oceanic Micropaleontology: Academic Press, London, v. 2, p. 847–912.

THEYER, F., and HAMMOND, S., 1974a, Paleomagnetic polarity sequence and radiolarian zones, Brunhes to Polarity Epoch 20: Earth and Planetary Sci. Letters, v. 22, p. 307–319.

———, 1974b, The Cenozoic magnetic time scale: Completion of the Neogene: Geology, v. 2, p. 487–492.

STRATIGRAPHIC STUDIES

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 233–251, 1980

PLANKTON BIOSTRATIGRAPHY OF THE REFUGIAN AND ADJOINING STAGES OF THE PACIFIC COAST TERTIARY

A. D. WARREN[1] AND J. H. NEWELL[2]

ABSTRACT

Nannoplankton and planktonic foraminiferal data are presented in order to demonstrate that the Refugian Stage of the Pacific Coast Tertiary may be equated with the *Discoaster barbadiensis* Zone, *Isthmolithus recurvus* Subzone, and with the P.16 and P.17 foraminiferal zones. Data derived from sediments assigned to the adjacent Narizian and Zemorrian Stages are also considered in order to delimit the extent of the Refugian Stage with respect to plankton zonations. The Refugian Stage is considered to be correlative to all or parts of the Jacksonian Stage of the Atlantic and Gulf Coastal Province, the Priabonian Stage of Europe, and the Kaiatan and Runangan Stages of New Zealand.

INTRODUCTION

The Refugian Stage was proposed and formalized by Schenck and Kleinpell (1936) with the Gaviota and lowermost Sespe (now considered Alegria) Formations in Cañada de Santa Anita, Santa Barbara County, California, designated as the stratotype; definition of the stage was based on mollusks and benthonic foraminifers and it was originally considered to be probably equivalent in age to part of the late Eocene or early Oligocene of Europe. Mallory (1959) and Kleinpell (1938) proposed and defined, respectively, the subjacent Narizian and superjacent Zemorrian Stages in California. Kleinpell and Weaver (1963) placed the Refugian Stage in the Oligocene sensu lato of the Santa Barbara Embayment, but they also indicated (1963, Fig. 2) the lower Refugian to be Eocene and the upper Refugian to be Oligocene in age. Weaver and Frantz (1967) presented evidence from which they concluded that the entire Alegria Formation, rather than only the lowermost part in the Refugian type area, is of late Refugian Age. Tipton, Kleinpell, and Weaver (1973) discussed further the faunal definition of the Refugian Stage and Tipton (this volume) has now formally proposed and documented a threefold zonation based largely on benthonic Foraminifera for that unit in part from data on the Arroyo el Bulito continuum in the type area of the stage. Many others have contributed importantly to the literature on the Refugian Stage, but in the interests of brevity, only those pertinent to the present study are cited in the bibliography.

The purpose of this report is to demonstrate the relationship of the calcareous microplankton disciplines, which have developed in large part over the past three decades, to the Refugian and adjacent stages of the Pacific Coast Tertiary. The vertical distribution of calcareous nannoplankton and planktonic Foraminifera within the Refugian and adjoining stages as manifested in several areas will be examined and discussed. Both nannofossils and planktonic foraminifers are scarce and of spasmodic occurrence in strata of Refugian Age. Nevertheless, both groups are present in most exposures and serve as perhaps the only means of correlating the Refugian directly with the stages of the Atlantic and Gulf Coastal Province, Europe, New Zealand, and other areas. It will be obvious that there are discrepancies between traditional Pacific

---

[1] Anderson, Warren & Associates, Inc., San Diego, California.

[2] Superior Oil Company, Geoscience Laboratory, Houston, Texas.

Coast provincial age assignments and those currently favored by most specialists studying planktonic microfossils. All age assignments herein based on calcareous microplankton will reflect the opinions as expressed by most plankton investigators unless otherwise indicated. All new data on the relationships of nannofossil and planktonic foraminiferal zones to the stages of the Pacific Coast Tertiary will be referred to in the text in terms of the calcareous nannoplankton zonation of Bukry (1973, 1975) and in terms of the planktonic foraminiferal letter/number zones proposed by Blow (1969). Both Martini (1971) and Berggren (1972) have attempted to correlate the nannoplankton zones of the former author to the planktonic foraminiferal letter/number zones of Blow (1969). By and large, their correlations have been confirmed by integration of data in both disciplines from reports of the Deep Sea Drilling Project, although there still remain some conflicts. During the following discussion, it will be necessary to equate nannoplankton zones to planktonic foraminiferal zones and vice versa; these correlations are based on both the opinions of Martini (1971) and Berggren (1972), but also, to some degree, on the personal observations of the present writers. Exact integration of nannoplankton, planktonic foraminiferal, and benthonic foraminiferal zonations is far from being perfected, so the reader is cautioned that all interdisciplinary correlations to follow should be taken in a general sense. For example, in Figure 5, planktonic foraminiferal Zones P.10 through P.15 are correlated with nannoplankton Zones NP 15 through NP 18, which is an essentially valid equation. However, no exact correlation of planktonic foraminiferal zone to nannoplankton zone is intended, rather the equations of P Zones to NP Zones are to be taken in a general and approximate sense until such time as more data are available to provide more refined correlations.

NANNOPLANKTON BIOSTRATIGRAPHY, REFUGIAN AND ADJACENT STAGES

Previously Published Data and Opinions

Bramlette and Sullivan (1961) described a nannoflora from the Canoas Member, basal Kreyenhagen Formation of Garza Canyon, Kings County, California, which may be assigned with certainty to the *Nannotetrina quadrata* Zone of Bukry (1973); this flora was noted in two samples approximately 10 m and 16 m above the base of the Canoas. A third sample 1.2 m above the base of the Canoas may be assigned tentatively to the *Discoaster sublodoensis* Zone, *Rhabdosphaera inflata* Subzone of Bukry (1973). Originally, Mallory (1959, p. 51) did not consider the foraminiferal fauna from the basal Canoas at this locality sufficiently diagnostic to determine whether it should be placed definitely within the Ulatisian Stage; subsequently, Mallory, in personal communication with Sullivan (1965, p. 23), indicated that the basal part of the Canoas at Garza Canyon could just as well be Narizian in age. However, the senior author interprets the upper 25 m of the 34 m thick Canoas Member at Garza Canyon to be definitely Narizian in age based on absence of Ulatisian index Foraminifera and presence of 40 foraminiferal species reported by Cushman and Siegfus (1942, checklist) and 61 foraminiferal species reported by Mallory (1959, Table 12) all of which species are now known to be typical and diagnostic of the earliest Narizian Stage. The lowermost 2 m of the Canoas Member at Garza Canyon are Ulatisian in age based on the presence of Ulatisian index foraminifers noted by the senior author in two samples from the basal Canoas Member 0.33 m and 1.2 m above the Avenal Formation at that locality; both of these samples contained rare to few specimens of *Globorotalia aragonensis twisselmanni*, *Nodosaria latejugata*, and *Uvigerina lodoensis miriamae* all of which are typical of the Ulatisian Stage while the first and last named species do not occur above the Ulatisian Stage. The Canoas Member at Oil City, Oil Canyon, Little Tar Canyon, and Coal Mine Canyon localities contains sediments Ulatisian in age based on foraminiferal occurrences reported by Cushman and Siegfus (1942, checklist) and by Mallory (1959, Tables 7, 8, and 18). At any rate, the two samples of Bramlette and Sullivan (1961) from the Canoas Member at Garza Canyon here assigned to the *Nannotetrina quadrata* Zone are earliest Narizian in age.

Sullivan (1965) identified species typical of his "Faunizone IV" (equivalent to the *Nannotetrina quadrata* Zone of Bukry, 1973) from the early Narizian portions of the "Vacaville shale" in Solano County, Alhambra Formation in Contra Costa County, upper Los Muertos Creek Formation in San Benito County, the middle "Tejon" Formation in Kern County, and lower Cozy Dell Formation in Santa Barbara County, California.

Lipps (1967b) listed 6 species of long-ranging nannofossils from the Zemorrian Stage of California but did not specifically indicate the locality from which they were obtained. From comments elsewhere in his text, it would appear that these species are from late Zemorrian strata at Los Sauces Creek, Ventura County, California, which he correlated with the *Globoro-*

talia opima opima planktonic foraminiferal zone of Bolli (1957a). The *G. opima opima* Zone is equivalent to the greater part of Zone P.21 (N.2) of Blow (1969) which is middle to late Oligocene in age.

Lipps (1968) listed 10 species of nannofossils and mentioned one more in the text as being present in rocks from the Zemorrian Stage in Los Sauces Creek, Ventura County, California. He suggested that the species noted support correlation with the *Globorotalia opima opima* and *Globigerina ciperoensis ciperoensis* Zones of Trinidad; these two planktonic foraminiferal zones are equivalent to the greater parts of Zones P.21 (N.2) and P.22 (N.3) of Blow (1969) and are middle to latest Oligocene in age.

Nannoplankton data developed from the Refugian of the Church Creek Formation, near Monterey, California, were published by Brabb, Bukry, and Pierce (1971) who concluded that the Stage is late Eocene in age and correlative to the *Discoaster barbadiensis* Zone although no data were presented from the delimiting and adjoining stages.

Lipps and Kalisky (1972) reported that a sample from the Refugian portion of the Gaviota Formation in Arroyo el Bulito, Santa Barbara County, California, contained nannofossils indicative of the late Eocene NP 19 and NP 20 nannoplankton zones of Martini (1971); these two zones are equivalent to the *Discoaster barbadiensis* Zone, *Isthmolithus recurvus* Subzone of Bukry (1975). They also listed 7 nannofossil species from the late Zemorrian of Los Sauces Creek, all of which were previously listed by Lipps (1968); Lipps and Kalisky considered some of these 7 species as suggestive of middle and upper Oligocene NP 24 and NP 25 nannoplankton zones of Martini (1971) which are equated here with the *Sphenolithus ciperoensis* Zone of Bukry (1973).

McKeel and Lipps (1972) reported the presence of *Isthmolithus recurvus* and 4 other long-ranging species of nannofossils from the Refugian portion of the Alsea Formation of Oregon; they suggested correlation of this association with an uppermost Eocene nannoflora described by Stradner (1969).

Worsley and Crecelius (1972) reported on 60 nannofossil species in 23 samples from the Olympic Peninsula of Washington from the Crescent, Boundary, Lyre, and Twin River Formations and from an unnamed sequence at Scow Bay, northeast Olympic Peninsula. It would appear that they assigned the Ulatisian Stage to the NP 14 and NP 15 nannoplankton zones and considered that stage to be middle Eocene in age. The Narizian Stage was assigned to the NP 16 nannoplankton zone and was shown to be late Eocene in age, while the Refugian Stage was charted as Oligocene in age and shown to contain nannofossil associations that those authors interpret as indicating the NP 21 and NP 23 nannoplankton zones. Most of the above interpretations are in serious conflict with data developed from the Narizian, Refugian, and Zemorrian Stages of California and Oregon to be discussed in paragraphs to follow. However, as Worsley and Crecelius do not present any documentation of the interdisciplinary controls utilized nor precise stratigraphic allocations, it is impossible to evaluate their opinions from a biostratigraphic point of view.

Warren and Newell (1976) presented preliminary nannoplankton data from the Sacate and Gaviota Formations of Arroyo el Bulito, Santa Barbara County, California, to support their conclusion that the Refugian Stage in California is late Eocene in age and equivalent to all or parts of the Jacksonian Stage of the Atlantic and Gulf Coastal Province, the Priabonian/Bartonian Stages of Europe, and the Kaiatan and Runangan Stages of New Zealand. Subsequently, Cavelier and Pomerol (1976), and Hardenbol and Berggren (1978), reported the Bartonian Stage to be middle Eocene in age. Thus, the Refugian Stage is not equivalent to the Bartonian Stage of Europe as was once believed.

Bukry, Brabb and Vedder (1977) reported on nannoplankton associations from strata of the Narizian and Zemorrian as well as other stages in California; they demonstrated that the *Nannotetrina quadrata* and *Reticulofenestra umbilica* Zones are present in the Narizian Stage and suggested that the *Sphenolithus predistentus* to *Sphenolithus ciperoensis* Zones may be present in the Zemorrian Stage.

Warren and Newell (1977) presented preliminary foraminiferal and nannoplankton data to support their conclusion that the middle and upper Bastendorff Formation of southwest Oregon are late Eocene in age.

NEW DATA, ARROYO EL BULITO CONTINUUM (FIG. 1)

Tipton (this volume) has documented the Narizian and Refugian Age of the upper Sacate and Gaviota Formations in Arroyo el Bulito within the type area of the Refugian Stage. Working with sample material furnished by Tipton, the authors assign a portion of the late Narizian within the upper Sacate Formation at this location to the *Reticulofenestra umbilica* Zone, *Discoaster bifax* Subzone. The *Discoaster saipanensis* Subzone was not noted in samples available for study from this section. The latest Narizian within the

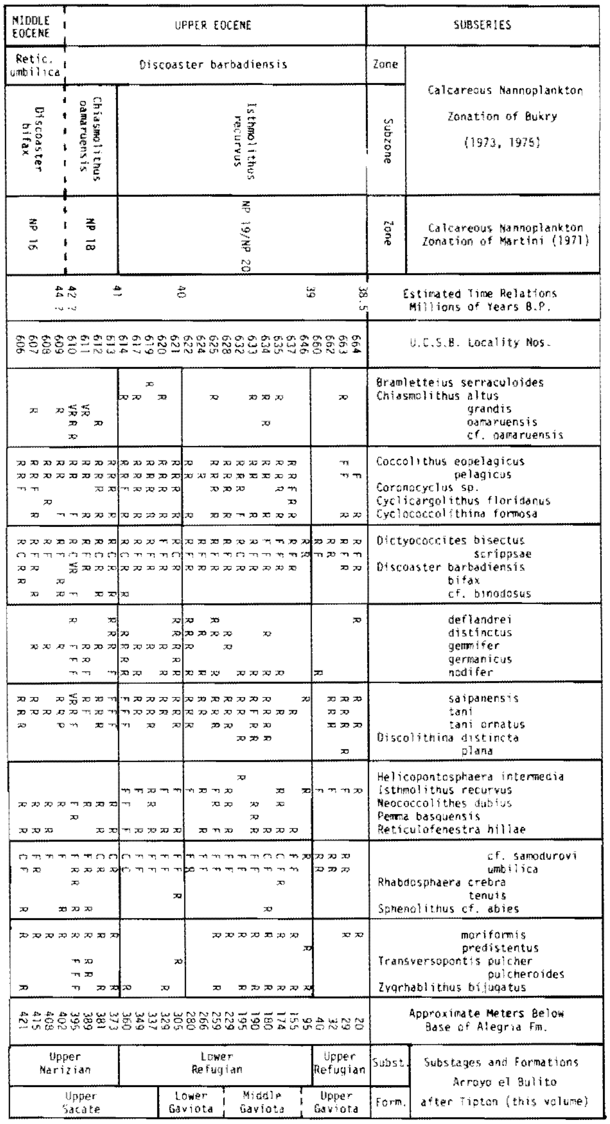


FIGURE 1

Stratigraphic distribution of nannoplankton species observed in the upper Sacate and Gaviota Formations of Arroyo el Bulito, Santa Barbara County, California. University of California, Santa Barbara locality numbers 606 through 664 are documented in Donnelly (1976, p. 29–31, and 289–290).

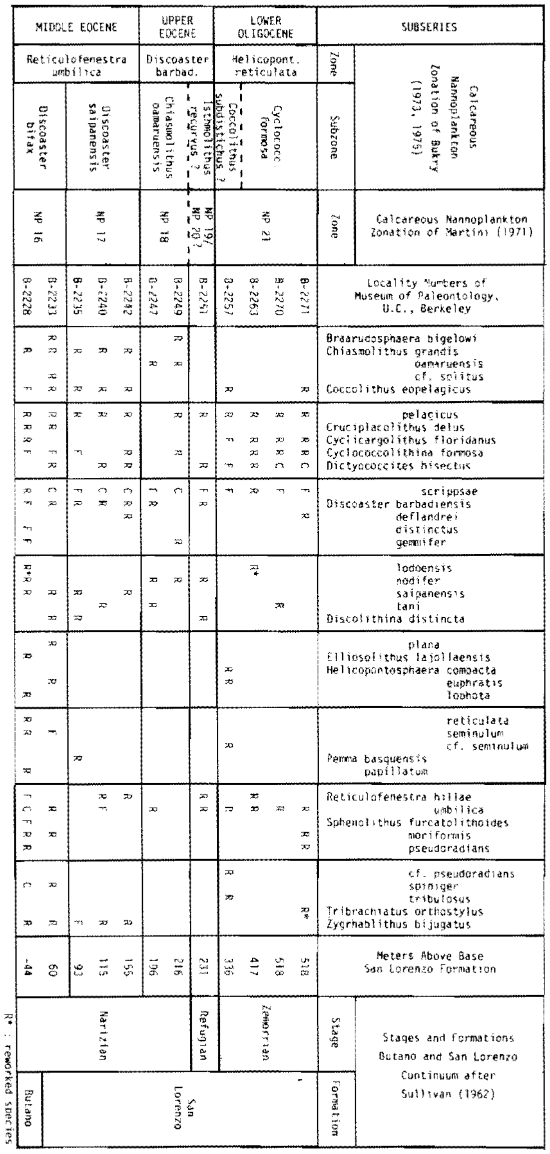


FIGURE 2

Stratigraphic distribution of nannoplankton species observed in the Butano and type San Lorenzo Formations, Santa Cruz County, California. University of California, Berkeley, Museum of Paleontology locality numbers B-2228 through B-2271 are documented in Sullivan (1962, Figs. 3, 4, p. 288–293).

upper Sacate Formation is assigned to the *Discoaster barbadiensis* Zone, *Chiasmolithus oamaruensis* Subzone. The microfossiliferous portion of the Refugian Stage as manifested in the uppermost Sacate and entire Gaviota Formations is assigned to the *Discoaster barbadiensis* Zone, *Isthmolithus recurvus* Subzone. That part of the Refugian Stage which may lie within the Alegria Formation is devoid of nannofossils and is, therefore, not definitely assigned to any nannoplankton zone based on data from this exposure.

NEW DATA, SAN LORENZO CONTINUUM (FIG. 2)

Small splits from 39 of the original 50 samples used by Sullivan (1962) for his study of the Butano and type

San Lorenzo Formations in Santa Cruz County, California, were made available to the authors by the late Gordon Hornaday of the Museum of Paleontology, University of California, Berkeley. Of these 39 samples, 12 were found to contain sufficient frequency and diversity of nannofossils to permit assignment to the nannoplankton zones and subzones of Bukry (1973, 1975). Two of the lower samples, one from the Butano and one from the lowermost San Lorenzo, are assigned to the *Reticulofenestra umbilica* Zone, *Discoaster bifax* Subzone; these samples are placed in the Narizian Stage by Sullivan (1962). The succeeding 3 higher samples from the San Lorenzo Formation containing diverse nannofossil associations are assigned to the *Reticulofenestra umbilica* Zone, *Discoaster saipanensis* Subzone; these samples are also placed in the Narizian Stage by Sullivan (1962). The next two nannofossiliferous samples above are assigned to the *Discoaster barbadiensis* Zone, *Chiasmolithus oamaruensis* Subzone; Sullivan (1962) places these samples from the San Lorenzo Formation in the latest Narizian Stage. Four samples from the earliest Zemorrian portion of the San Lorenzo Formation can be no younger than the *Helicopontosphaera reticulata* Zone, *Cyclococcolithina formosa* Subzone and the lowest of these samples may belong to the older *Coccolithus subdistichus* Subzone by virtue of the presence of *Sphenolithus tribulosus* which was described originally from the basal Oligocene of the Gulf Coast (Roth, 1970); this latter sample within the San Lorenzo Formation is only 20 m above the approximate top of the Refugian Stage according to Sullivan (1962).

NEW DATA, BASTENDORFF BEACH CONTINUUM (FIG. 3)

Tipton (1975) documented the Narizian and Refugian Age of the type Bastendorff Formation, Coos County, Oregon. Again, working with sample material furnished by Tipton, the authors assign the latest Narizian portion of the type Bastendorff Formation to the *Discoaster barbadiensis* Zone, *Chiasmolithus oamaruensis* Subzone. All of the early Refugian and part of the late Refugian within the Bastendorff are assigned with certainty to the *Discoaster barbadiensis* Zone, *Isthmolithus recurvus* Subzone. The highest two samples of the late Refugian portion of the Bastendorff may be assigned to either the late *Discoaster barbadiensis* Zone or to the *Helicopontosphaera reticulata* Zone, *Coccolithus subdistichus* Subzone. Due to the rarity and erratic occurrence of *Discoaster barbadiensis* and *Discoaster saipanensis* in marine strata from higher latitudes, the authors prefer to consider the latest Refugian of the Bastendorff Formation as probably assignable to the late *Discoaster barbadiensis* Zone.

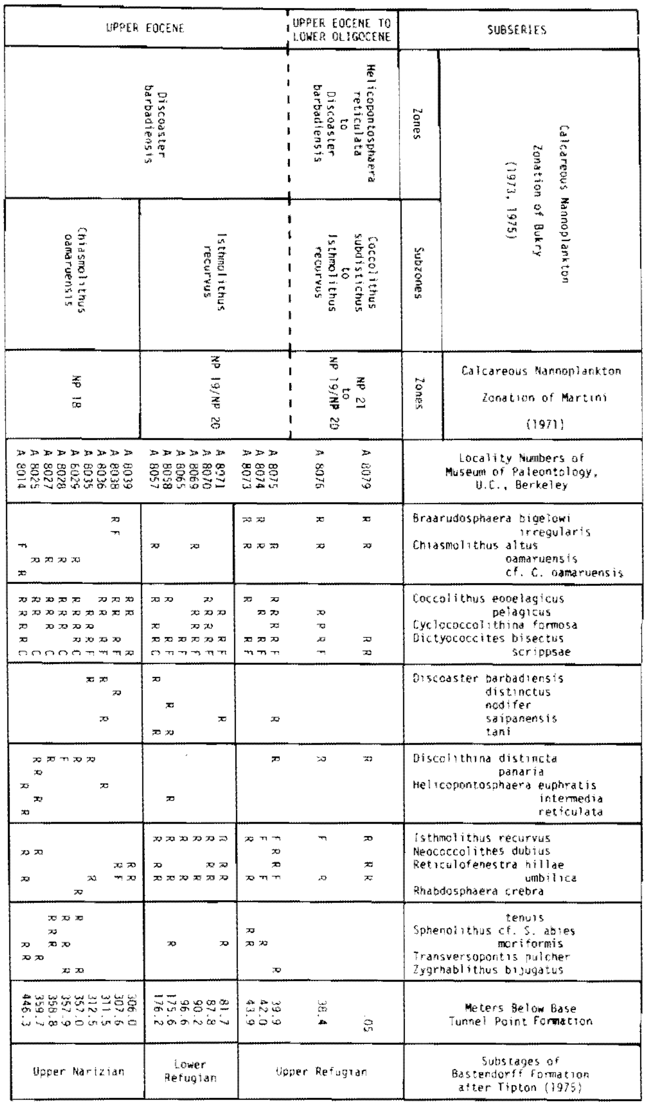


FIGURE 3

Stratigraphic distribution of nannoplankton species observed in the type Bastendorff Formation, Coos County, Oregon. University of California Museum of Paleontology locality numbers A-8014 through A-8079 are documented in Tipton (1975, Figs. 6, 7, p. 580–582).

NEW DATA, ROADS END BEACH CONTINUUM (FIG. 4)

D. R. McKeel collected 16 samples from an exposure of a portion of the Nestucca Formation at Roads End Beach, Lincoln County, Oregon, 13 of which contained calcareous nannofossils. According to McKeel (1975, pers. comm.), the lowest 3 samples are of Narizian Age and the higher 13 samples are of early Refugian Age. The lowest two surface samples from the Narizian of the Nestucca Formation exposed at this location are here assigned to the *Discoaster barbadiensis* Zone, *Chiasmolithus oamaruensis* Subzone while 11 nannofossiliferous samples from the early Refugian portion of the Nestucca are assigned to the *Discoaster barbadiensis* Zone, *Isthmolithus recurvus* Subzone.

UPPER EOCENE													SUBSERIES	
Discoaster barbadiensis													Zone	Calcareous Nannoplankton Zonation of Bukry (1973, 1975)
Chiasmolithus oamaruensis		Isthmolithus recurvus											Subzone	
NP 18		NP 19/NP20											Zone	Calcareous Nannoplankton Zonation of Martini (1971)
75-02-1	75-02-2	75-02-4	75-02-5	75-02-6	75-02-7	75-02-8	75-02-9	75-02-10	75-02-11	75-02-12	75-02-13	75-02-14		Locality Numbers of D. R. McKeel
		R	R		R	R		R	R	R	R			Braarudosphaera bigelowi
	R						F			R		F		Chiasmolithus altus
	R													titus
	R				R		R							Coccolithus eopelagicus
	R	R	R	R	R		R		R		R			pelagicus
				R	F	R	F			R	R	R		Cyclicargolithus floridanus
					R		R							Cyclococcolithina formosa
R	R	R												sp.
R		R	F	R	R		R		R					Dictyococcites bisectus
F	R	F		F	F	R	F	R	R	F	R	R		scrippsae
		R		R							R			Discoaster barbadiensis
							R			R				deflandrei
							R					R		distinctus
R							R			R				nodifer
							R							saipanensis
							R					R		tani ornatus
				R										Discolithina cf. distincta
		R		R		R				F				Isthmolithus recurvus
			R		R		R		R		R			Neococcolithes dubius
				R		R								Reticulofenestra hillae
	R	R	R	R	R	R	R			R				umbilica
					R									Rhabdosphaera sp.
												R		Sphenolithus cf. abies
							R							moriformis
					R									Zygrhablithus bijugatus
0.6	3	20	30	40	49	64	76	88	94	111	120	133		Approximate Meters Above Base of Exposed Nestucca Formation
Narizian		Refugian											Stage	Stages of Nestucca Formation as Exposed at Roads End Beach, Oregon After D. R. McKeel (pers. comm. to A. D. Warren)
Nestucca													Form.	

FIGURE 4

Stratigraphic distribution of nannoplankton species observed in the Nestucca Formation at Roads End Beach, Lincoln County, Oregon. Locality numbers 75-02-1 through 75-02-14 and their stratigraphic allocations are those of D. R. McKeel (1975, pers. comm.). See also McKeel and Lipps (1975, Fig. 2) for location of this exposure.

NEW DATA, SANTA ROSA ROAD EXPOSURE

Hornaday (1965) reported a foraminiferal faunule from a roadcut exposure mapped as undifferentiated Sacate-Gaviota Formations by Dibblee (1950) on Santa Rosa Road near Buellton, California; Hornaday assigned these strata to the *Amphimorphina jenkinsi* Zone of the late Narizian Stage. Small splits of his original samples were furnished by Hornaday and additional material was collected by the senior author for study of the nannofossil associations. In two samples from Locality D-969 of Hornaday (1965) the nannofossil assemblage includes *Chiasmolithus grandis*, *C. titus*, *Sphenolithus furcatolithoides*, and *S. spiniger*. Three samples from Locality D-971 contain *Chiasmolithus altus*, *C. grandis*, *C. solitus*, *C. titus*, *Discoaster bifax*, *Sphenolithus furcatolithoides*, and *S. spiniger*. The presence of these species suggests that both localities may be assigned to the *Reticulofenestra umbilica* Zone, *Discoaster bifax* Subzone. This assignment must remain tentative because of the presence of very rare *Nannotetrina* cf. *N. quadrata* in one sample from Locality D-969 and a very rare occurrence of *Isthmolithus recurvus* in two of the samples from Locality D-971. The presence of rare specimens of *Nannotetrina* in the *Discoaster bifax* Subzone has been remarked upon by Bukry (1973, p. 690). However, the occurrence of *Isthmolithus recurvus* in conjunction with most of the other diagnostic nannofossil species observed from Locality D-971 is considered a totally incompatible association. Either the specimens of *Isthmolithus recurvus* are present as contaminants somehow introduced into the samples, or, if *Isthmolithus recurvus* be indigenous to Locality D-971, then most of the other nannofossil taxa observed must be assumed to be redeposited older species. Should the latter be the case, then this would suggest that Locality D-971 would lie in the very latest part of the Narizian Stage and within a basal portion of the *Discoaster barbadiensis* Zone, *Isthmolithus recurvus* Subzone not yet observed nor recognized elsewhere in California. Further investigation of this anomalous situation may provide a solution. Meanwhile, assignment of these samples to some interval within the *Reticulofenestra umbilica* to early *Discoaster barbadiensis* Zones would seem to be reasonably certain.

NEW DATA, OTHER SECTIONS INVESTIGATED

The authors have examined material from the early Narizian Cozy Dell Formation exposed at Las Cruces, Santa Barbara County, California. Samples from the lower part of this exposure contain *Nannotetrina* *quadrata* and *Chiasmolithus gigas* dictating assignment to the *Nannotetrina quadrata* Zone, *Chiasmolithus gigas* Subzone. Samples from the upper part of this exposure from 2 to 10 m beneath the Sacate Formation contain *Reticulofenestra umbilica* and *Discoaster bifax* and are consequently assigned to the *Reticulofenestra umbilica* Zone, *Discoaster bifax* Subzone.

D. R. McKeel provided the authors with a sample from the type Alsea Formation at Alsea Bay, Lincoln County, Oregon. This sample is Sample Number 13 (67-12-13) as reported by McKeel and Lipps (1972). Benthonic foraminifers present are *Cassidulina galvinensis*, *Ceratobulimina washburnei*, *Eponides kleinpelli*, and *Sigmomorphina schencki*, a typical assemblage of the *Cassidulina galvinensis* Zone as reported by Rau (1975) who considers this zone to be late Refugian in age. *Isthmolithus recurvus* is common in this sample, but other diagnostic nannofossil taxa are extremely rare or absent. However, the presence of this nannofossil index species demands assignment of this sample from the Alsea Formation to either the *Discoaster barbadiensis* Zone, *Isthmolithus recurvus* Subzone, or to the *Helicopontosphaera reticulata* Zone, *Coccolithus subdistichus* Subzone.

Samples of the basal Rincon Formation of Arroyo el Bulito from strata assigned to the Zemorrian Stage contain a significant nannofossil association. These samples are University of California, Santa Barbara Localities 599, 600, and 601 which are located, respectively, 6, 12, and 18 m above the top of the Vaqueros Formation in Arroyo el Bulito, Santa Barbara County, California. Some of the nannofossils noted here are *Chiasmolithus altus*, *Coccolithus miopelagicus*, *Cyclicargolithus floridanus*, *C. neogammation*, *Dictyococcites scrippsae*, *Discoaster deflandrei*, *Helicopontosphaera euphratis*, and *H. intermedia*. This assemblage is most typical of the *Sphenolithus ciperoensis* Zone, *Dictyococcites bisectus* Subzone of Bukry (1975).

The senior author has studied material from the late Zemorrian, lower Rincon Formation of Los Sauces Creek, Ventura County, California, which immediately underlies the stratotype of the Saucesian Stage. Samples from the late Zemorrian approximately 76 to 91 m above the top of the Vaqueros Formation and within the lower Rincon Formation contain the highest occurrence noted of *Dictyococcites bisectus* in association with *Dictyococcites scrippsae*, *Coccolithus miopelagicus*, *Helicopontosphaera intermedia*, and *Cyclicargolithus neogammation* s.s. and the benthonic foraminifers *Hanzawaia americana crassisepta*, *Nonion ynezianum*, and *Uvigerinella sparsicostata*. Samples from the late Zemorrian from 152 to 198 m above the Vaqueros Formation and 30 to 76 m below the *Siphogenerina transversa* flood of the earliest Saucesian Stage contain the highest noted occurrence of *Dictyococcites scrippsae* in association with *Coccolithus miopelagicus* and *Cyclicargolithus neogammation* and the benthonic foraminifers *Hanzawaia americana crassisepta*, *Siphogenerina nodifera*, *S. transversa*, and *Valvulineria casitasensis*. Based on these data, the senior author places the top of the *Sphenolithus ciperoensis* Zone within the late Zemorrian of the lower Rincon Formation approximately 91 m above the Vaqueros Formation at Los Sauces Creek as dictated by the last occurrence of *Dictyococcites bisectus*. Some investigators may prefer to interpret the top of the *Sphenolithus ciperoensis* Zone based on the last occurrence of *Dictyococcites scrippsae* which is approximately 198 m above the top of the Vaqueros Formation, but still within the late Zemorrian Stage at least 15 m below the base of the type Saucesian Stage. In either case, some portion of the latest Zemorrian Stage may be equated to at least a part of the *Triquetrorhabdulus carinatus* Zone, *Cyclicargolithus abisectus* Subzone unless a hiatus occurs in that part of the section, in which case those strata present might belong to a younger subzone of the *Triquetrorhabdulus carinatus* Zone. However, the *Discoaster druggii* Subzone has been recognized by the senior author in the upper (but not uppermost) part of the Rincon Formation near the top of the early Saucesian Stage at Los Sauces Creek so that the latest Zemorrian here must be assigned to one of the subzones of the *Triquetrorhabdulus carinatus* Zone.

PLANKTONIC FORAMINIFERAL BIOSTRATIGRAPHY, REFUGIAN AND ADJACENT STAGES

PREVIOUSLY PUBLISHED DATA AND OPINION

Bandy and Kolpack (1963) reported 9 species of planktonic Foraminifera from strata of Narizian Age in the Cozy Dell and Coldwater Formations of the Tecolote Tunnel, Santa Barbara County, California. They considered those strata to be middle Eocene (Lutetian) in age, as the planktonic associations observed are typical for the middle Eocene elsewhere. These authors also reported one long-ranging planktonic species from strata of the Zemorrian Stage within the tunnel section.

Lipps (1965) listed 22 species of planktonic Foraminifera from the Zemorrian of the lower Rincon Formation at Los Sauces Creek, Ventura County, California, and assigned these strata to the *Globigerina oligocaenica* Zone of Eames, Banner, Blow, and Clarke (1962). The latter zone is a correlative of Zone P.19 of Blow (1969).

Lipps (1967a) reported finding *Subbotina linaperta, Turborotalia planoconica, T. centralis* and *Globigerapsis semiinvoluta* in samples from the Refugian Gaviota Formation in Arroyo el Bulito in the type area of the Refugian Stage; consequently, Lipps assigned the Refugian Stage to the *Globigerapsis semiinvoluta* Zone of Bolli (1957b). However, *Globorotalia (Turborotalia) planoconica* does not occur indigenously above the Ulatisian Stage in California and so cannot be a natural constituent within the Refugian Stage. Until Bolli (1972) provided a comprehensive study of the genus *Globigerinatheka* (previously *Globigerapsis*), the distinction between species and subspecies of this complex group were very poorly understood and it is easy to comprehend how early workers may have confused the various species and subspecies.

At any rate, the senior author has had the opportunity to critically examine numerous specimens of *Globigerinatheka* from the Narizian and Refugian Stages of California and Oregon and has yet to observe *Globigerinatheka semiinvoluta* s.s. in any section including the Refugian Gaviota Formation of Arroyo el Bulito. On the other hand, relatively frequent occurrences of *Globigerinatheka index tropicalis* have been observed in the early Refugian and Narizian of the Gaviota, Sacate, Bastendorff, and Nestucca Formations as well as in the early Refugian and Narizian of other formations within the Pacific Coast Tertiary. It is suggested that Lipps may have found *Globigerinatheka index tropicalis* rather than *G. semiinvoluta* in the Refugian strata at Arroyo el Bulito. Lipps (1967a) listed 10 species of planktonic Foraminifera, all of which he had listed previously with 12 additional species (Lipps, 1965), from the Zemorrian of Los Sauces Creek. He suggests, this time, a correlation of the late Zemorrian with the *Globorotalia opima opima* and *Globigerina ciperoensis* Zones of Bolli (1957a) and to Zones N.2 (P.21) and N.3 (P.22) of Banner and Blow (1965). It is not clear whether Lipps has here revised his original interpretation, as he does not mention the precise stratigraphic allocation of his material in either report. Should this not be a change in interpretation, then the implication is that the late Zemorrian as manifested in the lower Rincon Formation at Los Sauces Creek should be equated with Zones P.1[illegible] to P.22 (N.3) of Blow (1969). This interpretation is in partial conflict with new nannoplankton data from that location as will be discussed in later paragraphs.

Schmidt (1970) listed 12 species of planktonic Foraminifera from the Narizian Stage in the Sidney Flat and Kellogg Formations of Contra Costa County, the Kreyenhagen Formation of Kings County, and the Sacate-Gaviota Formations (undifferentiated) and Cozy Dell Formation of Santa Barbara County, California. Schmidt's Locality 0429 (which is from Locality D-971 of Hornaday, 1965) from within the undifferentiated Sacate-Gaviota Formations contains, among others, *Clavigerinella eocanica, Globigerinatheka index, Guembelitria columbiana,* and *Truncorotaloides rotundimarginatus* (a junior synonym of *Truncorotaloides collacteus*). The presence of these species in the Santa Rosa Road faunule assigned by Hornaday (1965) to the late Narizian *Amphimorphina jenkinsi* Zone would suggest equivalence to some part of Zone P.13 of Blow (1969). This interpretation would further suggest that the tentative assignment of Locality D-971 to the *Reticulofenestra umbilica* Zone, *Discoaster bifax* Subzone in an earlier paragraph is probably valid and that the very rare *Isthmolithus recurvus* found there are contaminants somehow introduced into our samples.

Steineck and Gibson (1971) reported *Globorotaloides suteri* and *Truncorotaloides collacteus* from the Poway Formation of Narizian Age in San Diego County, California, and considered that formation to be late middle Eocene in age.

McKeel and Lipps (1972) reported the occurrence of *Chiloguembelina cubensis, C. victoriana, Globigerina minima, G. praeturritilina, G. senilis,* and *G. wilsoni* in the late Refugian portion of the type Alsea Formation of Oregon; they concluded that the Alsea Formation is latest Eocene or earliest Oligocene in age. Rau (1975) equated this section with his *Cassidulina galvinensis* Zone (equivalent to the *Eponides kleinpelli* Zone of Rau, 1958).

Bandy (1972) considered the Ulatisian and Narizian Stages to be equivalent to Zones P.10 through P.14, the Refugian Stage to be equivalent to Zones P.15 through P.17 and the Zemorrian Stage to be equivalent to Zones P.18 through P.22 of Blow (1969). Bandy (1972, p. 41 and Fig. 1) also stated that "the Refugian Stage, as with other stages based upon benthic species, should be shown as a time-transgressive stage. . ."; this opinion appears to be contradicted by data from the present report.

Steineck, Gibson, and Morin (1972) listed 9 species of planktonic Foraminifera from the Narizian Poway

Formation in San Diego County, California, which they contend suggested equivalence with the *Orbulinoides beckmanni* Zone, a correlative to Zone P.13 of Blow (1969).

Rooth (1974) conducted a comprehensive study of the biostratigraphy and paleoecology of the Coaledo and Bastendorff Formations utilizing both benthonic and planktonic Foraminifera is his biostratigraphic analysis. He lists *Globigerapsis index, Globigerina prasaepis?, Globigerina senilis,* and *Subbotina linaperta* from the middle Bastendorff and *Chiloguembelina cubensis, Globigerina prasaepis?, Globigerina tripartita tripartita, Globorotalia gemma, Globorotalia* cf. *G. gemma, Globorotalia increbescens, Globorotalia opima nana,* and *Globorotalia* sp. from the upper Bastendorff at the stratotype locality. He concluded (p. 93) that the Coaledo and Bastendorff Formations are late Eocene in age and that they can be correlated confidently with the Runangan Stage of New Zealand and tentatively with the "P.17" partial range zone of Blow (1969) and others. Rooth's description and illustration of *Globorotalia* sp. from the uppermost Bastendorff Formation (22 meters below the Tunnel Point Formation) are sufficient to permit identification of the two specimens found as *Globorotalia insolita,* a late Eocene index species originally described from New Zealand by Jenkins (1966). In addition, the specimens identified *and* illustrated by Rooth as *Globorotalia gemma* and *Globorotalia* aff. *G. gemma* also appear to be specimens of *Globorotalia insolita.*

McKeel and Lipps (1975) documented the occurrence of *Chiloguembelina cubensis, Globorotaloides* aff. *G. pseudokugleri, Globigerinatheka index index,* and *Globigerina (Subbotina) wilsoni* from the late Narizian portion of the type Bastendorff Formation of Oregon as defined by Tipton (1975); the former authors also reported the occurrence of *Globigerina praebulloides* and *Globigerina* sp. in the late Refugian portion of the type Bastendorff. They equated their material from the Bastendorff Formation respectively to Zones P.15 and P.16 of late Eocene age.

Poore and Brabb (1977) studied the planktonic Foraminifera of the Butano and type San Lorenzo Formations in the Santa Cruz Mountains of the central California Coast Ranges. They concluded that the upper part of the Butano Sandstone (Narizian in age) and lower part of the Twobar Shale Member (late Narizian in age) contained assemblages typical of Zones P.13 to P.14 of Blow (1969), while the middle part of the Twobar Shale (late Narizian in age) was assigned to Zones P.15 to P.16. Those samples from the early Zemorrian in the lower part of the Rices Mudstone Member were considered referable to Zones P.19 to P.20. The Refugian Stage at this locality, in the basal 60 to 90 m of the Rices Mudstone Member, is practically barren of planktonic microfossils, but can be logically related to one or more of the planktonic foraminiferal zones between and including Zones P.16 to P.19.

Other workers, mainly concerned with the benthonic Foraminifera, cited the occurrence of specimens which they assign to *Globigerina triloculinoides* from the Narizian and Refugian Stages. These forms may be *Globigerina angiporoides, G. brevis, G. galavisi, G. linaperta,* or other homeomorphic species, but not *Globigerina triloculinoides* s.s. The latter species appears to be everywhere restricted to strata of Paleocene age.

NEW DATA, ARROYO EL BULITO CONTINUUM

Planktonic Foraminifera are present but rare in several samples from the upper Sacate and Gaviota Formations furnished by Tipton (this volume). The stratigraphically highest occurrence of *Globigerinatheka index tropicalis* noted is in U.C.S.B. 633 from the Gaviota Formation approximately 190 m below the base of the Alegria Formation and within the middle of the *Uvigerina atwilli* Subzone of the early Refugian Stage. *Pseudohastigerina micra* is present in U.C.S.B. 616, 621, and 635 all of which localities are in the early Refugian of the upper Sacate and Gaviota Formations. A single specimen of *Globorotalia cerroazulensis cerroazulensis* is recorded here from U.C.S.B. 664 in association with *Globigerina galavisi* and *Globigerina gortanii gortanii*; this locality is in the uppermost Gaviota Formation approximately 20 m below the base of the Alegria Formation and within the *Uvigerina vicksburgensis* Zone of the late Refugian Stage. No Foraminifer were noted in samples available from the Alegria Formation, and that unit is considered to be Refugian in age based on megafossil evidence alone (see Weaver and Frantz, 1967). The highest occurrence of *Globigerinatheka index tropicalis* here seen in U.C.S.B. 633 from the early Refugian portion of the Gaviota Formation is equated with the lower part of Zone P.16 (equivalent to the lower part of the *Globorotalia cerroazulensis* Zone of Bolli, 1966). Presence of *Globorotalia cerroazulensis cerroazulensis* and *Globigerina gortanii gortanii* together in U.C.S.B. 664 from the late Refugian portion of the uppermost Gaviota Formation suggests that this sample be assigned to Zone P.17 (equivalent to the upper part of the *Globorotalia cerroazulensis* Zone of Bolli, 1966).

NEW DATA, BASTENDORFF BEACH CONTINUUM

Samples from the type Bastendorff Formation utilized by Tipton (1975) in her study of that section were examined for planktonic Foraminifera by the senior author. Planktonic species were noted as rare to frequent constituents in 7 of these samples. *Globigerinatheka index index* and *G. index tropicalis* were found in a sample from Locality A-8014 of the late Narizian portion of the Bastendorff Formation 446 m below the base of the Tunnel Point Sandstone. The highest occurrence noted for *Globigerinatheka index index* at this exposure is from Locality A-8029 and is still within the late Narizian portion of the Bastendorff Formation 357 m below the base of the Tunnel Point; other occurrences of that species are from Localities A-8024 and A-8028. Also noted from Localities A-8028 and A-8029 are *Globigerina angiporoides angiporoides*, *Globigerinatheka index tropicalis*, and *Globorotaloides suteri*. The highest occurrence noted at this exposure of *Globigerinatheka index tropicalis* is from Locality A-8046 in the early Refugian portion of the Bastendorff Formation 217 m below the base of the Tunnel Point Sandstone. A single specimen of *Globorotalia cerroazulensis pomeroli* occurred in a sample from Locality A-8047 approximately 2 m above Locality A-8046 within the early Refugian Stage. *Globigerina linaperta* was found in a sample from Locality A-8058, still in the early Refugian Stage and approximately 176 m below base of the Tunnel Point.

No identifiable planktonic species were noted from localities within the late Refugian portion of the Bastendorff in this study, although McKeel and Lipps (1975) reported and figured two species from Locality A-8079 in the upper Refugian of the uppermost Bastendorff Formation only 5 cm below the base of the Tunnel Point Sandstone; their figured specimens appear to be *Globigerina praebulloides* and a single specimen of *Globigerina angiporoides angiporoides*. Also, Rooth (1974) was successful in isolating several planktonic species from the late Refugian portion of the Bastendorff Formation, the most significant being *Globorotalia insolita* (described and illustrated by Rooth as both *Globorotalia* sp. and *Globorotalia* cf. *G. gemma*) found within 22 m of the top of the formation.

The highest occurrence of *Globigerinatheka index index* in Locality A-8029 of the late Narizian portion of the Bastendorff Formation is equated with Zone P.15 (essentially equivalent to the *Globigerinatheka semiinvoluta* Zone of Bolli, 1972). The highest occurrence of *Globigerinatheka index tropicalis* from Locality A-8046 in close association with *Globorotalia cerroazulensis pomeroli* and within the early Refugian portion of the Bastendorff Formation is assigned to the lower part of Zone P.16 (essentially equivalent to the lower part of the *Globorotalia cerroazulensis* Zone of Bolli, 1966). The 2 species reported from the late Refugian of the Bastendorff Formation by McKeel and Lipps (1975) are long ranging and do not permit assignment of those strata to a particular planktonic zone. However, the presence of *Globorotalia insolita* in the late Refugian only 22 m below the top of the Bastendorff is considered sufficient evidence for assigning this part of the formation to Zone P.17 which is essentially equivalent to the upper part of the *Globorotalia cerroazulensis* Zone of Bolli, 1966.

NEW DATA, ROADS END BEACH CONTINUUM

D. R. McKeel (1975, personal communication) observed several important species of planktonic Foraminifera from samples of Narizian and Refugian Age in the Nestucca Formation exposed in continuum at Roads End Beach, Lincoln County, Oregon; the senior author has also examined McKeel's material in order to confirm those occurrences. *Globigerinatheka index index* has its highest occurrence here in Sample No. 75-02-1 in association with *Chiloguembelina cubensis*, *Globigerina* cf. *G. wilsoni*, and *Pseudohastigerina micra*; this sample is from the late Narizian portion of the Nestucca Formation 60 cm above the base of the Nestucca continuum. The highest occurrence of *Globigerinatheka index tropicalis* is in Sample No. 75-02-14 near the top of the sequence collected and in association with *Globorotaloides suteri*; this sample is from the early Refugian Stage and is 133 m above the base of the exposed continuum. Sample No. 75-02-1 from the late Narizian of the Nestucca Formation is assigned to Zone P.15 based on highest occurrence of *Globigerinatheka index index*. Sample No. 75-02-14 containing *G. index tropicalis* and from the early Refugian of the Nestucca Formation is equated with a part of lower Zone P.16. Zones P.15 and P.16 are in turn correlated with the *Globigerinatheka semiinvoluta* and lower *Globorotalia cerroazulensis* Zones of Bolli (1966, 1972). An isolated sample collected by McKeel from older Nestucca strata south of the Nestucca continuum contained *Chiloguembelina cubensis*, *Globigerinatheka index index*, *G. index tropicalis*, *Globigerinatheka* sp., *Globigerinita unicava primitiva*, *Globorotaloides suteri*, *Guembelitria columbiana*, *Pseudohastigerina micra*, and *Truncorotaloides rohri* var.; this sample, No. 73-12-A, is from the Narizian Stage and is older than any samples from the Nestucca continuum although its exact stratigraphic position is uncertain due to slumping. However, this sample is assigned to Zone P.13 based on concurrence of *Chiloguembelina cubensis, Globorotaloides suteri, Guembelitria columbiana,* and *Truncorotaloides rohri* (recte *T. pseudodubia,* teste Bandy, 1964). The rare specimens of *Truncorotaloides* recorded here are most similar to the variety described as *T. rohri* var. *guaracaraensis* by Bronnimann and Bermúdez (1953).

NEW DATA, OTHER SECTIONS INVESTIGATED

A sample from the Alsea Formation utilized by McKeel and Lipps (1972) in their study of calcareous plankton from the Oregon Tertiary was provided by D. R. McKeel for further examination by the senior author. Their Sample No. 13 (67-12-13) from the middle Alsea Formation, northwest side of Alsea Bay near Waldport, Lincoln County, Oregon, yielded rare specimens of *Globigerina ampliapertura, G. prasaepis,* and *Globorotalia increbescens* in addition to the 7 other species of planktonic Foraminifera reported by those authors. Benthonic Foraminifera noted in this sample and partially listed in an earlier paragraph are indicative of the *Cassidulina galvinensis* Zone of Rau (1975) who considers that zone to represent the late Refugian Stage in the Pacific Northwest.

Concurrence of *Globigerina ampliapertura, G. gortanii praeturritilina,* and *G. prasaepis* suggests that Sample No. 13 from the Alsea Formation should be equated with uppermost Zone P.17; the total planktonic fauna is the most diverse observed from the Refugian Stage by the senior author and also represents the youngest late Eocene planktonic assemblage so far recorded from the Pacific Coast.

R. S. Boettcher (1971, pers. comm.) identified *Globorotalia insolita* s.s. in the subsurface late Refugian of the Pacific Northwest and this occurrence was confirmed by the senior author. *Globorotalia insolita,* recorded as *Globorotalia* sp., *G. gemma,* and *G.* cf. *G. gemma* from the uppermost Bastendorff Formation by Rooth (1974), has also been observed in the Keasey Formation of northwest Oregon by Kristin McDougall (1978, pers. comm.). Originally described by Jenkins (1966) from the late Kaiatan Stage (and ranging upwards through most of the Runangan Stage, see Jenkins, 1971) of New Zealand, *Globorotalia insolita* has also been recorded in a deep sea core from the eastern equatorial Pacific by Jenkins and Orr (1972) where it was associated with other species of late Eocene age. To date, no occurrences have been recorded in California. Based on associated planktonic species occurring in the Kaiatan and Runangan Stages of New Zealand, in the late Refugian Stage of the Pacific Northwest, and in the late Eocene of Deep Sea Drilling Project Site 77B, *Globorotalia insolita* is considered here to be restricted essentially to sections equivalent to planktonic foraminiferal Zone P.17; occurrences of that species in the surface and subsurface late Refugian of the Pacific Northwest are also equated with that zone.

SUMMARY AND CONCLUSIONS
(FIG. 5)

AGE AND ZONAL ASSIGNMENTS, NARIZIAN STAGE

The Narizian Stage of the Pacific Coast Tertiary may be equated with the *Nannotetrina quadrata* and *Reticulofenestra umbilica* Zones and *Chiasmolithus oamaruensis* Subzone of the *Discoaster barbadiensis* Zone of Bukry (1973, 1975); these zones and subzones are correlated with the NP 15 through NP 18 nannoplankton zones of Martini (1971). Previously reported and new data from several formations in California support the older zonal assignment and new data from the type Bastendorff Formation and the Nestucca Formation in Oregon and the type San Lorenzo Formation and upper Sacate Formation of California support the younger zonal assignments within the Narizian Stage. Consequently, the Narizian is considered to be equivalent to the middle Eocene and the early late Eocene as recognized by nannoplankton investigators.

Utilizing both previously published and new planktonic foraminiferal data, the senior author equates the latest Narizian Stage with Zone P.15 of Blow (1969). This is based on the highest observed occurrence of *Globigerinatheka index index* in the late Narizian of the type Bastendorff and the Nestucca Formations of Oregon. Bolli (1972, Fig. 83) indicates that *G. index index* ranges to near the top of Zone P.15 (*Globigerinatheka semiinvoluta* Zone) and that *G. index tropicalis* ranges higher into Zone P.16 (early *Globorotalia cerroazulensis* Zone). This same relationship appears to exist within the Bastendorff and Nestucca Formations where *G. index index* has its highest occurrence in the late Narizian, while *G. index tropicalis* ranges upwards into the early Refugian Stage. Most investigators of planktonic Foraminifera consider Zone P.15 to be early late Eocene in age. Therefore, the latest Narizian is assigned here to the early late Eocene.

AGE AND ZONAL ASSIGNMENTS, REFUGIAN STAGE

The Refugian Stage of the Pacific Coast Tertiary is equated here with the *Discoaster barbadiensis* Zone, *Isthmolithus recurvus* Subzone; this subzone is equivalent to the NP 19 and NP 20 nannoplankton zones of

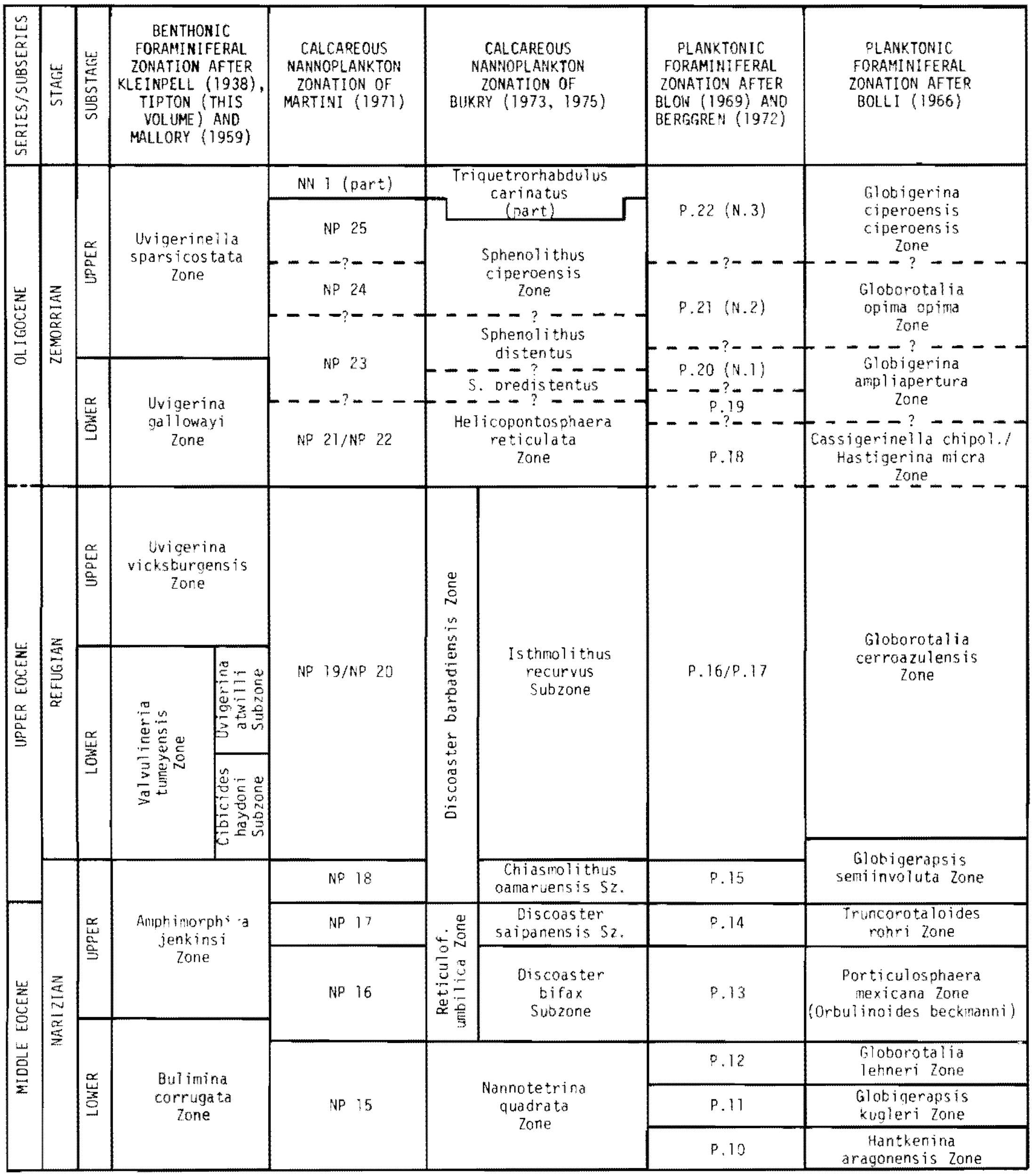


FIGURE 5

Correlation chart illustrating the relationship of the Narizian, Refugian and Zemorrian Stages of the Pacific Coast Tertiary to the planktonic zonations proposed by Martini (1971), Bukry (1973, 1975), Blow (1969), Berggren (1971, 1972), and Bolli (1966).

Martini (1971). All previous and new nannofossil data reported from California and Oregon would seem to support this conclusion. New data from the Alsea and Bastendorff Formations might suggest that the Refugian Stage could include younger nannoplankton zones, but other new data from the early Zemorrian of the type San Lorenzo Formation severely limit this possibility. The authors believe that the Refugian Stage as manifested in California does not include any of the *Helicopontosphaera reticulata* Zone and is, therefore, late Eocene in age throughout based on currently accepted nannoplankton chronology. However, they maintain the possibility that the upper part of the *Cassidulina galvinensis* Zone in the Pacific Northwest, considered to be late Refugian in age, might be younger than the late Refugian observed in California sections. Nevertheless, the nannoplankton evidence from most exposures would dictate that the Refugian Stage be considered entirely late Eocene in age.

In contradiction to some previously published data, new data developed by the senior author based on planktonic foraminiferal distribution indicate that the Refugian Stage is equivalent to all or parts of Zones P.16 and P.17 (*Globorotalia cerroazulensis* Zone of Bolli, 1966) rather than to Zone P.15 (approximate *Globigerapsis semiinvoluta* Zone of Bolli, 1957b) as postulated by Lipps (1967a). Presence of *Globigerinatheka index tropicalis* and *Globorotalia cerroazulensis pomeroli* and absence of *Globigerinatheka index index* in the early Refugian coupled with the presence of *Globigerina ampliapertura, G. gortanii gortanii, G. gortanii praeturritilina, G. prasaepis, Globorotalia cerroazulensis cerroazulensis,* and *G. insolita* in the late Refugian strongly suggests assignment of the entire Refugian Stage to Zones P.16 and P.17 which are late and latest Eocene in age.

AGE AND ZONAL ASSIGNMENTS, ZEMORRIAN STAGE

New nannoplankton data developed from the earliest Zemorrian of the type San Lorenzo Formation and the latest Zemorrian of the Rincon Formation at Los Sauces Creek and Arroyo el Bulito suggest that the Zemorrian Stage of the Pacific Coast Tertiary ranges from the early *Helicopontosphaera reticulata* Zone at the base to, and including part of, the early *Triquetrorhabdulus carinatus* Zone at the top; in terms of the nannoplankton zonation of Martini (1971), the Zemorrian Stage would range from NP 21 to, and include part of, the NN 1 nannoplankton zone. Except for the upper part of the *Sphenolithus ciperoensis* Zone, which is present in the late Zemorrian of Arroyo el Bulito and Los Sauces Creek (and equivalent to NP 25 of Martini, 1971), none of the intervening Oligocene nannoplankton zones have yet been definitely recognized from the Pacific Coast. During investigation of the late Zemorrian and early Saucesian strata from Los Sauces Creek, the top of the *Cyclicargolithus abisectus* Subzone, lowest subzone of the *Triquetrorhabdulus carinatus* Zone and latest Oligocene in age, was not observed. However, it is reasonable to conclude that this subzone must be limited either to the latest Zemorrian or includes the latest Zemorrian and some part of the earliest Saucesian Stage at Los Sauces Creek. In either event, the Oligocene/Miocene boundary as recognized by nannoplankton investigators must occur at or very close to the top of the Zemorrian Stage as manifested at this locality. Consequently the Zemorrian Stage is considered here to be wholly Oligocene in age based on nannoplankton distribution.

No sections of early Zemorrian Age containing well preserved or diagnostic planktonic Foraminifera were available for study as of this writing, although it is suspected that such sections exist. Perhaps these are present in the subsurface of the western San Joaquin Valley of California or in surface and subsurface sections of the Pacific Northwest that have not yet come under scrutiny by plankton investigators.

A planktonic foraminiferal assemblage from the late Zemorrian at Los Sauces Creek is assigned to the *Globigerina oligocaenica* Zone (equivalent to Zone P.19) of Eames, Banner, Blow, and Clarke (1962) by Lipps (1965). This surprisingly diverse association contains 22 species which can only occur together in Zone P.19 according to Blow (1969). However, as mentioned in earlier paragraphs, nannoplankton associations recorded from identical strata at Los Sauces Creek and equivalent strata at Arroyo el Bulito call for assignment to either the *Sphenolithus ciperoensis* Zone, *Dictyococcites bisectus* Subzone or *Triquetrorhabdulus carinatus* Zone, *Cyclicargolithus abisectus* or younger Subzone of Bukry (1973, 1975); these zones and subzones are equivalent to NP 25 and early NN 1 nannoplankton zones of Martini (1971). Both Martini (1971) and Berggren (1972) have indicated that the NP 25 and early NN 1 nannoplankton zones are equivalent to the P.22 planktonic foraminiferal zone. Lipps (1965) must consider this planktonic foraminiferal assemblage from the late Zemorrian at Los Sauces Creek to be early Oligocene in age by virtue of the species he lists as present. However, nannoplankton species from the late Zemorrian of Los Sauces Creek and Arroyo el Bulito are late Oligocene in age. Consequently, a contradiction exists here for which no satisfactory explanation can be offered at this time.

CONCLUSIONS

Calcareous nannofossils and planktonic Foraminifera are relatively scarce and erratic in occurrence in strata of late Narizian, Refugian, and Zemorrian Age within the Pacific Coast Tertiary. However, both groups are present in sufficient numbers in the marine sediments so that a persistent investigator may develop data from which zonal assignments can be determined. Experience would indicate that, of the two disciplines, the calcareous nannoplankton provide the greater stratigraphic resolution by virtue of their more consistent presence. Care must be taken so as not to

SERIES AND SUBSERIES	TENTATIVE CORRELATION OF NARIZIAN, REFUGIAN AND ZEMORRIAN STAGES OF THE PACIFIC COAST TERTIARY WITH THOSE OF THE ATLANTIC AND GULF COASTAL PROVINCE, EUROPE AND NEW ZEALAND BASED ON VERTICAL DISTRIBUTION OF NANNOPLANKTON AND PLANKTONIC FORAMINIFERA			
	PACIFIC COAST This Report	ATLANTIC AND GULF Murray (1961)	EUROPE Berggren (1972), Hardenbol and Berggren (1978)	NEW ZEALAND Jenkins (1971)
LOWER MIOCENE (part)	Saucesian (part)	Anahuacian	Aquitanian (part)	Otaian (part)
OLIGOCENE	Zemorrian		Chattian	Waitakian
		Chickasawhayan		Duntroonian
		Vicksburgian	Rupelian	Whaingaroan
UPPER EOCENE	Refugian	Jacksonian	Priabonian	Runangan
				Kaiatan
	Narizian			
MIDDLE EOCENE		Claibornian	Bartonian	
				Bortonian
			Lutetian	
				Porangan
LOWER EOCENE (part)	Ulatisian (part)	Sabinian (part)	Ypresian (part)	Heretaungan (part)

FIGURE 6

Tentative correlation of Narizian, Refugian, and Zemorrian Stages of the Pacific Coast Tertiary to those of the Atlantic and Gulf Coastal Province, Europe and New Zealand.

be misled by reworked and redeposited nannofossils which seem to be all too prevalent in sediments of the Pacific Coast Tertiary. Consequently, it is best to avoid working with isolated single samples whenever possible; a series of samples collected from an exposed continuum offers the best chance of recognizing alien specimens that are incompatible with the indigenous nannoflora which might be present within that section.

The focal point of this study is the Refugian Stage of the Pacific Coast Tertiary, but in order to properly delimit that unit it has been necessary to examine also the subjacent Narizian and superjacent Zemorrian Stages. Considerable new data have been presented on both the calcareous nannoplankton and planktonic foraminiferal associations and distributions within these three stages. Based on this data and applying the plankton chronology accepted by most investigators the authors conclude that: (1) the latest Narizian Stage is at least in part equivalent to the *Discoaster barbadiensis* Zone, *Chiasmolithus oamaruensis* Subzone of Bukry (1973, 1975) and to Zone P.15 of Blow (1969) and is earliest late Eocene in age; (2) the Refugian Stage is equivalent to the *Discoaster barbadiensis* Zone, *Isthmolithus recurvus* Subzone and to Zones P.16 and P.17 and is late Eocene in age; and (3) the earliest Zemorrian Stage in California includes all or most of the *Helicopontosphaera reticulata* Zone and is earliest Oligocene in age.

By collating previously published plankton data, new data, and the authors' personal knowledge, a tentative correlation can be made between the Pacific Coast stages and those of the U.S. Atlantic and Gulf

Coast Province, Europe and New Zealand (Fig. 6). The authors have drawn upon the works of Berggren (1971, 1972), Hardenbol and Berggren (1978), Jenkins (1971), and Murray (1961) plus their personal, but unpublished, knowledge of Gulf Coast planktonic biostratigraphy in illustrating the relationships between the Narizian, Refugian, and Zemorrian Stages of the Pacific Coast Tertiary and those of the Atlantic and Gulf Coast, Europe, and New Zealand.

During this investigation, no hard evidence was uncovered to suggest that the Pacific Coast stages under study, and as based on benthonic foraminiferal distribution, might be time-transgressive in nature. The senior author has followed with interest the debate that developed between proponents of plankton biostratigraphy and advocates of benthonic foraminiferal biostratigraphy regarding this controversial issue (see Steineck and Gibson, 1971; Bandy, 1972; McWilliams, 1972; Gibson and Steineck, 1972; Phillips, 1972; and Steineck and Gibson, 1972). There certainly appears to be some basis in fact from the plankton investigator's point of view to consider that some of the early Tertiary marine stages of the Pacific Coast as manifested in various areas may not have the degree of temporal integrity that has been traditionally assigned to them. On the other hand, it has not been proven how much the semantics of the various disciplines may have magnified the problem. Also, some plankton investigators have failed to include all of the documentary details in their presentations necessary to convince a skeptical audience that their conclusions are justified by hard fact, and, therefore, merit serious consideration. It is the senior author's belief that additional carefully prepared data on the distribution of planktonic and benthonic Foraminifera and calcareous nannoplankton will settle the controversy. Hopefully, such documention will be accomplished in a spirit of cooperation, rather than one of contention, between the various disciplines.

ACKNOWLEDGMENTS

We are grateful to the late G. R. Hornaday, and to D. R. McKeel and Ann Tipton who provided much of the sample material necessary to this investigation. For stimulating and informative discussions relevant to the subject, we thank R. E. Anderson, R. S. Boettcher, L. N. Edwards, J. A. Forman, R. M. Kleinpell, D. R. McKeel, R. W. Morin, S. F. Percival, H. L. Tipsword, Ann Tipton, and D. W. Weaver. David Bukry kindly agreed to review the manuscript prior to publication.

NANNOPLANKTON REFERENCE LIST

Preferred modern names are followed by the original designation and reference.

Bramletteius serraculoides Gartner, 1969, Micropaleontology, v. 15, no. 1, p. 31, pl. 1, figs. 1–3.

Braarudosphaera bigelowi (Gran & Braarud) = *Pontosphaera bigelowi* Gran & Braarud, 1935, Biol. Board Canada Jour., v. 1, p. 388, fig. 67.

Braarudosphaera irregularis Bybell & Gartner, 1972, Micropaleontology, v. 18, no. 3, p. 324, pl. 1, figs. 1, 2.

Chiasmolithus altus Bukry and Percival, 1971, Tulane Studies Geology and Paleontology, v. 8, no. 3, p. 126, pl. 2, figs. 1, 2.

Chiasmolithus gigas (Bramlette & Sullivan) = *Coccolithus gigas* Bramlette & Sullivan, 1961, Micropaleontology, v. 7, no. 2, p. 140, pl. 1, figs. 6a–d.

Chiasmolithus grandis (Bramlette & Riedel) = *Coccolithus grandis* Bramlette & Riedel, 1954, Jour. Paleontology, v. 28, no. 4, p. 391, pl. 38, figs. 1a, b.

Chiasmolithus oamaruensis (Deflandre) = *Tremalithus oamaruensis* Deflandre in Deflandre & Fert, 1954, Annales de Paleontologie, v. 40, p. 154, pl. 11, fig. 22; text. figs. 72–74.

Chiasmolithus solitus (Bramlette & Sullivan) = *Coccolithus solitus* Bramlette & Sullivan, 1961, Micropaleontology, v. 7, no. 2, p. 140, pl. 2, figs. 4a–c.

Chiasmolithus titus Gartner, 1970, North Am. Paleont. Convention, Sept. 1969, Proc. G, p. 945, fig. 17.

Coccolithus eopelagicus (Bramlette & Riedel) = *Tremalithus eopelagicus* Bramlette & Riedel, 1954, Jour. Paleontology, v. 28, p. 392, pl. 38, figs. 2a, b.

Coccolithus miopelagicus Bukry, 1971, San Diego Soc. Nat. History Trans., v. 16, no. 4, p. 310, pl. 2, figs. 6–9.

Coccolithus pelagicus (Wallich) = *Coccosphaera pelagica* Wallich, 1877, Ann. Mag. Nat. History, ser. 4, v. 19, p. 348, figs, 1, 2, 5, 11, 12.

Cruciplacolithus delus (Bramlette & Sullivan) = *Coccolithites delus* Bramlette & Sullivan, 1961, Micropaleontology, v. 7, no. 2, p. 151, pl. 7, figs. 1a–c, 2a, b.

Cyclicargolithus floridanus (Roth & Hay) = *Coccolithus floridanus* Roth & Hay in Hay and others, 1967, Gulf Coast Assoc. Geol. Soc. Trans., v. 17, p. 445, pl. 6, figs. 1–4.

Cyclicargolithus neogammation (Bramlette & Wilcoxon) = *Cyclococcolithus neogammation* Bramlette & Wilcoxon, Tulane Studies Geology and Paleontology, v. 5, no. 3, p. 104, pl. 1, figs. 1–3; pl. 4, figs. 3–5.

Cyclococcolithina formosa (Kamptner) = *Cyclococcolithus formosus* Kamptner, 1963, Ann. Naturh. Mus. Wien, v. 66, p. 163, pl. 2, fig. 8; text. fig. 20.

Dictyococcites bisectus (Hay, Mohler & Wade) = *Syracosphaera bisecta* Hay, Mohler & Wade, 1966, Eclogae Geol. Helvetiae, v. 59, p. 393, pl. 10, figs. 1–6.

Dictyococcites scrippsae Bukry & Percival, 1971, Tulane Studies Geology and Paleontology, v. 8, no. 3, p. 128, pl. 2, figs. 7, 8.

Discoaster barbadiensis Tan, 1927, Koninkl. Nederlandse Akad. Wetensch. Proc., Sec. Sc., v. 30, p. 415 (not figured).

Discoaster bifax Bukry, 1971, San Diego Soc. Nat. History Trans., v. 16, no. 14, p. 313, 314, pl. 3, figs. 6–11.

Discoaster binodosus Martini, 1958, Senckenbergiana Lethaea, v. 39, p. 362, pl. 4, fig. 18a, b.

Discoaster deflandrei Bramlette & Riedel, 1954, Jour. Paleontology, v. 28, p. 399, pl. 39, fig. 6, text-figs. 1a–c.

Discoaster distinctus Martini, 1958, Senckenbergiana Lethaea, v. 39, p. 363, pl. 4, figs. 17a, b.

Discoaster gemmifer Stradner, 1961, Erdoel-Zeitschrift, v. 77, p. 86, fig. 83.

Discoaster germanicus Martini, 1958, Senckenbergiana Lethaea, v. 39, p. 360, pl. 3, figs. 15a, b.

Discoaster lodoensis Bramlette & Riedel, 1954, Jour. Paleontology, v. 28, no. 4, p. 398, pl. 39, figs. 3a, b.

Discoaster nodifer Bramlette & Riedel = *Discoaster tani nodifer* Bramlette & Riedel, 1954, Jour. Paleontology, v. 28, no. 4, p. 397, pl. 39, fig. 2.

Discoaster saipanensis Bramlette & Riedel, 1954, Jour. Paleontology, v. 28, no. 4, p. 298, pl. 39, fig. 4.

Discoaster tani Bramlette & Riedel, 1954, Jour. Paleontology, v. 28, no. 4, p. 397, pl. 39, fig. 1.

Discoaster tani ornatus Bramlette & Wilcoxon, 1967, Tulane Studies Geology and Paleontology, v. 5, no. 3, p. 112, 114; pl. 7, figs. 7, 8.

Discolithina distincta (Bramlette and Sullivan) = *Discolithus distinctus* Bramlette & Sullivan, 1961, Micropaleontology, v. 7, no. 2, p. 141, pl. 2; figs. 8a, b, 9a–c.

Discolithina panaria (Deflandre) = *Discolithus panarium* Deflandre in Deflandre & Fert, 1954, Annales de Paleontologie, v. 40, p. 141, text-figs. 39, 40.

Discolithina plana (Bramlette & Sullivan) = *Discolithus planus* Bramlette & Sullivan, 1961, Micropaleontology, v. 7, no. 2, p. 143, pl. 3, figs. 7a–c.

Helicopontosphaera compacta (Bramlette & Wilcoxon) = *Helicosphaera compacta* Bramlette & Wilcoxon, 1967, Tulane Studies Geology and Paleontology, v. 5, no. 3, p. 105, pl. 6, figs. 5–8.

Helicopontosphaera euphratis (Haq) = *Helicosphaera euphratis* Haq, 1966, Stockholm Contr. Geology, v. 15, no. 3, p. 33, pl. II, figs. 1, 3 (= *Helicosphaera parallela* Bramlette & Wilcoxon).

Helicopontosphaera intermedia (Martini) = *Helicosphaera intermedia* Martini, 1965, Proc. XVII Symp. Colston Res. Soc., v. 17, p. 404, pl. 35, figs. 1, 2.

Helicopontosphaera lophota (Bramlette & Sullivan) = *Helicosphaera seminulum lophota* Bramlette & Sullivan, 1961, Micropaleontology, v. 7, no. 2, p. 144, pl. 4, figs. 3a, b, 4.

Helicopontosphaera reticulata (Bramlette & Wilcoxon) = *Helicosphaera reticulata* Bramlette & Wilcoxon, 1967, Tulane Studies Geology and Paleontology, v. 5, no. 3, p. 106, pl. 6, fig. 15.

Helicopontosphaera seminulum (Bramlette & Sullivan) = *Helicosphaera seminulum seminulum* Bramlette & Sullivan, 1961, Micropaleontology, v. 7, no. 2, p. 144, pl. 4, figs. 1a–c, 2.

Isthmolithus recurvus Deflandre & Fert, 1954, Ann. Paleont., v. 40, p. 169, pl. 12, figs. 9–13, text-figs. 119–122.

Nannotetrina quadrata (Bramlette & Sullivan) = *Chiphragmalithus ? quadratus* Bramlette & Sullivan, 1961, Micropaleontology, v. 7, no. 2, p. 157, pl. 10, figs. 14, 15.

Neococcolithes dubius (Deflandre) = *Zygolithus dubius* Deflandre in Deflandre & Fert, 1954, Ann. Paleont., v. 40, p. 149, text-figs. 43–44, 68.

Pemma basquensis (Martini) = *Micrantholithus basquensis* Martini, 1959, Senckenbergiana Lethaea, v. 40, p. 417, pl. 1, figs. 9, 10, 12.

Pemma papillatum Martini, 1959, Erdol u. Kohle, v. 12, p. 139, text-fig. 1.

Reticulofenestra hillae Bukry & Percival, 1971, Tulane Studies Geology and Paleontology, v. 8, no. 3, p. 136, pl. 6, figs. 1–3.

Reticulofenestra samodurovi (Hay, Mohler & Wade) = *Apertapetra samodurovi* Hay, Mohler & Wade, 1966, Eclogae Geol. Helvetiae, v. 59, p. 388, pl. 6, figs. 1–7.

Reticulofenestra umbilica (Levin) = *Coccolithus umbilicus* Levin, 1965, Jour. Paleontology, v. 39, p. 265, pl. 41, fig. 2.

Rhabdosphaera crebra (Deflandre) = *Rhabdolithus creber* Deflandre in Deflandre & Fert, 1954, Ann. Paleont., v. 40, p. 157, pl. 12, figs. 31–33, text. figs. 81, 82.

Rhabdosphaera tenuis Bramlette & Sullivan, 1961, Micropaleontology, v. 7, no. 2, p. 147, pl. 5, figs. 14a, b.

Sphenolithus abies Deflandre in Deflandre & Fert, 1954, Ann. Paleont., v. 40, p. 164, pl. 10, figs. 1–4.

Sphenolithus furcatolithoides Locker, 1967, Geologie, v. 16, p. 363, figs. 7–8.

Sphenolithus moriformis (Bronnimann & Stradner) = *Nannoturbella moriformis* Bronnimann & Stradner, 1960, Erdoel-Z., v. 76, p. 368, figs. 11–16.

Sphenolithus predistentus Bramlette & Wilcoxon, 1967, Tulane Studies Geology and Paleontology, v. 5, no. 3, p. 136, pl. 2, figs. 10, 11.

Sphenolithus pseudoradians Bramlette & Wilcoxon, 1967, Tulane Studies Geology and Paleontology, v. 5, no. 3, p. 126, pl. 2, figs. 12–14.

Sphenolithus spiniger Bukry, 1971, San Diego Soc. Nat. History Trans., v. 16, no. 14, p. 321, pl. 6, figs. 11, 12; pl. 7, figs. 1, 2.

Sphenolithus tribulosus Roth, 1970, Eclogae Geol. Helvetiae, v. 61, p. 870, pl. 14, fig. 5.

Transversopontis pulcher (Bramlette & Sullivan) = *Discolithus pulcher* Bramlette & Sullivan, 1961, Micropaleontology, v. 7, no. 2, p. 143, pl. 3, figs. 8a–c.

Tribrachiatus orthostylus (Bramlette & Riedel) = *Discoaster tribrachiatus* Bramlette & Riedel, 1954, Jour. Paleontology, v. 28, no. 4, p. 397, pl. 38, fig. 11.

Zygrhablithus bijugatus (Deflandre) = *Zygolithus bijugatus* Deflandre, 1954 (part), in Deflandre & Fert, Ann. Paleont., v. 40, p. 148, pl. 11, fig. 21 (not text fig. 59).

FORAMINIFERAL REFERENCE LIST

All species of Foraminifera reported here as new data are listed alphabetically by preferred modern name and followed by the original designation and reference.

Cassidulina galvinensis Cushman and Frizzell, 1940, Cushman Lab. Foram. Research Contr., v. 16, pt. 2, p. 43, pl. 8, figs. 10a–c.

Ceratobulimina washburnei Cushman and Schenck, 1928, California Univ., Dept. Geol. Sci. Bull., v. 17, no. 9, p. 314, pl. 45, figs. 1a–c.

Chiloguembelina cubensis (Palmer) = *Gümbelina cubensis* Palmer, 1934, Soc. Cubana Hist. Nat. Mem., v. 8, p. 74, text figs. 1–6.

Eponides kleinpelli Cushman and Frizzell, 1940, Cushman Lab. Foram. Research Contr., v. 16, pt. 2, p. 42, pl. 8, figs. 11a–c.

Globigerina ampliapertura Bolli, 1957, U.S. Natl. Mus. Bull. 215, p. 108, pl. 22, figs. 4a–7b.

Globigerina angiporoides angiporoides Hornibrook = *Globigerina angiporoides* Hornibrook, 1965, New Zealand Jour. Geology and Geophysics, v. 8, no. 5, p. 834, figs. 1, 2.

Globigerina brevis Jenkins, 1966, New Zealand Jour. Geology and Geophysics, v. 10, no. 6, p. 1100, fig. 7, nos. 58–63.

Globigerina galavisi Bermúdez, 1961, de Geologia, Caracas, p. 1.183, pl. 4, fig. 3.

Globigerina gortanii gortanii Borsetti = *Globigerina gortanii* Borsetti, 1959, Gior. Geologia (2), v. 27, p. 205–212, pl. 1.

Globigerina gortanii praeturritilina (Blow and Banner) = *Globigerina turritilina praeturritilina* Blow and Banner, 1962, Fundamentals of mid-Tertiary stratigraphical correlation (2), p. 99, pl. XIII, figs. A–C.

Globigerina linaperta Finlay, 1939, Royal Soc. New Zealand Trans., v. 69, pt. 1, p. 125, pl. 23, fig. 54–7.

Globigerina praebulloides Blow, 1959, Bulls. Am. Paleontology, v. 39, no. 178, p. 180, pl. 8, figs. 47a–c; pl. 9, fig. 48.

Globigerina prasaepis Blow, 1969, Internat. Planktonic Conf., 1st Proc., v. 1, p. 382, pl. 10, fig. 13; pl. 18, figs. 3–7.

Globigerina triloculinoides Plummer, 1926, Univ. Texas Bull. 2644, p. 134–135, pl. 8, figs. 10a–c.

Globigerina wilsoni Cole, 1927, Bulls. Am. Paleontology, v. 14, no. 51, p. 34, pl. 4, figs. 8, 9.

Globigerinatheka index index (Finlay) = *Globigerinoides index* Finlay, 1939, Royal Soc. New Zealand Trans., v. 69, pt. 1, p. 125, pl. 14, figs. 85–88.

Globigerinatheka index tropicalis (Blow and Banner) = *Globigerapsis tropicalis* Blow and Banner, 1962, Fundamentals of mid-Tertiary stratigraphic correlation (2), p. 124, 125, pl. XV, figs. D–F.

Globigerinatheka semiinvoluta (Keijzer) = *Globigerinoides semiinvolutus* Keijzer, 1945, Univ. Utrecht Geogr. en Geol. Med., Phys.-Geol. Reeks, ser. 11, no. 6, p. 206, pl. 4, figs. 58a–e.

Globigerinita unicava primitiva Blow and Banner, 1962, Fundamentals of mid-Tertiary stratigraphic correlation (2), p. 114, pl. XIV, figs. J–L.

Globorotalia aragonensis twisselmanni Mallory, 1959, Lower Tertiary Biostratigraphy of the California Coast Ranges, Am. Assoc. Petroleum Geologists, Tulsa, p. 252, pl. 23, fig. 1a–c.

Globorotalia cerroazulensis cerroazulensis (Cole) = *Globigerina cerro-azulensis* Cole, 1928, Bulls. Am. Paleontology, v. 14, no. 53, p. 217, pl. 1, figs. 11–13.

Globorotalia cerroazulensis pomeroli Toumarkine and Bolli, 1970, Rev. Micropaleontologie, v. 13, no. 3, p. 140, pl. I, figs. 10–18.

Globorotalia increbescens (Bandy) = *Globigerina in-*

crebescens Bandy, 1949, Bulls. Am. Paleontology, v. 32, no. 131, p. 120, pl. 23, figs. 3a–c.

Globorotalia insolita Jenkins, 1966, New Zealand Jour. Geology and Geophysics, v. 8, no. 6, p. 1120, fig. 13, no. 113–118.

Globorotaloides suteri Bolli, 1957, U.S. Natl. Mus. Bull. 215, p. 117, pl. 27, figs. 9a–13b.

Guembelitria columbiana Howe = *Gümbelitria columbiana* Howe, 1939, Louisiana Geol. Survey Bull. 14, p. 62, pl. 8, figs. 12, 13.

Hanzawaia americana crassisepta (Cushman and Laiming) = *Cibicides americanus crassiseptus* Cushman and Laiming, 1931, Jour. Paleontology, v. 5, no. 2, p. 119, pl. 14, figs. 7a–c.

Nodosaria latejugata Gumbel, 1868, Beitrage zur Foraminiferenfauna der nordalpinen Eocangebilde, K. Bayer, Akad. Wiss. München, Math.-Physik. Cl., Abh., München, Deutschland, bd. 10 (1870), abt. 2, p. 619.

Nonion ynezianum Kleinpell, 1938, Miocene stratigraphy of California, Am. Assoc. Petroleum Geologists, Tulsa, p. 237, pl. 11, figs. 1, 2.

Pseudohastigerina micra (Cole) = *Nonion micrus* Cole, 1927, Bulls. Am. Paleontology, v. 14, no. 51, p. 22, pl. 5, fig. 12.

Sigmomorphina schencki Cushman and Ozawa, 1930, U.S. Natl. Mus. Proc., v. 77, art. 6, p. 133, pl. 35, figs. 6a, b.

Siphogenerina nodifera Cushman and Kleinpell, 1934, Cushman Lab. Foram. Research Contr., v. 10, pt. 1, p. 13, pl. 2, figs. 15, 16.

Siphogenerina transversa Cushman = *Siphogenerina raphanus transversus* Cushman, 1918, U.S. Natl. Mus. Bull. 103, p. 64, pl. 22, fig. 8.

Truncorotaloides rohri Bronnimann and Bermúdez, 1953, Jour. Paleontology, v. 27, no. 6, p. 818, 819, pl. 87, figs. 7–9.

Uvigerina lodoensis miriamae Mallory, 1959, Lower Tertiary Biostratigraphy of the California Coast Ranges, Am. Assoc. Petroleum Geologists, Tulsa, p. 209, pl. 17, figs. 8a–c, 9a–c; pl. 40. fig. 9.

Uvigerinella sparsicostata Cushman and Laiming, 1931, Jour. Paleontology, v. 5, no. 2, p. 112, pl. 12, figs. 12a, b.

Valvulineria casitasensis Cushman and Laiming, 1931, Jour. Paleontology, v. 5, no. 2, p. 113, pl. 13, figs. 1a–c.

REFERENCES

BANDY, O. L., 1964, Cenozoic planktonic foraminiferal zonation: Micropaleontology, v. 10, p. 1–17.

———, 1972, Late Paleogene-Neogene planktonic biostratigraphy and its geological implications, California: Pacific Coast Miocene Biostratigraphy Symposium, Proc., Pacific Section, S.E.P.M., Bakersfield, Calif., p. 37–51.

BANDY, O. L., and KOLPACK, R. L., 1963, Foraminiferal and sedimentological trends in the Tertiary section of Tecolote Tunnel, California: Micropaleontology, v. 9, p. 117–170.

BANNER, F. T., and BLOW, W. H., 1965, Progress in the planktonic foraminiferal biostratigraphy of the Neogene: Nature, v. 208, p. 1164–1166.

BERGGREN, W. A., 1971, Tertiary boundaries and correlations, *in* The Micropaleontology of Oceans: Cambridge, Cambridge Univ. Press, p. 693–809.

———, 1972, A Cenozoic time-scale—some implications for regional geology and paleobiogeography: Lethaia, v. 5, p. 195–215.

BLOW, W. H., 1969, Late middle Eocene to Recent planktonic foraminiferal biostratigraphy, *in* Bronnimann, P., and Renz, H. H., eds., First Internat. Conf. Planktonic Microfossils, 1st, Geneva, Proc. Leiden: E. J. Brill, v. 1, p. 199–422.

BOLLI, H. M., 1957a, Planktonic Foraminifera from the Oligocene-Miocene Cipero and Lengua Formations of Trinidad, B.W.I.: U.S. Natl. Mus. Bull. 215, p. 97–123.

———, 1957b, Planktonic Foraminifera from the Eocene Navet and San Fernando Formations of Trinidad, B.W.I.: U.S. Natl. Mus. Bull. 215, p. 155–172.

———, 1966, Zonation of Cretaceous to Pliocene marine sediments based on planktonic Foraminifera: Asoc. Venezolana Geologia, Mineria y Petroleo, Bol. Inf., v. 9, p. 3–32.

———, 1972, The genus Globigerinatheka Bronnimann: Jour. Foram. Research, v. 2, p. 109–136.

BRABB, E. E., BUKRY, D., and PIERCE, R. L., 1971, Eocene (Refugian) nannoplankton in the Church Creek Formation near Monterey, central California: U.S. Geol. Survey, Prof. Paper 750-C, p. C44–C47.

BRAMLETTE, M. N., and SULLIVAN, F. R., 1961, Coccolithophorids and related nannoplankton of the early Tertiary in California: Micropaleontology, v. 7, p. 129–174.

BRONNIMANN, P., and BERMÚDEZ, P. W., 1953, Truncorotaloides, a new foraminiferal genus from the Eocene of Trinidad, B.W.I.: Jour. Paleontology, v. 27, p. 817–820.

BUKRY, D., 1973, Low-latitude coccolith biostratigraphic zonation: Deep Sea Drilling Proj., Initial Repts., v. 15, p. 685–703.

———, 1975, Coccolith and silicoflagellate stratigraphy, northwestern Pacific Ocean, Deep Sea Drilling Project Leg 32: Deep Sea Drilling Proj., Initial Repts., v. 32, p. 677–701.

BUKRY, D., BRABB, E. E., and VEDDER, J. G., 1977, Correlation of Tertiary nannoplankton assemblages from the Coast and Peninsular Ranges of California: Cong. Latino-Americano de Geologia, 2nd, Caracas, 1973, Memoria, t. 3, p. 1461–1483.

CAVALIER, C., and POMEROL, C., 1976, Les rapports entre le Bartonien et le Priabonien, Incidence sur la position de la limite Eocene moyen-Eocene supérieur. Soc. Geol. France Compte Rendu, v. 2, p. 49–51.

CUSHMAN, J. A., and SIEGFUS, S. S., 1942, Foraminifera from the type area of the Kreyenhagen Shale of California: San Diego Soc. Natl. History Trans., v. IX, no. 34, p. 385–426.

DIBBLEE, T. W., 1950, Geology of southwestern Santa Barbara County, California: California Div. Mines Bull. 150, p. 1–95.

DONNELLY, A. TIPTON, 1976, The Refugian Stage of the California Tertiary: foraminiferal zonation, geologic history, and correlations with the Pacific Northwest. California Univ. Santa Barbara, unpub. Ph.D. dissert., p. 1–316.

EAMES, F. E., BANNER, F. T., BLOW, W. H., and CLARKE, W. J., 1962, Fundamentals of mid-Tertiary stratigraphical correlation: Cambridge, Cambridge Univ. Press, p. 1–163.

Gibson, J. M., and Steineck, P. L., 1972, Age and correlation of the Ulatisian and Narizian Stages, California: Reply. Geol. Soc. America Bull., v. 83, p. 2225–2232.

Hardenbol, J., and Berggren, W. A., 1978, A new Paleogene numerical time scale: Am. Assoc. Petroleum Geologists, Studies in Geol., no. 6, p. 213–234.

Hornaday, G. R., 1965, An Eocene foraminiferal faunule from the northwestern Santa Ynez Mountains, California: Cushman Found. Foram. Research Contr., v. 16, pt. 1, p. 29–39.

Jenkins, D. G., 1966, Planktonic foraminiferal zones and new taxa from the Danian to Lower Miocene of New Zealand: New Zealand Jour. of Geol. and Geophys., v. 8, p. 1088–1126.

———, 1971, New Zealand Cenozoic planktonic Foraminifera: New Zealand Geol. Survey Paleontology Bull. 42, p. 1–278.

Jenkins, D. G., and Orr, W., 1972, Planktonic foraminiferal biostratigraphy of the eastern equatorial Pacific, Leg 9: Deep Sea Drilling Proj., Initial Repts., v. 8, p. 1059–1193.

Kleinpell, R. M., 1938, Miocene stratigraphy of California: Tulsa, Okla., Am. Assoc. Petroleum Geologists, p. 1–450.

Kleinpell, R. M., and Weaver, D. W., 1963, Oligocene biostratigraphy of the Santa Barbara embayment, California: California Univ. Pub. Geol. Sci., Pt. 1, v. 43, p. 1–77.

Lipps, J. H., 1965, Oligocene in California? Nature, v. 208, p. 885–886.

———, 1967a, Planktonic Foraminifera, intercontinental correlation and age of California mid-Cenozoic microfaunal stages: Jour. Paleontology, v. 41, p. 994–999.

———, 1967b, Miocene calcareous plankton, Reliz Canyon, California: A.A.P.G.-S.E.P.M. Pacific Secs., Guidebook, Oct. 1967, p. 54–60.

———, 1968, Mid-Caenozoic calcareous nannoplankton from western North America: Nature, v. 218, p. 1151–1152.

Lipps, J. H., and Kalisky, M., 1972, California Oligo-Miocene calcareous nannoplankton biostratigraphy and paleoecology: Pacific Coast Miocene Biostratigraphy Symposium, Pacific Sec. S.E.P.M., Proc., Bakersfield, Calif., p. 239–254.

Mallory, V. S., 1959, Lower Tertiary biostratigraphy of the California Coast Ranges: Am. Assoc. Petroleum Geologists, p. 1–416.

Martini, E., 1971, Standard Tertiary and Quaternary calcareous nannoplankton zonation: Internat. Planktonic Conf., 2d, Roma, 1970, Proc., v. II, p. 739–786.

McKeel, D. R., and Lipps, J. H., 1972, Calcareous plankton from the Tertiary of Oregon: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 12, p. 75–93.

———, 1975, Eocene and Oligocene planktonic Foraminifera from the central and southern Oregon Coast Range: Jour. Foram. Research, v. 5, p. 249–269.

McWilliams, R. G., 1972, Age and correlation of the Eocene Ulatisian and Narizian Stages, California: Geol. Soc. America Bull., v. 83, p. 533–534.

Murray, G. E., 1961, Geology of the Atlantic and Gulf Coastal Province of North America: New York, Harper & Bros., p. 1–659.

Phillips, F. J., 1972, Age and correlation of the Eocene Ulatisian and Narizian Stages, California: Discussion: Geol. Soc. America Bull., v. 83, p. 2217–2223.

Poore, R. Z., and Brabb, E. E., 1977, Eocene and Oligocene planktonic foraminifers from the Upper Butano Sandstone and type San Lorenzo Formation, Santa Cruz Mountains, California: Jour. of Foram. Research, v. 7, p. 249–272.

Rau, W. W., 1958, Stratigraphy and foraminiferal zonation in some of the Tertiary rocks of southwestern Washington: U.S. Geol. Survey Oil and Gas Inv. Chart O.C. 57.

———, 1975, Foraminifera and biostratigraphy of the Alsea Formation of western Oregon, *in* Paleogene Symposium and Selected Technical Papers: A.A.P.G., S.E.P.M., S.E.G. Pacific Sec. Joint Ann. Meeting, Long Beach, Calif., p. 409–416.

Rooth, G. H., 1974, Biostratigraphy and paleoecology of the Coaledo and Bastendorff Formations, Southwestern Oregon: Oregon State Univ., unpub. Ph.D. dissert., p. 1–270.

Roth, P. H., 1970, Oligocene calcareous nannoplankton biostratigraphy: Eclogae Geol. Helvetiae, v. 63, p. 879–902.

Schenck, H. G., and Kleinpell, R. M., 1936, Refugian Stage of Pacific Coast Tertiary: Am. Assoc. Petroleum Geologists Bull., v. 20, p. 215–225.

Schmidt, R. R., 1970, Planktonic Foraminifera from the lower Tertiary of California. California Univ. Los Angeles, unpub. Ph.D. dissert.

Steineck, P. L., and Gibson, J. M., 1971, Age and correlation of the Eocene Ulatisian and Narizian Stages, California: Geol. Soc. America Bull., v. 82, p. 477–480.

———, 1972, Age and correlation of the Eocene Ulatisian and Narizian Stages, California: Reply. Geol. Soc. America, v. 83, p. 535–536.

Steineck, P. L., Gibson, J. M., and Morin, R. W., 1972, Foraminifera from the middle Eocene Rose Canyon and Poway Formations, San Diego, California: Jour. Foram. Research, v. 2, p. 137–144.

Stradner, H., 1969, Upper Eocene calcareous nannoplankton from Austria and problems of inter-hemispherical correlation: *in* Bronnimann, P., and Renz, H. H., eds., Proc. Internat. Conf. Planktonic Microfossils, 1st, Geneva, 1967, Proc., E. J. Brill, Leiden, v. 2, p. 663–669.

Sullivan, F. R., 1962, Foraminifera from the type section of the San Lorenzo Formation, Santa Cruz County, California: California Univ. Pub. Geol. Sci., v. 37, p. 233–352.

———, 1965, Lower Tertiary nannoplankton from the California Coast Ranges. II Eocene: California Univ. Pub. Geol. Sci., v. 53, p. 1–53.

Tipton, Ann, 1975, Foraminiferal biostratigraphy of the late Eocene and early Oligocene type Bastendorff Formation, near Coos Bay, Oregon, *in* Paleogene Symposium and Selected Technical Papers: A.A.P.G., S.E.P.M., S.E.G. Pacific Sec. Joint Ann. Meeting, Long Beach, Calif., p. 563–585.

———, 1980, Foraminiferal zonation of the Refugian Stage, uppermost Eocene of California, *in* O. L. Bandy Memorial Volume, Cushman Found. Spec. Pub. No. 19, p. 258–277.

Tipton, A., Kleinpell, R. M., and Weaver, D. W., 1973, Oligocene biostratigraphy, San Joaquin Valley, California: California Univ. Pub. Geol. Sci., v. 105, p. 1–72.

Warren, A. D., and Newell, J. H., 1976, Nannoplankton biostratigraphy of the upper Sacate and Gaviota Formations, Arroyo el Bulito, Santa Barbara County, California (abs): Am. Assoc. Petroleum Geologists Abs. with Programs, Pacific Sections Ann. Meeting, 1976, San Francisco, p. 19–20.

———, and ———, 1977, Calcareous plankton biostratigraphy of the type Bastendorff Formation, southwest Oregon (abs): Geol. Soc. America Abs. with Programs, Ann. Meeting, 1977, Seattle, p. 1217–1218.

Weaver, D. W., and Frantz, J. D., 1967, Re-evaluation of the type Refugian Stage of the Pacific Coast Tertiary (abs): Geol. Soc. America, Cordilleran Sec. Meeting Program, Santa Barbara, Calif., p. 69–70.

Worsley, T. R., and Creceliuss, E., 1972, Paleogene calcareous nannofossils from the Olympic Peninsula, Washington: Geol. Soc. America Bull., v. 83, p. 2859–2862.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 252–257, 1980

BIOSTRATIGRAPHY OF THE LOWER SECTION OF SWEDISH CORE 234 (EQUATORIAL ATLANTIC): PALEOECOLOGY AND AN AGE REASSIGNMENT

BARBARA H. LIDZ[1]
Rosenstiel School of Marine and Atmospheric Science,
University of Miami, Miami, Florida 33149

ABSTRACT

In contrast to the strongly cyclic isotopic record of late Pleistocene deep-sea cores, the isotopic record of earlier deep-sea sediment sections is much more uniform. The first pre-Pleistocene sediment sections analyzed isotopically for paleotemperatures include the lower section of Swedish core 234, previously assigned either a lower-middle Miocene age or an upper Miocene age on the basis of limited foraminiferal studies. Both the oxygen isotopic curve and calcium carbonate percentages reflect a sequence of three stratigraphically distinct units in the core section. Because of the significance of the isotopic results in terms of pre-Pleistocene climate and the paucity of paleontological data from the cursory foraminiferal examinations, a refined micropaleontologic investigation of the core section was carried out for more complete paleoclimatic information. The results confirm that: (1) the lower portion of the core is not as disturbed as previously thought; (2) clearly, three distinct biostratigraphic units are indicated, the bottommost being Pleistocene in age; (3) environment of deposition was tropical and deep-water; (4) the core penetrated through Pleistocene into only Pliocene sediments; (5) species in the fine fraction (<250 μm) are important to a complete faunal study and should not be eliminated from analyses; and (6) pelagic species often exhibit temperature-related trends in distribution, abundance and test morphology.

INTRODUCTION

Oxygen isotope analysis of deep-sea cores (Emiliani, 1955, 1956, 1966, 1978; Shackleton and Opdyke, 1973, 1976) has led to a complete revision of Pleistocene climate. In lieu of the four classical glaciations proposed by Penck and Brückner (1909), a picture has emerged of many, short, intense glaciations alternating with warm interglacials with a quasi-periodicity of approximately 100,000 years. These consistent, strong, quasi-periodic variations are interpreted as an effect of temperature variations and variations in the oxygen isotopic composition of sea water related to glacial/interglacial cycles (Emiliani, 1955, 1958, 1966, 1972, 1978; Shackleton and Opdyke, 1973, 1976). The strong isotopic variations observed in deep-sea sediment sections of Pleistocene age are attenuated in sediment sections older than approximately 3 m.y. (Shackleton and Opdyke, 1977).

Three core sections of presumably Tertiary age were analyzed isotopically by Emiliani (1956). The longest section is the lower portion (702.5 to 1,474.5 cm) of Swedish core 234 (lat. 5°45′N, long. 21°43′W; 3,577 m depth) raised from the Sierra Leone Rise in the eastern equatorial Atlantic. This portion exhibits very small, erratic oxygen isotope variations throughout, in marked contrast to the strong isotopic variations in the upper portion of the same core. The upper portion, 693.5 to 0 cm, consisting of undisturbed sed-

---

[1] Present address: U.S. Geological Survey, Fisher Island Station, Miami Beach, Florida 33139.

iments, was readily assigned a late Pleistocene to Holocene age, ranging from stage 8 to stage 1, on the basis of intercore correlation (Emiliani, 1955). Micropaleontological analysis, based largely on a few pelagic foraminifera, led Phleger and others (1953) to assign a Miocene age, not younger than upper Miocene, to the bottom of core 234. These authors noted, however, the continued presence of modern species throughout the section. They also observed that the section is lithologically more compact and indurated than that above and interpreted the lithologic boundary as an unconformity occurring at approximately 1,100 cm below core top. Emiliani (1956) assigned a lower-middle Miocene age to the same sediments on the basis of selected benthic and pelagic foraminifera. None of the three Tertiary core sections analyzed isotopically by Emiliani (1956) shows significant isotopic variations of the type characteristic of Quaternary cores. This was interpreted as a corollary to absence of glaciation during the time when these core sections were deposited.

In view of the significance of the isotopic data, a more precise investigation of foraminiferal stratigraphy of core 234 was conducted for the purpose of obtaining a clearer picture of the pre-Pleistocene climatic record. Significant progress made in stratigraphic micropaleontology during the past 20 years yielded an additional effect, that the bottom sediments are younger than previously thought, thus leading to an age reassignment to the lower portion of the core.

METHODS

A thorough micropaleontologic examination was conducted initially on a sample (1,412.5–1,414.5 cm) 52 cm from the bottom. A total of 51 species was identified and their stratigraphic ranges determined on the basis of foraminiferal zonations of Parker (1967), Blow (1969), Berggren and Van Couvering (1974), and Stainforth and others (1975). Distribution of those species most diagnostic biostratigraphically was then determined throughout the core section at sedimentary intervals of 10 to 50 cm (Table 1), the closer interval being used when significant changes in faunal assemblages were noted. Each sample was sieved into three size fractions (>500 μm, 250–500 μm, <250 μm) and each fraction was examined separately. An entire sample, ranging from 0.3 to 2.8 grams, was used for the taxonomic study.* Test preservation throughout the core section varied from good to poor, the latter apparently resulting from post-depositional dissolution (i.e., Emiliani, 1955).

Micropaleontological analysis is often restricted to those species present in the coarser size fractions of a sample, a procedure which can lead to biostratigraphic misinterpretation of the faunal assemblage by omission of species whose adult forms occur only in the fine fraction. For instance, as shown in Table 1, some species (e.g., *Globigerina rubescens* and *Globigerinoides tenella*, and others examined from the 1,412.5–1,414.5 cm sample but not listed in the Table, such as *Globigerina bradyi*, *G. decoraperta*, *G. hexagona*, many *Globigerinita* species, and *Globigerinoides bolli*) are present largely or exclusively in the fine fraction. Accurate analysis, therefore, must be directed at close examination of all size fractions, thereby reducing the error and increasing the stratigraphic resolution. Inherent bias, however, exists in fine fraction faunal analyses. Thin-walled forms are often broken, rendering identification impossible, and there is the danger of misidentification of any species whose adult tests are found normally in the coarser fractions (i.e., Stainforth and others, 1975). Micropaleontologic analysis of the fine fraction should be restricted, therefore, to only those species occurring there as adults. Throughout the lower section of core 234, adult specimens of the subspecies *Sphaeroidinellopsis dehiscens immatura*, believed to be restricted in range to Blow's (1969) Zone N19 (upper Pliocene), resemble smaller than adult specimens of *S. dehiscens dehiscens* so closely that no attempt was made to distinguish between the two at the subspecific level.

DISCUSSION

It is evident from Table 1 that the lower section of core 234 is composed of three distinct biostratigraphic units, here referred to as core intervals A (top), B (middle), and C (bottom or basal unit). A Pleistocene fauna (*Globigerinita digitata digitata*, *G. eggeri eggeri*, pink *Globigerinoides rubescens* tests, *G. tenella*, *Globorotalia acostaensis pseudopima*, *G. hirsuta hirsuta*, *G. truncatulinoides*, and *Pulleniatina obliquiloculata finalis*) clearly dominates the pelagic foraminiferal assemblage in core intervals A (702.5–1,099.5 cm) and C (1,452.5–1,474.5 cm). Core interval B (1,132.5–1,444.5 cm), on the other hand, contains a mixture of species with varying ranges: Pliocene to Holocene (*Globigerinoides rubra*, *Pulleniatina obliquiloculata obliquiloculata*, and *Sphaeroidinella dehiscens*); middle Miocene to Holocene (*Globorotalia menardii*); middle and late Pliocene to Pleistocene (*Globigeri-*

---

* Gram weights given exclude specimens of *Globigerinoides sacculifera* and *G. rubra*, which had been removed from all >500 μm and most 250–500 μm size fractions for oxygen isotope analyses. As a result, no quantitative total faunal analysis was undertaken.

noides fistulosa, Globorotalia cultrata exilis, and *G. miocenica*); late Miocene to early Pleistocene (*Globigerinoides obliqua extrema, Globorotalia acostaensis acostaensis,* and *Pulleniatina obliquiloculata primalis*); and from the middle Miocene to the N21/N22 boundary of Blow (1969) (*Globorotalia multicamerata* and *Pulleniatina obliquiloculata praecursor*). Core interval B also includes *flexuosa*-type specimens (of *Globorotalia menardii, G. tumida,* and *G. multicamerata*) and specimens of *G. tosaensis,* whose respective ranges extend from early and late Pliocene into upper and lower Pleistocene. In addition, *Globigerina venezuelana, Globoquadrina altispira altispira, Globorotalia miozea cibaoensis, G. tumida merotumida, Sphaeroidinellopsis seminulina kochi,* and *S. subdehiscens subdehiscens* all occur in this core interval and all have extinction datum levels located at or near the Pliocene-Pleistocene boundary. *Globigerina nepenthes, Globorotalia margaritae,* and *G. tumida plesiotumida* are present and exhibit a middle Pliocene extinction. Two species (*Globoquadrina dehiscens* and *Sphaeroidinellopsis seminulina seminulina*) presumed to become extinct in the upper Miocene also occur, possibly because of redeposition, together with Pleistocene species which apparently have been reworked down the core (i.e., Gartner and Lidz, 1972). This mixing, however, was not sufficiently great to homogenize the sediment; a clear biostratigraphic distinction between the 702.5–1,099.5 cm interval and the 1,132.5–1,444.5 cm unit can still be made (see Table 1).

The presence of a thin unit of Pleistocene sediment at the very base of the core (core interval C: 1,452.5–1,474.5 cm) appears to indicate that the core barrel was dropped back into the sediment immediately after extraction or that the surface sediments of the sea floor were sucked up into the barrel. It should be noted that the basal unit again shows a lower carbonate concentration characteristic of the upper Pleistocene (i.e., Olausson, 1960). A similar trend is shown by oxygen isotopic analysis (Emiliani, 1956).

The fact that many species occurring in the lower portion of core 234 range from within the Miocene into the Pliocene, becoming extinct before the Pleistocene, and that a clear distinction exists between the two major biostratigraphic units (at approximately 1,100 cm below top), is consistent with the theory of a great, worldwide planktonic foraminiferal change during the middle Pliocene (i.e., Blow, 1969; Stainforth and others, 1975, Fig. 22); however, the added effect of an unconformity at 1,100 cm is probable. A Miocene species previously reported from this core as *Sphaeroidinellopsis rutschi* (Phleger and others, 1953; Emiliani, 1956) does not appear distinguishable from mature specimens of *Sphaeroidinellopsis subdehiscens,* a form whose horizon of extinction is unknown, according to Blow (1969), and may well occur within the Pliocene but whose datum is thought by Stainforth and others (1975) to be within the late Miocene near the Miocene/Pliocene boundary. Following the biostratigraphic controls established by Blow (1969) and subsequently used by Berggren and Van Couvering (1974), the coexistence of *Sphaeroidinellopsis* and *Sphaeroidinella* groups, plus the presence of *Globoquadrina altispira altispira,* characterize foraminiferal Zones N19 and N20, which are dated at 4.8 and 3.0 m.y. B.P. (Berggren and Van Couvering, 1974), and continue to occur together throughout the 5 to 3 m.y. B.P. interval. Based on these criteria, therefore, core interval B (1,132.5–1,444.5 cm) appears to be of middle to upper Pliocene age.

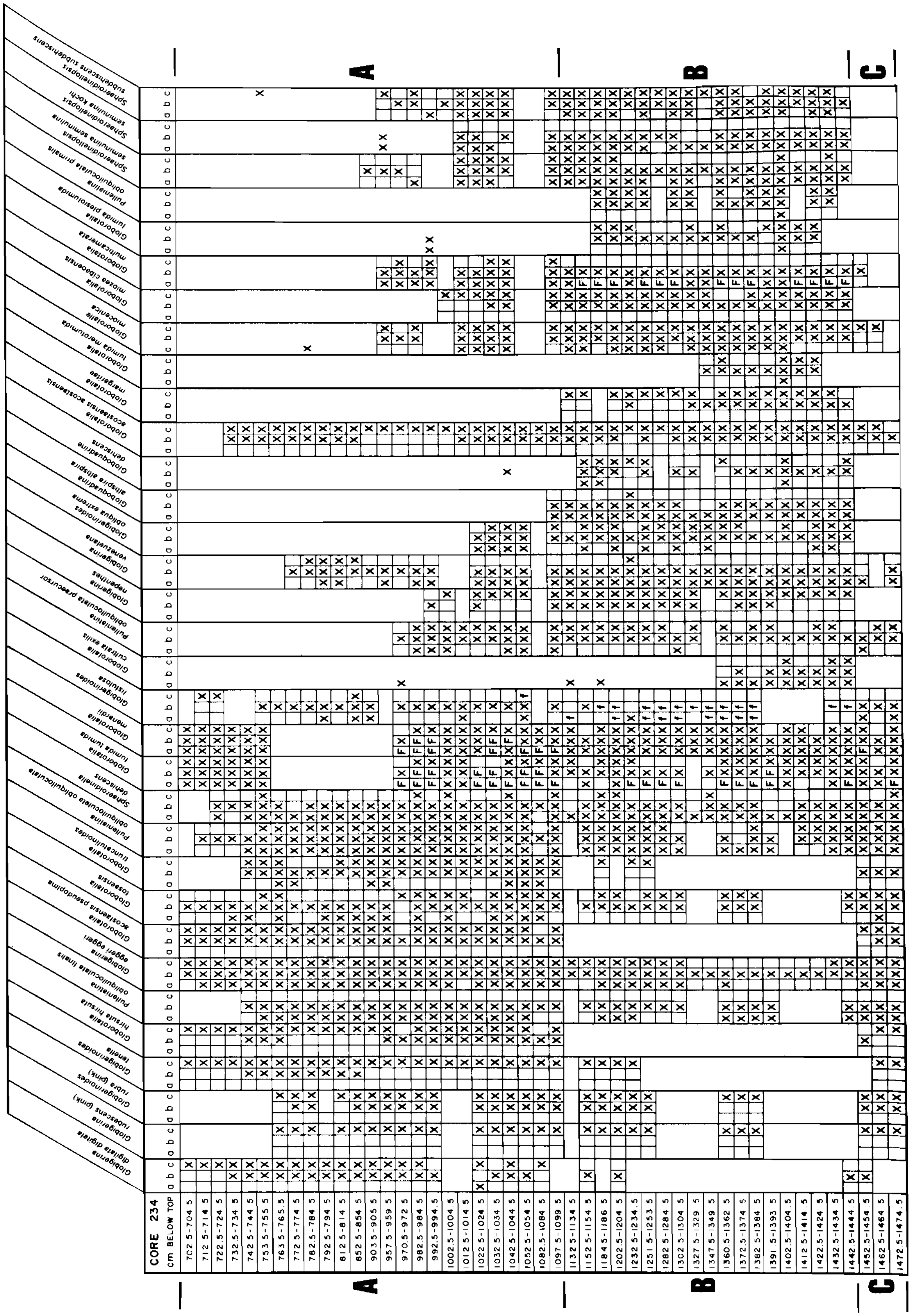
PALEOECOLOGY

Oxygen isotope analyses indicate that slightly more negative values are evident in the interval between 1,150 and 1,450 cm than in the portion between 750 and 1,100 cm (Emiliani, 1956). In addition, the isotopic composition of *Globigerinoides sacculifera/G. rubra* in the section from the bottom of the core to 702.5 cm is intermediate between glacial and interglacial values. This would indicate a temperature of about 2°C lower than today, but still quite tropical, as is also shown by the continued presence of such warm-water species as *Pulleniatina obliquiloculata* and *Sphaeroidinella dehiscens.* The *Globorotalia menardii* group, on the oth-

→

TABLE 1

Biostratigraphy of lower section of Swedish core 234: 33 stratigraphically significant species and their presence (X) or absence (blank) from 1,474.5 cm (total depth) to 702.5 cm below top of core. Core interval A of Pleistocene age; core interval B of middle to upper Pliocene age; core interval C of Pleistocene age. (a) >500 μm size fraction; (b) 250–500 μm size fraction; (c) <250 μm size fraction. *Globigerinoides fistulosa*: (f) highly spinose; (X) very lightly spinose, often identifiable with certain specimens of *G. sacculifera. Globorotalia menardii, G. multicamerata,* and *G. tumida tumida*: (F) *flexuosa*-type; (X) non-*flexuosa* type.


A
B
C
Sphaeroidinellopsis subdehiscens
Sphaeroidinellopsis seminulina kochi
Sphaeroidinellopsis seminulina seminulina
Pulleniatina primalis
Globorotalia plesiotumida
Globorotalia multicamerata
Globorotalia cibaoensis
Globorotalia miozea
Globorotalia miocenica
Globorotalia merotumida
Globorotalia margaritae
Globorotalia acostaensis acostaensis
Globoquadrina dehiscens
Globoquadrina altispira altispira
Globigerinoides obliqua extrema
Globigerina venezuelana
Globigerina nepenthes
Pulleniatina obliquiloculata praecursor
Globorotalia exilis
Globorotalia cultrata
Globigerinoides fistulosus
Globorotalia menardii
Globorotalia tumida
Sphaeroidinella dehiscens
Pulleniatina obliquiloculata
Globorotalia truncatulinoides
Globorotalia tosaensis
Globorotalia acostaensis pseudopima
Globigerina eggeri eggeri
Pulleniatina obliquiloculata finalis
Globorotalia hirsuta hirsuta
Globigerinoides tenella
Globigerinoides rubra (pink)
Globigerina rubescens (pink)
Globigerina digitata digitata
a b c
X
F
CORE 234
cm BELOW TOP
702.5-704.5
712.5-714.5
722.5-724.5
732.5-734.5
742.5-744.5
753.5-755.5
763.5-765.5
772.5-774.5
782.5-784.5
792.5-794.5
812.5-814.5
852.5-854.5
903.5-905.5
957.5-959.5
970.5-972.5
982.5-984.5
992.5-994.5
1002.5-1004.5
1012.5-1014.5
1022.5-1024.5
1032.5-1034.5
1042.5-1044.5
1052.5-1054.5
1082.5-1084.5
1097.5-1099.5
1132.5-1134.5
1152.5-1154.5
1184.5-1186.5
1202.5-1204.5
1232.5-1234.5
1251.5-1253.5
1282.5-1284.5
1302.5-1304.5
1327.5-1329.5
1347.5-1349.5
1360.5-1362.5
1372.5-1374.5
1382.5-1384.5
1391.5-1393.5
1402.5-1404.5
1412.5-1414.5
1422.5-1424.5
1432.5-1434.5
1442.5-1444.5
1452.5-1454.5
1462.5-1464.5
1472.5-1474.5

er hand, is conspicously absent between 763.5 and 959.5 cm, a clear example of nonlinear response by a major foraminiferal group to environmental parameters. Analogous nonlinear responses by the same group occur in the Gulf of Mexico (Kennett and Huddleston, 1972, Fig. 1) and in the Atlantic-Caribbean during warm stages 15 and 13 (Emiliani, 1964).

Benthic species identified randomly throughout the core section are deep-water forms (1,000–4,000 m or deeper; Bock, pers. comm., 1973).

Oxygen isotope values for the lower portion of core 234 show small (0.5 per mil) but well defined oscillations on a trend which indicates that sediment and/or coring disturbances were not sufficiently large to randomize this parameter (or other parameters, such as coarse fraction percentages, foraminiferal trends, etc.). From the point of view of faunal composition, the following observations are made:

1. Specimens of *Globigerina digitata digitata* are morphologically well developed in interval A, whereas the species is largely absent in interval B.
2. The warm-water species, *Sphaeroidinella dehiscens* and *Pulleniatina obliquiloculata,* are abundant between 750 and 900 cm, whereas the deep-water form, *Globorotalia tumida,* is absent.
3. Between 750 and 900 cm, specimens of *Globorotalia crassaformis* are large and abundant, number of chambers in the final coil is relatively high (5–6), and the periphery ranges from relatively acute to partially carinate, all parameters morphologically characteristic of warm temperatures in the Pleistocene (i.e., Emiliani, 1969; Lidz, 1972).
4. Both the *Globorotalia miocenica/G. multicamerata* and *G. tumida* groups exhibit strong changes in flexed *versus* non-flexed morphotypes; these variations do not appear to be correlated to each other within the two groups.
5. The fistulose characteristic of *Globigerinoides fistulosa* is strongly more developed in interval B than in the overlying interval A.
6. Of particular significance is the abundance of abnormal specimens, both benthic and pelagic, in the lowest 1 m of Pleistocene interval A (1,012–1,097 cm); neither the isotope nor the coarse fraction percentages indicate any significant gradient or change. The cause of the high incidence of abnormality remains, therefore, unknown.

Altogether, it appears that temperatures remained above the winter threshold for *Sphaeroidinella* and *Pulleniatina* species throughout interval B. This observation and the trend of the isotopic curve suggest that while winter temperatures may have been similar to those of today, summer temperatures may have been a few degrees centigrade lower. Present-day annual temperatures in the equatorial Atlantic range from 24.4° to 29.4°C (U.S. Naval Hydrographic Office, 1967). Isotopic temperatures for core 234 vary from 21.0° to 25.5°C (Emiliani, 1956) for the lower section discussed herein.

CONCLUSIONS

The lower portion of core 234 (702.5–1,474.5 cm) consists of three different biostratigraphic units: core interval A (top) of Pleistocene age (702.5–1,099.5 cm), core interval B (middle) of middle to late Pliocene age (1,132.5–1,444.5 cm), and core interval C (base), again of Pleistocene age (1,452.5–1,474.5 cm). This three-part division is borne out by oxygen isotope and calcium carbonate percentages. In addition to pelagic foraminiferal species characteristic of the three units mentioned, Pleistocene and Miocene species are present in the Pliocene interval, causing the appearance of disturbed sediments. Uniformity of the isotope curve and gradational trends in variation of foraminiferal parameters, however, are consistent with undisturbed sediments. Mixing apparently occurred during core sampling and was such that further differentiation of the three intervals into specific zones was not possible. The presence of *Sphaeroidinellopsis* and *Sphaeroidinella* species, along with *Globoquadrina altispira altispira,* which characterizes foraminiferal Zones N19 and N20 dated at 4.8 and 3.0 m.y. B.P., is good evidence that the core penetrated Pliocene and not Miocene sediments. Benthic species throughout the core section indicate a depositional environment of 1,000–4,000 m or greater.

The warm-water species, *Pulleniatina obliquiloculata obliquiloculata* and *Sphaeroidinella dehiscens,* remain abundant in the lower portion of the core, providing corroborative evidence for a tropical (but 2°C cooler than today) environment of deposition as determined by oxygen isotopic analysis. On the other hand, the warm-water *Globorotalia menardii* group is absent between 763.5 and 959.5 cm, indicating a nonlinear response by this group to environmental parameters.

Detailed examination of the fine (<250 μm) fraction of sediments precludes overlooking those species whose adult tests occur largely or exclusively in the fine fraction. In some cases, even in Quaternary and especially in Tertiary sediments, such pelagic species are good age indices and would otherwise be missed.

Applied to mature tests of selected species of pelagic foraminifera with respect to isotopic temperature variations, evolutionary changes and/or adaptations of test growth and structure, species abundance and distribution often are a reflection of changes in paleoenvironment. In core 234 selected species adapted to tropical waters demonstrate sensitivity to paleotemperature changes. Their variations in morphology, however, are not as pronounced as those exhibited by species adapted to higher latitudes, where glacial/interglacial temperature amplitudes are greater.

The basal 22 cm of Pleistocene sediment, which appear to underlie the older Pliocene interval, were probably artificially introduced into the core barrel upon extraction from the sea floor. This could have been accomplished by dropping the barrel back into the surface sediment or by suction upon extraction, causing sea floor sediment to "flow into" the barrel and be retained.

ACKNOWLEDGMENTS

Critical reviews and comments from J. Kennett, J. Ingle, E. Vincent and C. W. Poag are gratefully acknowledged. Particular thanks are extended to C. Emiliani for his continuing guidance, support and patience. Financial support was provided by National Science Foundation Grant OCE 23299. This research is a contribution from the Division of Marine Geology and Geophysics, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149.

REFERENCES

BERGGREN, W., and VAN COUVERING, J., 1974, The Late Neogene—biostratigraphy, geochronology and paleoclimatology of the last 15 million years in marine and continental sequences: Developments in Paleontology and Stratigraphy, 2: Amsterdam, Elsevier, 216 p.

BLOW, W. H., 1969, Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy: Internat. Conf. Planktonic Microfossils, 1st, Geneva, 1967, Proc., v. 1, 422 p.

EMILIANI, C., 1955, Pleistocene temperatures: Jour. Geology, v. 63, p. 538–578.

———, 1956, Oligocene and Miocene temperatures of the equatorial and subtropical Atlantic Ocean: Jour. Geology, v. 64, p. 281–288.

———, 1958, Paleotemperature analysis of core 280 and Pleistocene correlations: Jour. Geology, v. 66, p. 264–275.

———, 1964, Paleotemperature analysis of the Caribbean cores A254-BR-C and CP-28: Geol. Soc. America, Bull., v. 75, p. 129–144.

———, 1966, Paleotemperature analysis of Caribbean cores P6304-8 and P6304-9 and a generalized temperature curve for the past 425,000 years: Jour. Geology, v. 74, p. 109–126.

———, 1969, A new paleontology: Micropaleontology, v. 15, p. 265–300.

———, 1972, Quaternary paleotemperatures and the duration of the high temperature intervals: Science, v. 178, p. 398–401.

———, 1978, The cause of the ice ages: Earth and Planetary Sci. Letters, v. 37, p. 349–354.

GARTNER, S., and LIDZ, B., 1972, Reworking and apparent reworking of Neogene fossil plankton: Micropaleontology, v. 18, p. 115–118.

KENNETT, J. P., and HUDDLESTON, P., 1972, Abrupt climatic change at 90,000 Yrs BP: faunal evidence from Gulf of Mexico cores: Jour. Quaternary Research, v. 2, p. 384–395.

LIDZ, B., 1972, *Globorotalia crassaformis* morphotype variations in Atlantic and Caribbean deep-sea cores: Micropaleontology, v. 18, p. 194–211.

OLAUSSON, E., 1960, Description of sediment cores from the North Atlantic: Swedish Deep-Sea Exped. Repts., v. 7, p. 244–245.

PARKER, F. L., 1967, Late Tertiary biostratigraphy (planktonic foraminifera) of tropical Indo-Pacific deep-sea cores: Am. Paleontology Bull., v. 52, p. 115–208.

PENCK, A., and BRÜCKNER, E., 1909, Die Alten im Eiszeitalter: Leipzig, Tauchnitz, 1199 p.

PHLEGER, F. B., PARKER, F. L., and PEIRSON, J. F., 1953, North Atlantic foraminifera: Swedish Deep-Sea Exped. Repts., v. 7, p. 83–86.

SHACKLETON, N., and OPDYKE, J., 1973, Oxygen-isotope and paleomagnetic stratigraphy of equatorial Pacific core V28-238: oxygen isotope temperatures and ice volumes on a 10^5 year and 10^6 year scale: Jour. Quaternary Research, v. 3, p. 39–55.

———, 1976, Oxygen-isotope and paleomagnetic stratigraphy of Pacific core V28-239: Late Pliocene to Latest Pleistocene: Geol. Soc. America Mem. 145, p. 449–464.

———, 1977, Oxygen-isotope and paleomagnetic evidence for early northern hemisphere glaciation: Nature, v. 270, p. 216–219.

STAINFORTH, R. M., LAMB, J. L., LUTERBACHER, H., BEARD, J. H., and JEFFORDS, R. M., 1975, Cenozoic planktonic foraminiferal zonation and characteristics of index forms: Kansas Univ. Paleont. Contr., Art. 62, 425 p.

U.S. NAVAL HYDROGRAPHIC OFFICE, 1967, Oceanographic Atlas of the North Atlantic Ocean. Section II. Physical Properties: U.S. Naval Oceanog. Office, Pub., no. 700, 300 p.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 258–277, 1980

FORAMINIFERAL ZONATION OF THE REFUGIAN STAGE, LATEST EOCENE OF CALIFORNIA

ANN TIPTON
Resource Associates of Alaska, Inc., 5926 McIntyre St., Golden, Colorado 80401

ABSTRACT

The Refugian Stage of California contains two Oppelian zones, the *Valvulineria tumeyensis* Zone in the lower Refugian, and the *Uvigerina vicksburgensis* Zone in the upper Refugian. The *V. tumeyensis* Zone consists of the *Cibicides haydoni* Subzone, below, and the *Uvigerina atwilli* Subzone, above.

The Refugian Stage is equivalent to the *Globorotalia cerroazulensis* planktonic foraminiferal zone of Bolli (1957, 1966), and to the *Isthmolithus recurvus* Subzone of the *Discoaster barbadiensis* calcareous nanoplankton Zone of Bukry (1973, 1975), NP19 and NP20 of Martini (1971; see Warren and Newell, 1980).

The present zonation for the Refugian Stage is applicable to all known areas of California and the California borderland, as well as southern Oregon. Refugian foraminiferal faunas of northern Oregon and Washington are very similar in overall faunal content, but in details of faunal sequence differ sufficiently to be recognized as belonging to a separate Refugian biogeographic *subprovince*, within which the zonation of Rau (1958, 1966) is used instead.

INTRODUCTION

The foraminiferal "zones" previously used to subdivide the Refugian Stage in California are inadequately defined or purely local biostratigraphic units and are herein replaced by Oppelian zones (see Berry, 1966, 1968). The latter are based on faunal analysis, throughout the biogeographic province, of sequences representing numerous biofacies and paleoenvironments, to determine a succession of *diagnostic congregations* of fossils. The zones based on these faunal congregations are anchored in both time and space by accurately defined type sections.

The succession of congregations defining zones is independent of ecologic facies to the extent that faunas representing a wide range of biofacies and paleoenvironments, including a range of water depths, have been utilized in determining the succession.

In actuality, the range of these factors that has been considered is sometimes far from perfect. In the case of the Refugian Stage in California, deep-water forms predominate among the known benthic foraminiferal faunas, nearly to the exclusion of neritic assemblages (Donnelly, 1976), so that neritic forms are less well represented in the zonal congregations than are bathyal and deeper forms.

Downslope displacement and differences in rates of sedimentation also have the potential to affect appearances and extinctions of individual species or of assemblages in the stratigraphic record, but these factors are unlikely to disrupt the *successions* of rigorously defined zonal congregations from place to place. A discussion of the various physical and biological factors during sedimentation that affect the accumulation and preservation of fossils is beyond the scope of this paper, but they nonetheless are to be recognized as playing a role in further complicating the already complex task of paleontological correlations at the zonal level.

TABLE I

Primary references to foraminiferal data for the Refugian Stage in California. Locations of areas 1 through 9 are shown on Figure 1.

AREA	FORMATION	REFERENCE
1. Western Santa Ynez Mountains	Uppermost Sacate and Gaviota	Wilson (1954); Kleinpell and Weaver (1963); Donnelly (1976)
2. Santa Lucia Mountains	Church Creek	Waters (1963), Dickinson (1965)
3. San Juan Bautista	San Juan Bautista and (?) Pinecate	Castro (1967); Clark and Rietman (1973)
4. Santa Cruz Mountains	San Lorenzo	Sullivan (1962); Fairchild and others (1969); Smith (1971)
5. Sacramento Valley subsurface	"Markley Gorge fill"	Almgren and Schlax (1957)
6. Mount Diablo area of Contra Costa County	Kirker	Kleinpell (1938; Zemorrian microfauna); Refugian mollusks treated in Primmer (1964)
7. Diablo Range and subsurface	Tumey	Cushman and Simonson (1944); Phillips and others (1974); Donnelly (1976)
8. Temblor Range and subsurface	Wagonwheel ("Oceanic sand" and "Tumey shale" of subsurface)	Smith (1956); Tipton and others (1973)
9. San Emigdio Range and subsurface	upper San Emigdio and lower Pleito	Delise (1967); Tipton and others (1973)

Oppelian zonation of the Refugian Stage has lagged with respect to that of California's stages of the older Eocene (zonation of Mallory, 1959) and of the Oligocene and Miocene (Kleinpell, 1938) because of the scarcity of continuously microfossiliferous marine sequences through the Refugian interval. Lying above the Narizian and below the Zemorrian Stages, the Refugian is typically represented in California's outcrops by continental deposits (Sespe, Vasquez, Plush Ranch, Simmler Formations), non-foraminiferal, shallow-water marine beds (e.g., Alegria Formation) or hiatus. These features are indicative of regression of seas or uplift of source areas throughout much of western California during Refugian time.

The present zonation is based on analysis of the distribution of foraminiferal species in every known Refugian outcrop sequence (see Table 1 and Fig. 1) and in numerous subsurface sequences of onshore and offshore California. Details of each area, its foraminiferal taxonomy, biofacies, paleoenvironments, a discussion of Refugian paleogeography and of correlations to Refugian sequences in the Pacific Northwest are available in Donnelly (1976).

EOCENE OR OLIGOCENE?

The present study does not attempt to treat fully the controversial question of the Eocene-Oligocene boundary in the California sequence of stages. According to the usage of workers such as Kleinpell and Weaver (1963), it most probably falls somewhere *within* the Refugian Stage, whereas many planktonic microfossil specialists (e.g., Warren and Newell, 1976, 1980) place it at the top of the Stage. A full discussion of this subject is not presented here. Weaver and Tipton (1972) discussed the theoretical difficulties involved in pinpointing, at a stage or zonal level of refinement, the series-epoch boundaries of the Tertiary. Boundaries were never defined by Lyell in his designation of the Eocene or Miocene; the Oligocene of von Beyrich, defined for a time interval between the two, involves serious problems of correlation both at the top and the bottom of its type sequence in Europe.

These correlation problems are magnified in making long-distance correlations across the boundaries of zoogeographic provinces. In each region, usages inevitably differ for different groups of taxa, because the times of best-defined evolutionary change in one group do not necessarily coincide with those of another group. The molluscan faunas of the Refugian Stage bear closest affinities to the Eocene (e.g., the large venericards of the *Turritella variata* fauna; see Weaver and Kleinpell, 1963, p. 118). The benthic foraminiferal faunas of the Refugian Stage have notable elements in common with benthic faunas of the upper Jackson and Vicksburg Groups, lithogenetic units long considered of upper Eocene and Oligocene age. Recent correlations on the basis of the chronologically diagnostic nannoplankton of the *Isthmolithus recurvus* Subzone (A. D. Warren, pers. comm., 1975, and War-

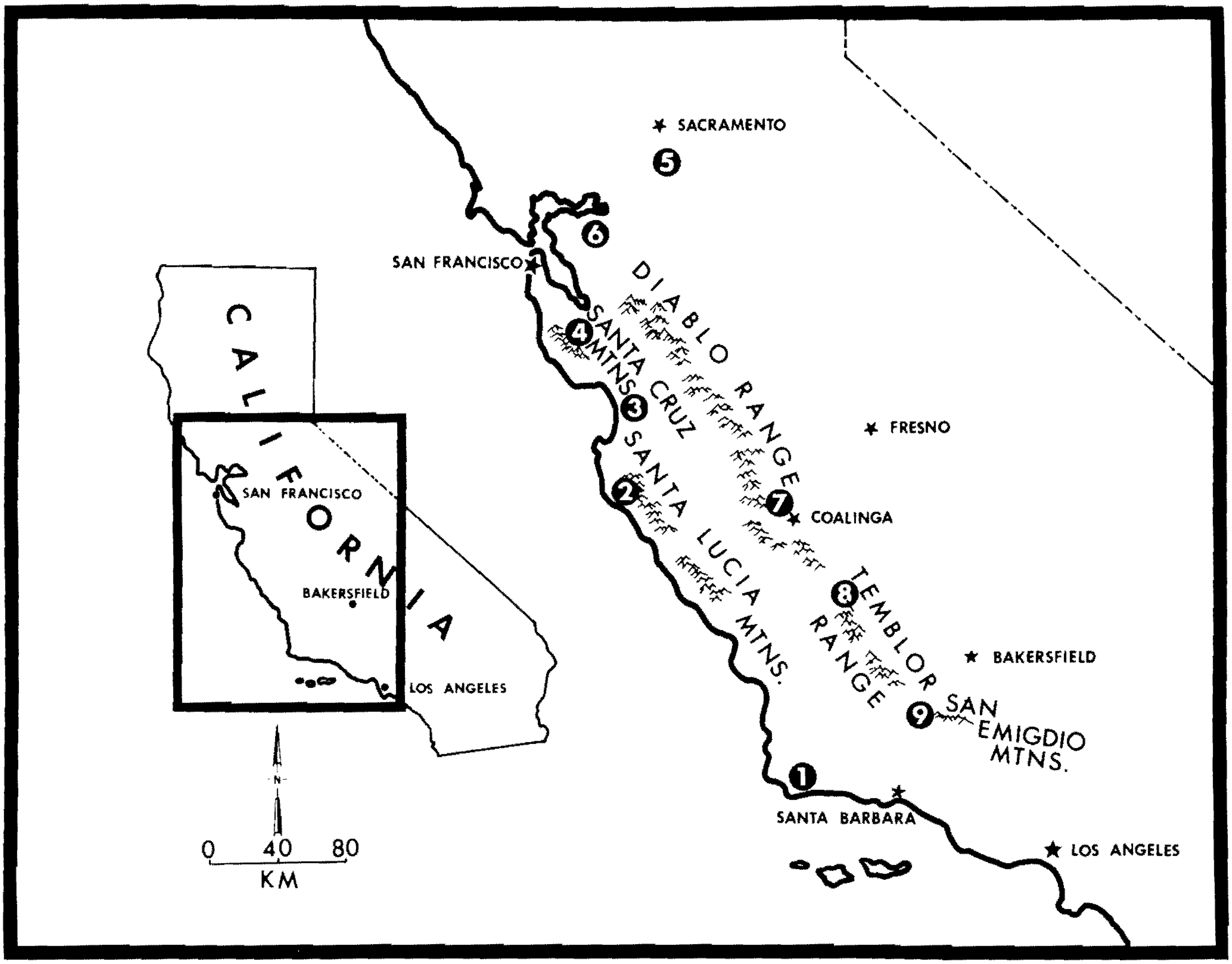


FIGURE 1
Primary areas of occurrence of Refugian foraminiferal sequences in California. Numbers 1 through 9 refer to Table 1.

ren and Newell, 1976) link the Refugian Stage of California with a portion of the upper Jackson Group that Warren regards as Eocene, but whether the upper Jackson Group is entirely Eocene, or perhaps partially Oligocene, is itself open to controversy.

The placing of the Eocene-Oligocene boundary within the context of the California provincial stages thus inevitably involves interpretation that varies both according to the group of organisms considered and the individual usage. To place it at all at the stage or zone level of refinement is falsely accurate, but is done nonetheless in order to relate California sequences generally with those of other regions. The usage followed here, based primarily on the general affinities of the *Turritella variata* molluscan assemblages, is that of uppermost Eocene age for the entire Refugian Stage.

PREVIOUS WORK

Schenck and Kleinpell (1936, p. 219) named the Refugian Stage of the West Coast for "the rocks deposited after the strata usually included with the Tejon (restricted) Formation were laid down and before the Zemorrian age . . . ." They left the Stage unsubdivided into Zones "until a more finely drawn control over the faunal sequence has been established" (p. 221).

Cushman and Simonson (1944) described the Refugian foraminiferal succession in cores of the Seaboard

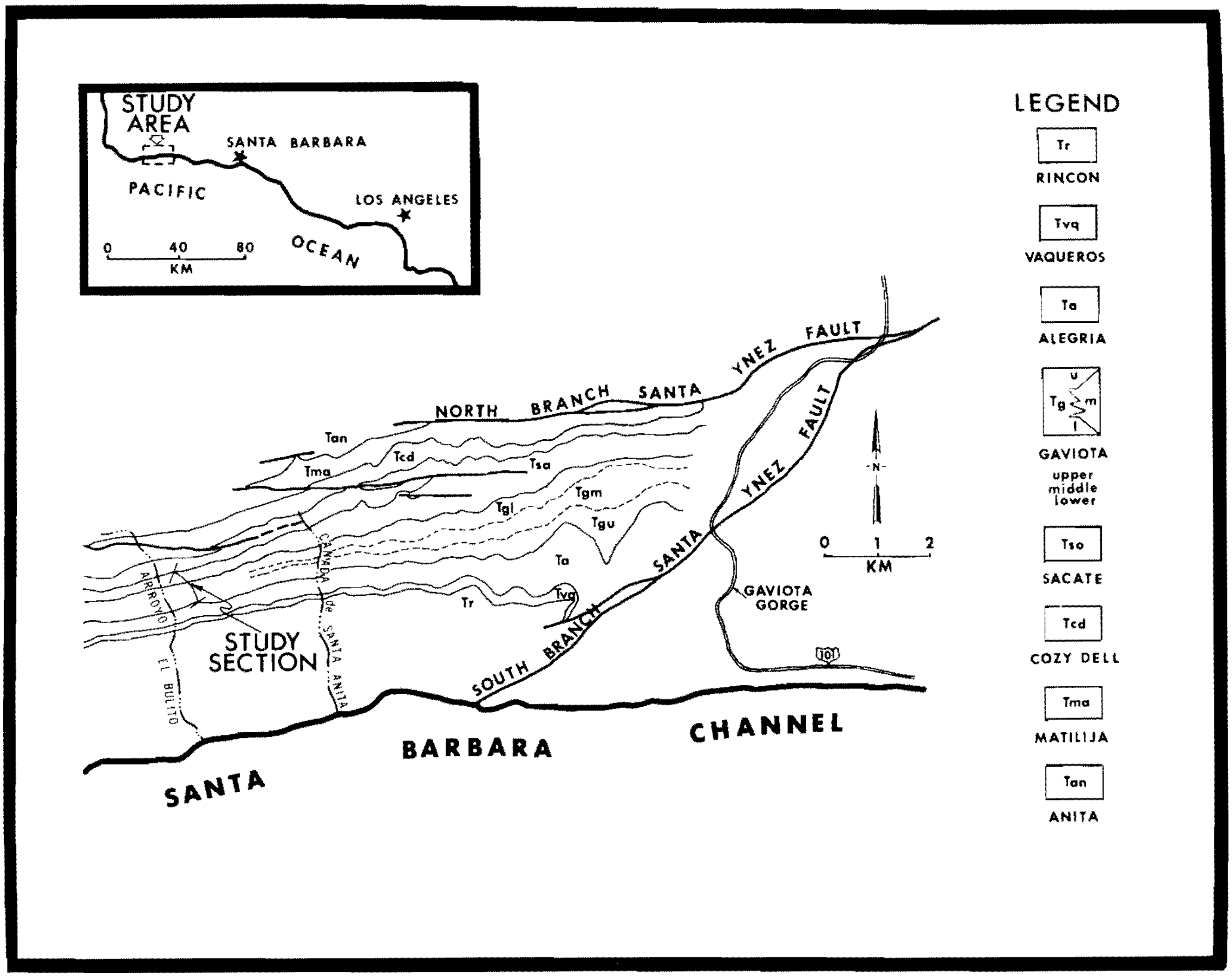


FIGURE 2

Geologic setting of collected section, Sacate and Gaviota Formations, Arroyo el Bulito, western Santa Ynez Mountains, California. Geology from Dibblee (1950) and Kleinpell and Weaver (1963).

Welch #1 Well near the type Tumey Formation (Atwill, 1935) of the Diablo Range in central California. Beneath the Zemorrian and younger faunas of the subsurface Temblor Formation, they distinguished three foraminiferal "zones" within the Tumey interval: the "*Leda* Zone," the "*Uvigerina cocoaensis* Zone" and the "Transition Zone." Beneath the latter, faunas of the Kreyenhagen Shales indicated definite pre-Refugian age.

The "zones" of Cushman and Simonson would, by present usage, be termed *zonules* (Fenton and Fenton, 1928), purely local biostratigraphic units that are not necessarily significant in terms of age.

Kleinpell and Weaver (1963, pp. 32–33) proposed tentatively that an upper Refugian *Uvigerina vicksburgensis* Zone is typified by occurrences of *Uvigerina vicksburgensis* in the "*Leda* Zone" of Cushman and Simonson (1944), in addition to the earliest occurrences of *Cassidulina galvinensis*, *Eponides kleinpelli*, *Uvigerina gallowayi*, and others.

In local investigations of Refugian sections in California (Table 1), the "*Uvigerina cocoaensis* Zone" of Cushman and Simonson (1944) and the tentative *Uvigerina vicksburgensis* Zone of Kleinpell and Weaver (1963) have commonly been used as lower and upper Refugian zonal subdivisions, respectively. Their use in regional biochronology has led to confusion and miscorrelations because they lack faunal criteria for

TABLE 2

Known occurrences of selected foraminiferal taxa in upper Narizian, Refugian, and lower Zemorrian Stages of California (+x = occurs lower than upper Narizian; x+ = occurs higher than lower Zemorrian).

TABLE 2

Continued.

STAGE	NARIZIAN	REFUGIAN			ZEMORRIAN
ZONE	A. jenkinsi	Valvulineria tumeyensis		Uvigerina vicksburgensis	U. gallowayi
SUBZONE		C. haydoni	U. atwilli		
Alabamina kernensis	x	x	x	x	
Anomalina californiensis	x	x	x	x	x+
Bifarina eleganta	+x				
Bolivina basisenta	x				
Bolivina jacksonensis	x	x	x	x	
Bolivina jacksonensis var. tumeyensis		x	x	x	
Bolivina marginata				x	x+
Bulimina corrugata	+x				
Bulimina schencki		x	x	x	
Bulimina sculptilis	+x	x	x	x	
Cancris joaquinensis	x		x	x	
Cassidulina galvinensis				x	
Cibicides cushmani	+x				
Cibicides elmaensis				x	x+
Cibicides haydoni		x	x	x	
Cibicides hodgei	x	x	x	x	
Cibicides natlandi	+x				
Cibicides pseudoungerianus var. evolutus	x	x	x	x	x+
Cibicidoides coalingensis	+x		x	x	
Dentalina consobrina	+x	x	x	x	x+
Eggerella elongata	+x				
Eggerella subconica	+x	x			
Epistomina eocenica	+x	x	x	x?	
Eponides gaviotaensis	+x		x	x	
Eponides kleinpelli				x	x+
Eponides mansfieldi var. oregonensis			x		x
Eponides yeguaensis	+x		x		
Globocassidulina globosa	+x	x	x	x	
Globocassidulina margareta				x	x+
Gyroidina condoni	+x	x	x	x	x+
Guttulina irregularis	x	x	x	x	x?
Lenticulina chirana	+x	x?	x		
Lenticulina welchi	+x				
Nonion planatum	+x			x	
Planularia tolmani	x	x	x		
Plectofrondicularia garzaensis	x	x	x	x	
P. packardi var. multilineata	+x	x	x	x	x
P. packardi var. packardi	x	x	x	x	
P. packardi var. robusta		x	x	x	
P. vaughani	x		x	x	x+
P. vokesi	x	x	x	x	
Pseudohastigerina micra	+x	x	x		
Spiroloculina wilcoxensis	+x	x	x	x	
Tritaxilina colei	+x	x	x		x+
Uvigerina atwilli			x	x	
Uvigerina cocoaensis			x	x	
Uvigerina gallowayi				x	x+
Uvigerina gardnerae	x	x	x	x?	
Uvigerina garzaensis	+x	x	x	x	
Uvigerina garzaensis var. nudorobusta	+x	x			
Uvigerina jacksonensis			x	x	
Uvigerina kernensis				x	x+
Uvigerina vicksburgensis				x	
Vaginulinopsis saundersi	+x		x		
Valvulineria jacksonensis var. welcomensis	+x	x			
Valvulineria menloensis				x	
Valvulineria tumeyensis	+x	x	x		
Vulvulina curta	+x	x	x		

recognition verified throughout the province, and because no type sections have been designated where superpositional and faunal relationships are clearly exemplified. Tipton, Kleinpell, and Weaver (1973, p. 20) emphasized the need for definition of Refugian zones and suggested tentative faunal criteria for the eventual designation of three such units.

NEW ZONATION

The zonation presented here is generalized from detailed foraminiferal investigations in each known area of Refugian occurrence in California (Table 1 and Donnelly, 1976). Biostratigraphic ranges of species in two important sections are newly published here (from Donnelly, 1976), first, the upper Sacate and Gaviota Formations at Arroyo el Bulito, western Santa Ynez Mountains (Figs. 2–5), and, second, the Kreyenhagen and Tumey Formations of the Seaboard Welch #1 Well (Figs. 6, 7; first reported by Cushman and Simonson, 1944) in the foothills of the Diablo Range

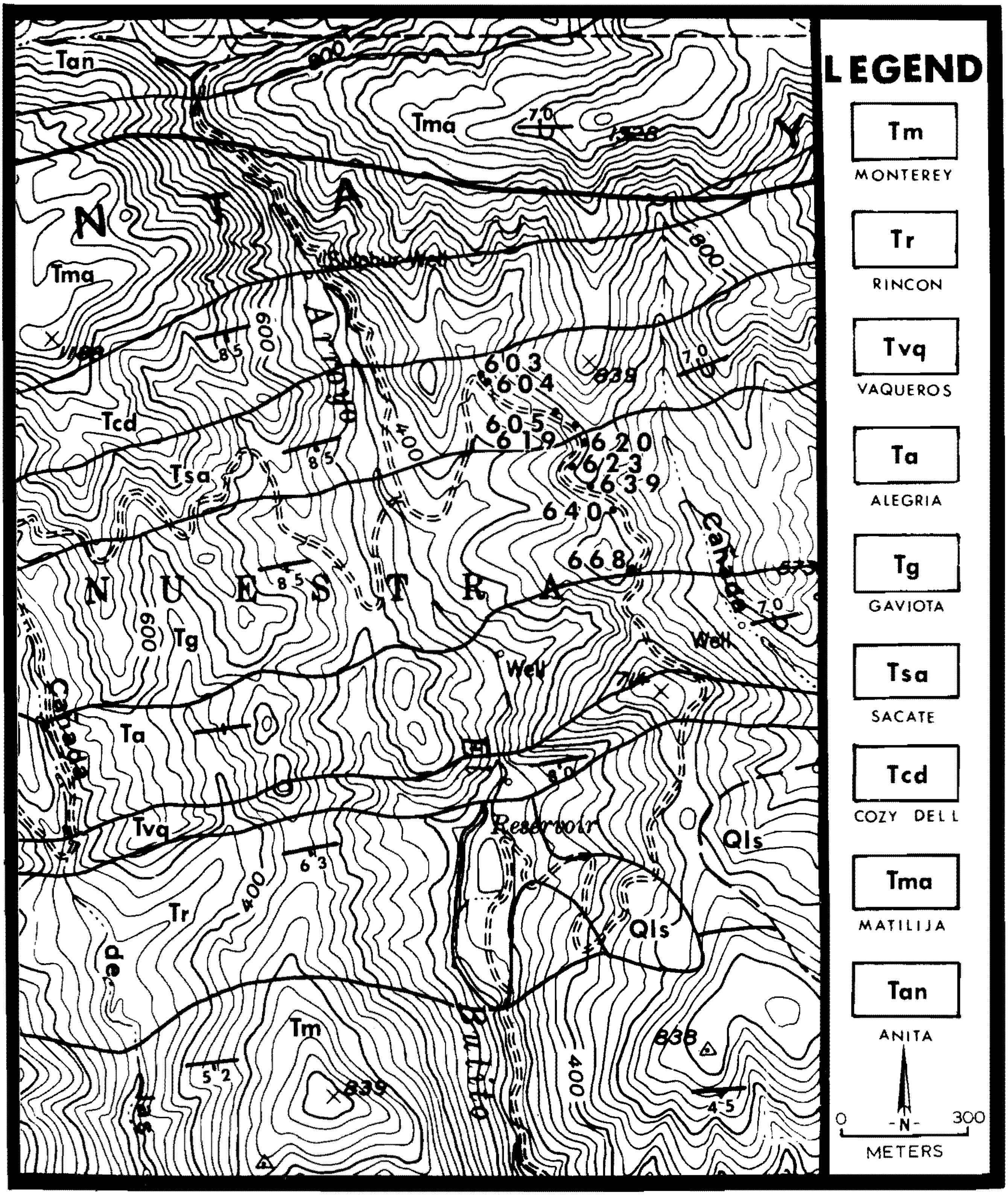
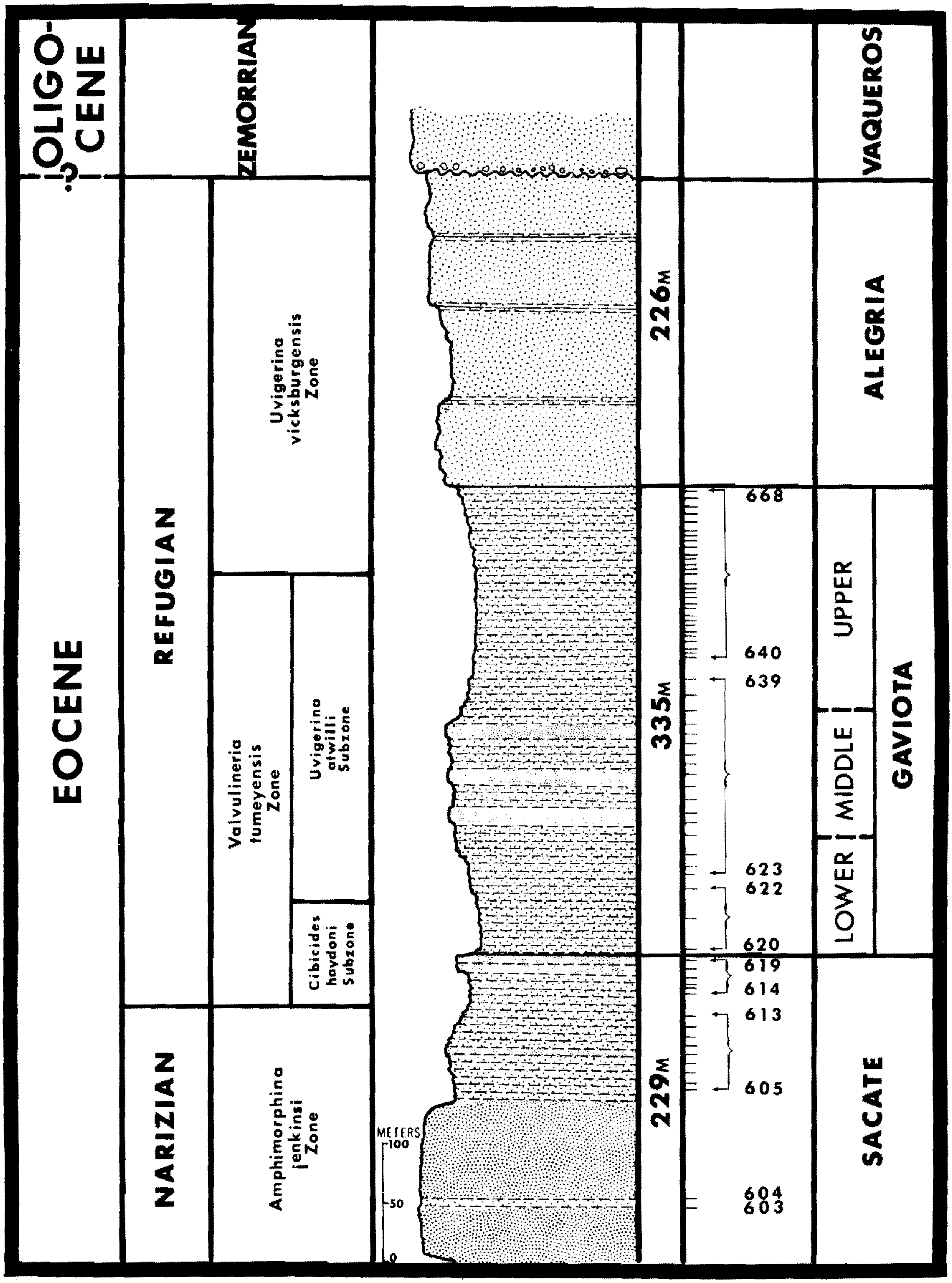


FIGURE 3

Location of University of California, Santa Barbara, microfossil localities 603 through 668, inclusive, Sacate and Gaviota Formations, Arroyo el Bulito, Sacate 7½′ U.S.G.S. Topographic Quadrangle. Geology from Dibblee (1950).


OLIGO-CENE
?
EOCENE
ZEMORRIAN
REFUGIAN
NARIZIAN
Uvigerina vicksburgensis Zone
Valvulineria tumeyensis Zone
Uvigerina atwilli Subzone
Cibicides haydoni Subzone
Amphimorphina jenkinsi Zone
METERS
100
50
0
226M
335M
229M
668
640
639
623
622
620
619
614
613
605
604
603
VAQUEROS
ALEGRIA
UPPER
MIDDLE
LOWER
GAVIOTA
SACATE

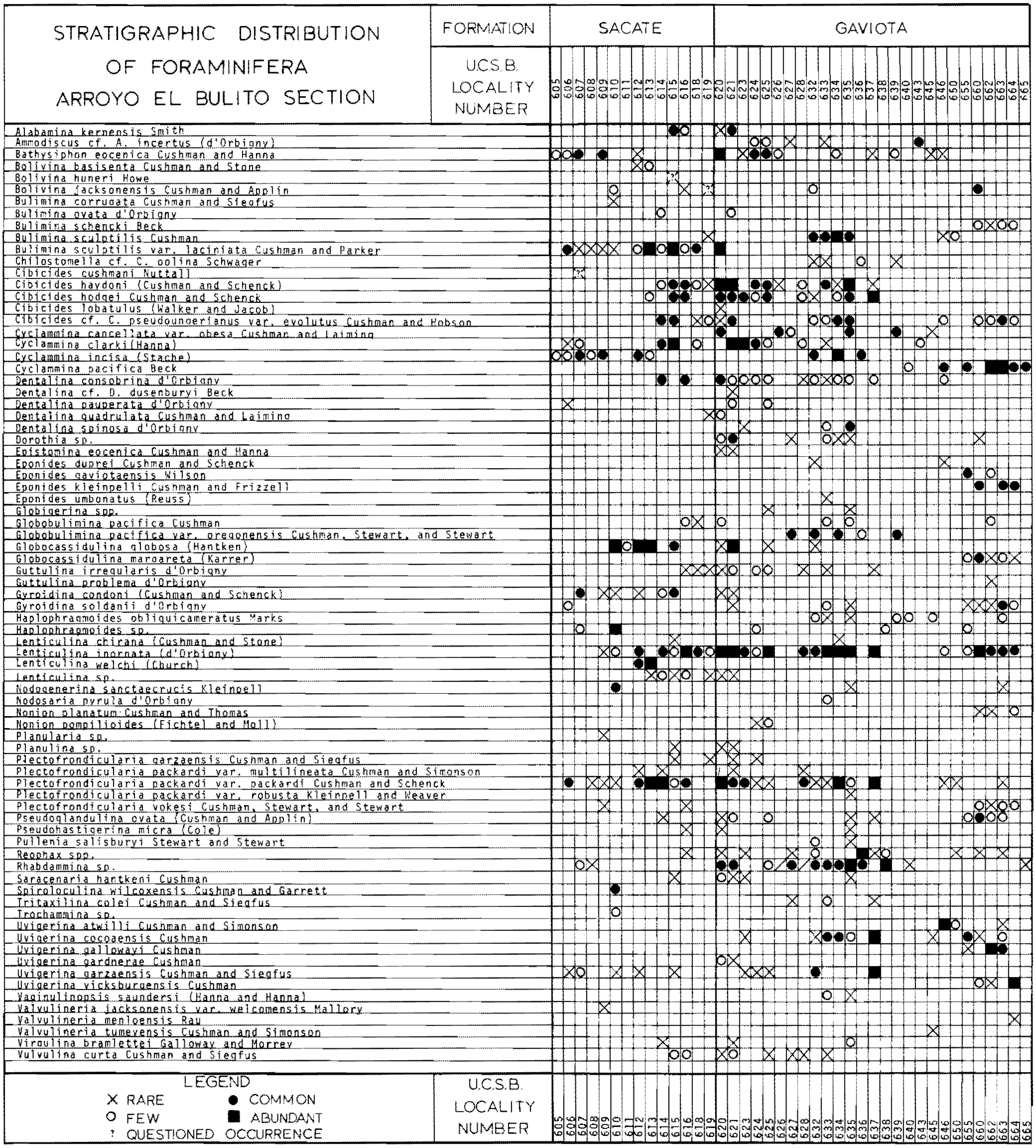


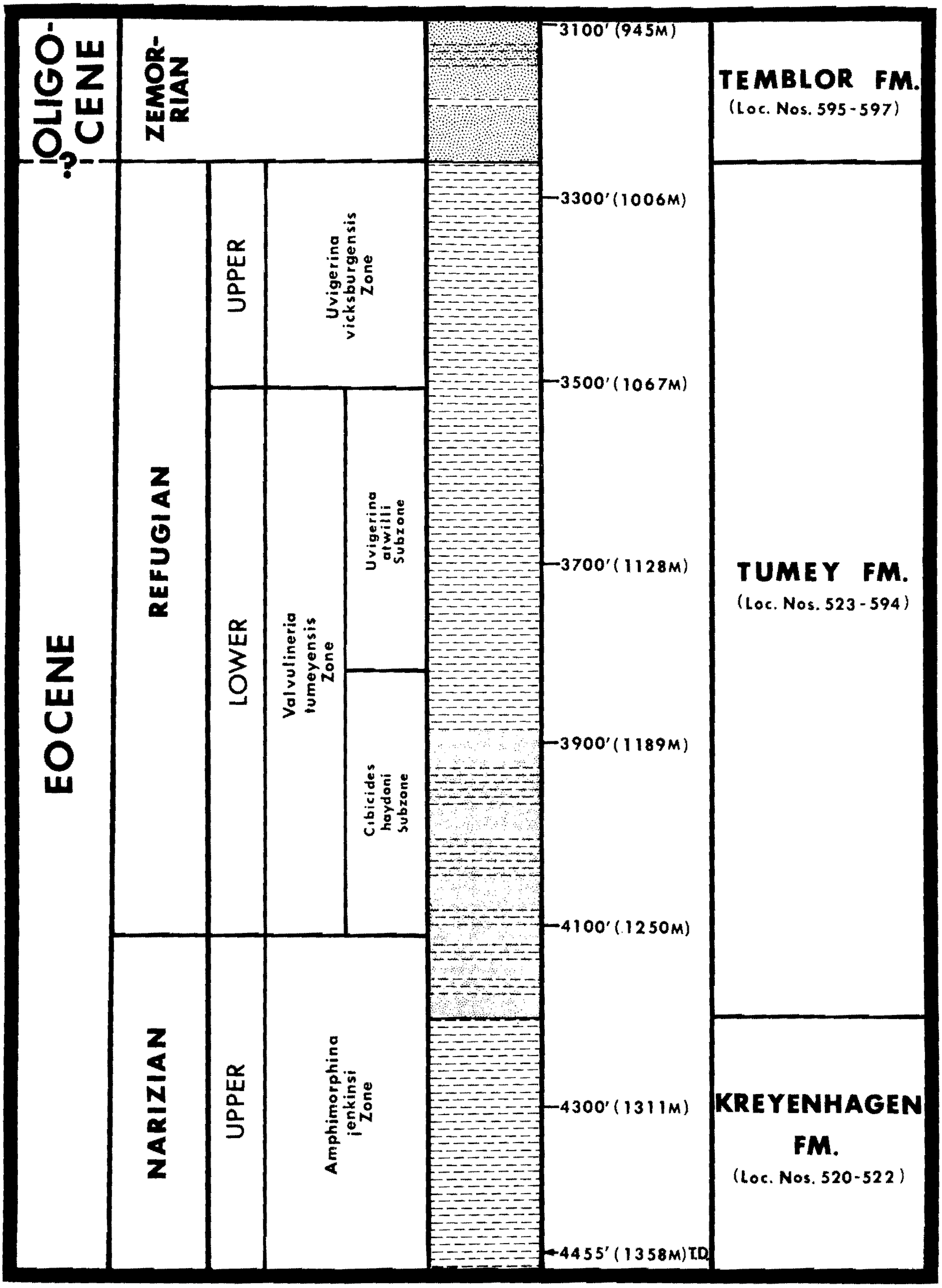
FIGURE 5

Stratigraphic distribution of Foraminifera, Arroyo el Bulito, from Donnelly (1976).

←

FIGURE 4

Stratigraphic distribution and Stage-Zone assignments of microfossil localities 603 through 668, inclusive, Sacate and Gaviota Formations, Arroyo el Bulito. Lithologies and thicknesses modified from Kleinpell and Weaver (1963, Fig. 8).


OLIGO-CENE
?
EOCENE
ZEMOR-RIAN
REFUGIAN
NARIZIAN
UPPER
LOWER
UPPER
Uvigerina vicksburgensis Zone
Valvulineria tumeyensis Zone
Uvigerina atwilli Subzone
Cibicides haydoni Subzone
Amphimorphina jenkinsi Zone
3100' (945M)
3300' (1006M)
3500' (1067M)
3700' (1128M)
3900' (1189M)
4100' (1250M)
4300' (1311M)
4455' (1358M) T.D.
TEMBLOR FM.
(Loc. Nos. 595-597)
TUMEY FM.
(Loc. Nos. 523-594)
KREYENHAGEN FM.
(Loc. Nos. 520-522)

north of Coalinga (see Fossil Localities). These sections provide dominantly fine-grained and nearly continuous foraminiferal sequences from the upper Narizian to the upper Refugian.

The stratigraphy and structure of the Arroyo el Bulito area are fully treated in Dibblee (1950) and Kleinpell and Weaver (1963). The nonforaminiferal Alegria Formation, which overlies the Gaviota at Arroyo el Bulito, is considered to be mainly, probably entirely, Refugian on the basis of its mollusks (Weaver and Kleinpell, 1963; Weaver and Frantz, 1967).

SUBJACENT NARIZIAN STAGE

Strata of the Narizian Stage (Mallory, 1959) underlie marine strata of the Refugian Stage with no apparent break in sedimentation in the western Santa Ynez Mountains (Sacate, Coldwater, and Gaviota Formations), in the Santa Cruz Mountains (San Lorenzo Formation), along the west side of the San Joaquin Valley (Kreyenhagen, Tumey, and Wagonwheel Formations), and on the southern border of the Great Valley (San Emigdio Formation). A similar Narizian-Refugian foraminiferal continuum is also to be found in the type Bastendorff Formation of southern Oregon (Tipton, 1975).

The upper limit of the Narizian Stage is defined in California by the highest stratigraphic occurrences of: *Amphimorphina jenkinsi* (Church), *Bifarina eleganta* (Plummer), *Bolivina basisenta* Cushman and Stone, *Bulimina microcostata* Cushman and Parker, *Bulimina corrugata* Cushman and Siegfus, *Cibicides natlandi* Beck, *Cibicides cushmani* Nuttall, *Lenticulina welchi* (Church), and *Eggerella elongata* Blaisdell.

The many other taxa listed by Mallory (1959, pp. 60–61) also become extinct at or near the end of the Narizian Age. However, as shown on Table 2, the following forms previously cited by Mallory as extinct near the end of the Narizian have since been found in Refugian assemblages: *Eponides yeguaensis* Weinzierl and Applin, *Nonion planatum* Cushman and Thomas, *Plectofrondicularia vokesi* Cushman, Stewart, and Stewart, *Lenticulina chirana* (Cushman and Stone), *Tritaxilina colei* Cushman and Siegfus, *Uvigerina garzaensis* var. *nudorobusta* Mallory, *Valvulineria jacksonensis* var. *welcomensis* Mallory, and *Vulvulina curta* Cushman and Siegfus. These taxa are thus no longer diagnostic of pre-Refugian age.

REFUGIAN STAGE

The Refugian Stage in California is here subdivided into two Oppelian zones, the *Valvulineria tumeyensis* Zone in the lower Refugian, and the *Uvigerina vicksburgensis* Zone in the upper Refugian. The *Valvulineria tumeyensis* Zone consists of the *Cibicides haydoni* Subzone in its lower part, and the *Uvigerina atwilli* Subzone in its upper part.

VALVULINERIA TUMEYENSIS ZONE

The *Valvulineria tumeyensis* Zone has its type locality at Arroyo el Bulito, western Santa Ynez Mountains (Figs. 2–5), in the uppermost Sacate Formation and all but the uppermost 61 meters of the overlying Gaviota Formation. The type section includes localities 614 to 654 of the present study; assemblages of localities 646 to 654 are zonally nondiagnostic or barren, but are arbitrarily included in the *V. tumeyensis* Zone because they lack the faunal criteria for younger age. The top of the *V. tumeyensis* Zone at Arroyo el Bulito is drawn below Sample 655, which is the lowest sample of diagnostically upper Refugian age.

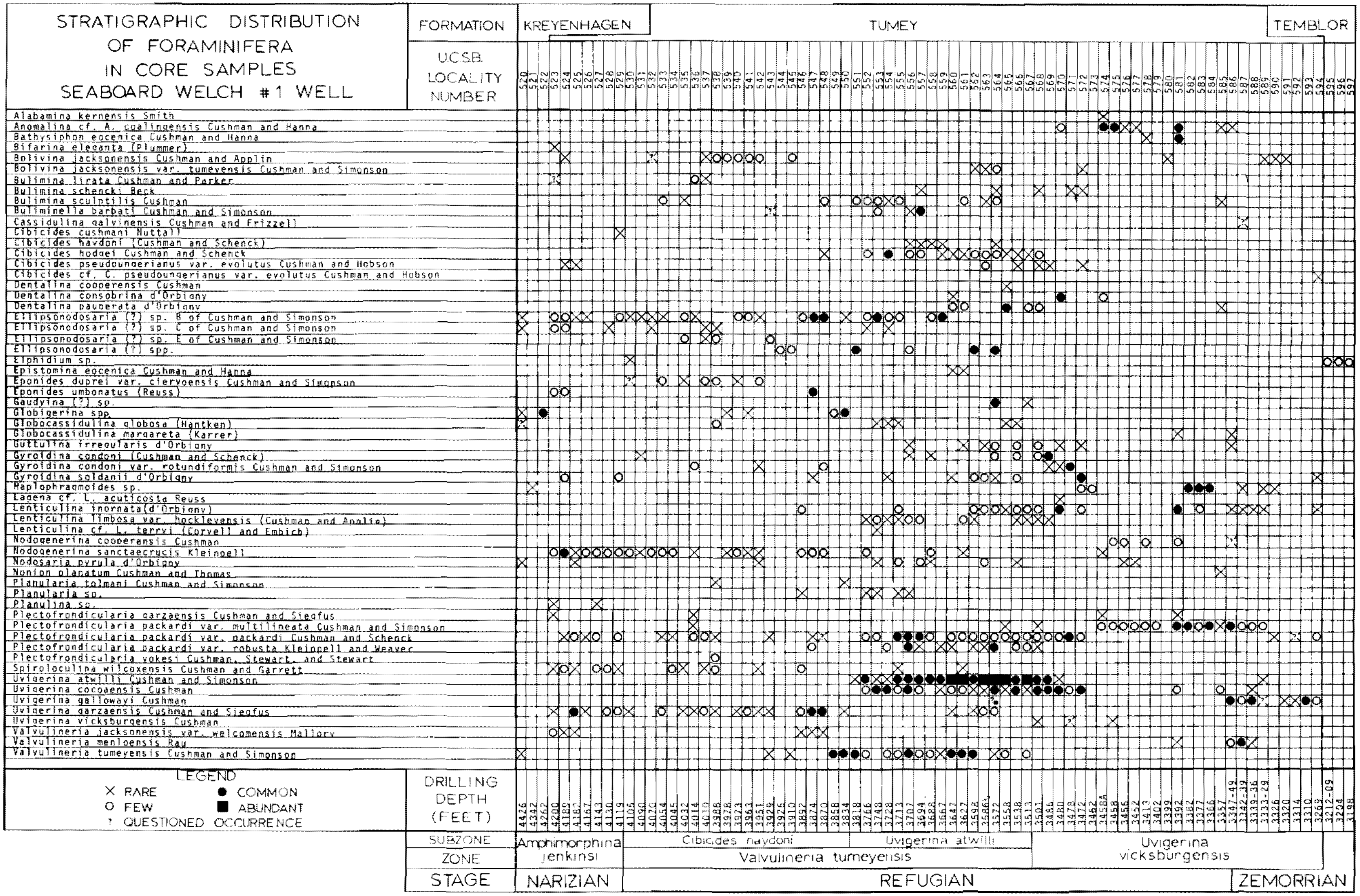
Faunas representative of this zone are also found within the type San Lorenzo Formation (samples B-2251 and B-2252 of Sullivan, 1962), the type Tumey Formation (see "lower Refugian" of Phillips, Tipton, and Watkins, 1974), the subsurface Tumey (Localities 530–568, Seaboard Welch #1 Well, this study), the type Wagonwheel Formation (lowermost 5 samples, Smith, 1956, Fig. 3), the subsurface Wagonwheel (see Tipton and others, 1973, Texaco Tulare Well section), and subsurface San Emigdio and Pleito Formations (see "lower Refugian," Texas P.U.P. #1 Well section, Tipton and others, 1973, Fig. 4).

The *Valvulineria tumeyensis* Zone is defined by the earliest occurrences of *Bolivina jacksonensis* var. *tumeyensis* Cushman and Simonson, *Cibicides haydoni* (Cushman and Schenck), and *Plectofrondicularia packardi* var. *robusta* Kleinpell and Weaver, and the highest occurrences of *Valvulineria tumeyensis* Cushman and Simonson, *Eponides yeguaensis* Weinzierl and Applin, *Lenticulina chirana* (Cushman and Stone), *Planularia tolmani* Cushman and Simonson, *Vaginulinopsis saundersi* (Hanna and Hanna), *Vulvulina curta* Cushman and Siegfus, and possibly *Uvigerina gardnerae* Cushman (occurs questionably in up-

←

FIGURE 6

Lithology and age of cored study interval, Seaboard Welch #1 Well, Fresno County, California.


STRATIGRAPHIC DISTRIBUTION OF FORAMINIFERA IN CORE SAMPLES SEABOARD WELCH #1 WELL

per Refugian). Of the planktonic species, *Pseudohastigerina micra* (Cole) and *Globigerinatheka index tropicalis* (Blow and Banner) have their highest known occurrences in this zone (Warren and Newell, 1980).

Two subzones are recognizable within the *Valvulineria tumeyensis* Zone, herein designated the *Cibicides haydoni* Subzone, below, and the *Uvigerina atwilli* Subzone, above.

Cibicides haydoni Subzone. This subzone is best represented at its type locality, Arroyo el Bulito, in samples 614 through 621 of the uppermost Sacate and lowermost Gaviota Formations. It is also recognizable faunally in the type San Lorenzo Formation (localities B-2251 and 2252 of Sullivan, 1962, and possibly sample B-4356 of Fairchild, Wesendunk, and Weaver, 1969), in the subsurface Tumey Formation (localities 530–550, Seaboard Welch #1 Well section, this study) and the subsurface San Emigdio Formation (localities D-4251, 4252, Texas P.U.P. #1 Well section, Tipton and others, 1973).

This lowermost Refugian Subzone is defined by the earliest occurrences of the relatively few taxa defining the base of the Refugian Stage and the *Valvulineria tumeyensis* Zone: *Cibicides haydoni* (Cushman and Schenck), *Plectofrondicularia packardi* var. *robusta* Kleinpell and Weaver, and *Bolivina jacksonensis* var. *tumeyensis* Cushman and Simonson in association with the highest occurrences of *Uvigerina garzaensis* var. *nudorobusta* Mallory, *Valvulineria jacksonensis* var. *welcomensis* Mallory, and *Eggerella subconica* Parr.

The Uvigerina atwilli Subzone. This subzone also has its type locality at Arroyo el Bulito, where it is represented by samples 623 through 654, spanning all but the lowermost and uppermost beds of the Gaviota Formation. It also is known to occur in subsurface equivalents of the Gaviota Formation beneath the Santa Barbara Channel. The subzone almost certainly occurs within the type San Lorenzo Formation (lower Rices Mudstone Member), though neither Sullivan (1962) nor Fairchild, Wesendunk, and Weaver (1969) report assemblages diagnostic of it. It is represented at Monocline Ridge, Fresno County, by much if not all of the "lower Refugian" Tumey of Phillips, Tipton, and Watkins (1974), and it is found in the nearby subsurface between depths 3,818′ (1,157 m) and 3,513′ (1,064 m) of the Seaboard Welch #1 Well. Much of the *Uvigerina cocoaensis* "zone" of Cushman and Simonson (1944) is referable to the *Uvigerina atwilli* Subzone.

The lowermost five assemblages checklisted from the type Wagonwheel Formation by H. P. Smith (1956, Fig. 3) are typical of this subzone, and Smith's single sample from the underlying Welcome Member, Kreyenhagen Formation, is also referable to it. It occurs within the subsurface equivalents of the middle Wagonwheel and lowermost Pleito Formations, southwestern San Joaquin Valley, typically localities D-4324 through 4335 and D-4253 of Tipton, Kleinpell, and Weaver (1973, Figs. 7 and 8, respectively).

The *Uvigerina atwilli* Subzone is defined by the lowest known occurrences of *Uvigerina atwilli* Cushman and Simonson, *Uvigerina cocoaensis* Cushman, *Uvigerina jacksonensis* Cushman, and *Eponides mansfieldi* var. *oregonensis* Cushman, Stewart and Stewart in conjunction with the highest occurrences of *Valvulineria tumeyensis* Cushman and Simonson, *Eponides yeguaensis* Weinzierl and Applin, *Lenticulina chirana* (Cushman and Stone), *Planularia tolmani* Cushman and Simonson, *Vaginulinopsis saundersi* (Hanna and Hanna), *Vulvulina curta* Cushman and Siegfus, and ?*Uvigerina gardnerae* Cushman.

UVIGERINA VICKSBURGENSIS ZONE

Kleinpell and Weaver (1963, p. 42) proposed a tentative zone of this name, constituting the upper portion of the Refugian Stage, but they could not at that time define the faunal criteria for recognizing it. They implied that the zone is best typified by the upper part of the Seaboard Welch #1 Well sequence, the "*Leda* zone" of Cushman and Simonson (1944).

The present study has confirmed the tentative zone of Kleinpell and Weaver essentially as originally conceived. For this reason, it seems unnecessary to search for a new zonal name, and the term *Uvigerina vicksburgensis* Zone is herein maintained, constituting an upper Refugian Substage.

Late Refugian time was characterized by the initiation of uplift and local folding on the borders of many of California's marine basins. Where strata of *Uvigerina vicksburgensis* age occur, an unconformity or disconformity is common, often truncating them, though

←

FIGURE 7

Stratigraphic distribution of Foraminifera, Seaboard Welch #1 Well (from Donnelly, 1976).

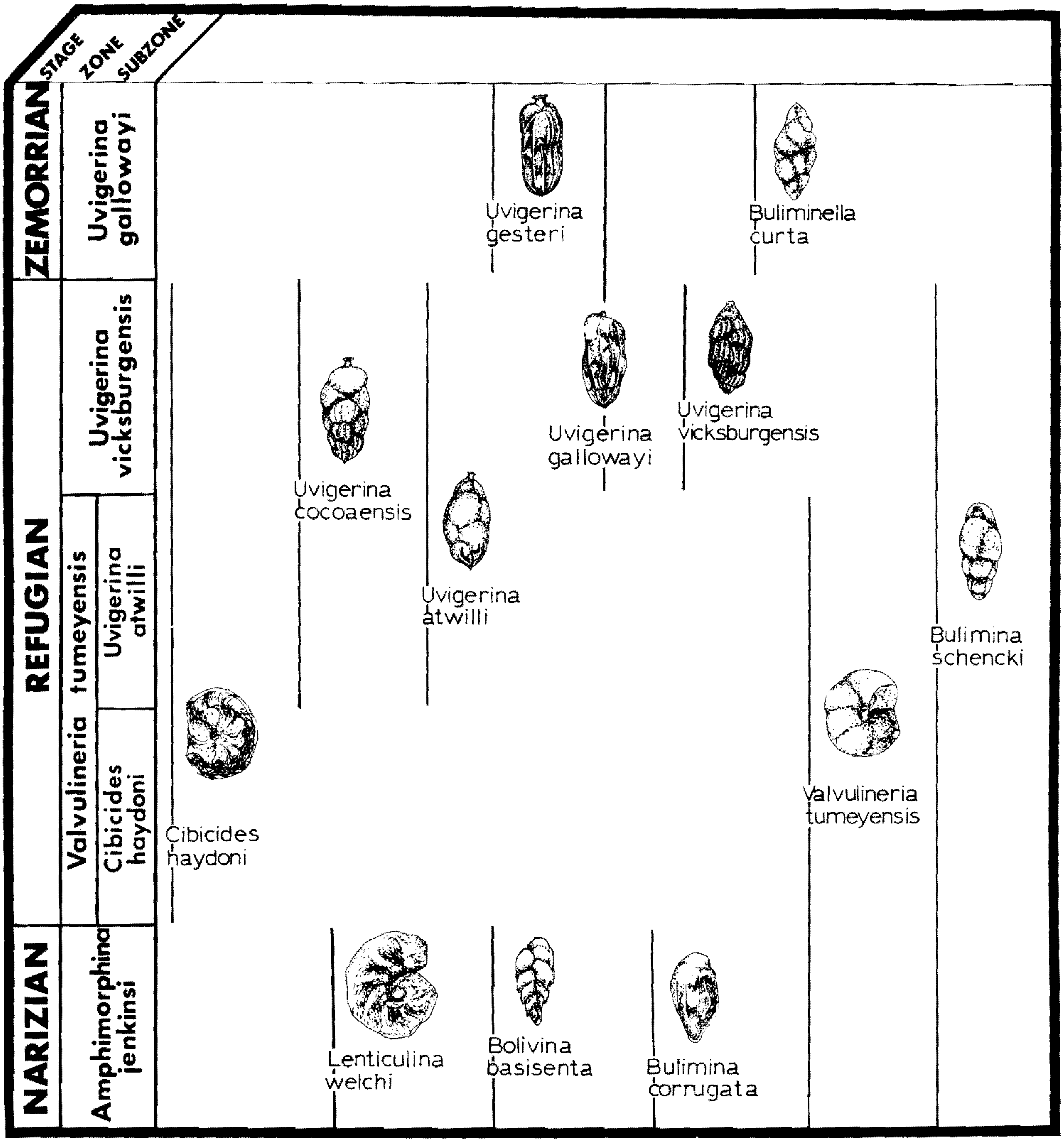


FIGURE 8

Known stratigraphic ranges of some foraminiferal species in the upper Narizian, Refugian, and lower Zemorrian Stages in California. Illustrations courtesy of David G. Howell.

not in every instance. Examples include them Alegria Formation of the western Santa Ynez Mountains (including subsurface Santa Barbara Channel), the type Tumey Formation, the type Wagonwheel Formation, and the subsurface equivalents of the latter two units, including the "*Leda* Zone" of Cushman and Simonson. At the Devils Kitchen syncline in the San Emigdio Mountains, the type Pleito Formation is upper Refugian in part, but the *Uvigerina vicksburgensis* Zone cannot be recognized because of lack of foraminifera in that interval (see Delise, 1967). The zone is well represented faunally in the Upper Church Creek Formation of the Santa Lucia Mountains (Dickinson, 1965; Waters, 1963), but the section is truncated by a fault at the top, and no Zemorrian assemblages have been found.

Foraminiferal beds of the *Uvigerina vicksburgensis* Zone are known to be overlain by diagnostically microfossiliferous lower Zemorrian in only three areas of California: (1) north and east of Coalinga, where the subsurface "*Leda* Zone" below the regional unconformity locally contains rare *Uvigerina gesteri* in its uppermost beds and is thus apparently as young as early Zemorrian, (2) in the upper San Lorenzo River area of the Santa Cruz Mountains, where the Rices Mudstone Member of the San Lorenzo Formation and the Vaqueros Formation provide a dominantly fine-grained and foraminiferal sequence from the early Refugian to the late Zemorrian or early Saucesian (see Fairchild, Wesendunk, and Weaver, 1969), and (3) the dominantly fine-grained subsurface equivalents of the Pleito Formation at the Pioneer anticline (see Texaco P.U.P. #1 Well, Tipton and others, 1973).

As the superpositional relationships are clearest and the faunal evidence most complete in the latter section, the type section of the *Uvigerina vicksburgensis* Zone is designated as the Texaco Pioneer Unit Plan #1 Well in the western San Emigdio Mountains, approximate drilling depths 7,725′ to 7,830′, including localities D-4254 through 4256 of Tipton and others (1973, Fig. 4). In addition to the checklisted species from that well, the authors (p. 23) report that *Uvigerina vicksburgensis* was recorded by R. M. Kleinpell in previous observations at the horizon of locality D-4254, upper Refugian, and that *Buliminella curta* was similarly observed at the horizon of sample D-4257, lowest Zemorrian.

Assemblage slides and lithologic information regarding the Texaco P.U.P. #1 Well section are housed at the Paleontological Laboratories of Texaco, Inc., Los Angeles.

It is far from ideal to designate a subsurface section as a biochronological type locality, and thus it seems advisable to designate supplementary outcrop sections where the faunas of the *Uvigerina vicksburgensis* Zone can be sampled from surface exposures, though those exposures are not in continunity with microfossiliferous Zemorrian strata. The supplementary sections are as follows:

1. The uppermost 61 meters of the Gaviota Formation at Arroyo el Bulito, localities 655–668 of the present study. (The overlying nonforaminiferal Alegria Formation is also upper Refugian, on the basis of mollusks.)
2. The interval embracing localities D-464, 463, 462, 468, 469, 471, 472, and 470 of Waters (1963), Section A, type Church Creek Formation (see also Dickinson, 1965, localities S. O. 7416, 7475, 7414, 7470, 7315, upper type Church Creek Formation).

The *Uvigerina vicksburgensis* Zone is defined by the lowermost occurrences of the following species: *Bolivina marginata* Cushman, *Cibicides elmaensis* Rau, *Eponides kleinpelli* Wilson, *Uvigerina gallowayi* Cushman, and *Uvigerina kernensis* Barbat and von Estorff in conjunction with the latest occurrences of *Alabamina kernensis* Smith, *Bolivina jacksonensis* Cushman, *Bolivina jacksonensis* var. *tumeyensis* Cushman and Simonson, *Bulimina schencki* Beck, *Bulimina sculptilis* Cushman, *Bulimina sculptilis* var. *laciniata* Cushman and Parker, *Cancris joaquinensis* Smith, *Cibicides haydoni* (Cushman and Schenck), *Cibicides hodgei* Cushman and Schenck, *Cibicidoides coalingensis* (Cushman and Hanna), *Epistomina eocenica* Cushman and Hanna, *Eponides gaviotaensis* Wilson, *Nonion planatum* Cushman and Thomas, *Plectofrondicularia garzaensis* Cushman and Siegfus, *Plectofrondicularia packardi* s.s. Cushman and Schenck, *Plectofrondicularia packardi* var. *robusta* Kleinpell and Weaver, *Plectofrondicularia vokesi* Cushman, Stewart, and Stewart, *Spiroloculina wilcoxensis* Cushman and Garrett, *Uvigerina atwilli* Cushman and Simonson, *Uvigerina cocoaensis* Cushman, *Uvigerina garzaensis* Cushman and Siegfus, and *Uvigerina jacksonensis* Cushman. The extinctions of the taxa just listed also define the upper limit of the Refugian Stage as a whole.

The following species are restricted in California to the *Uvigerina vicksburgensis* Zone: *Uvigerina vicksburgensis* Cushman and Ellisor, *Valvulineria menloensis* Rau, and *Cassidulina galvinensis* Cushman and Frizzell.

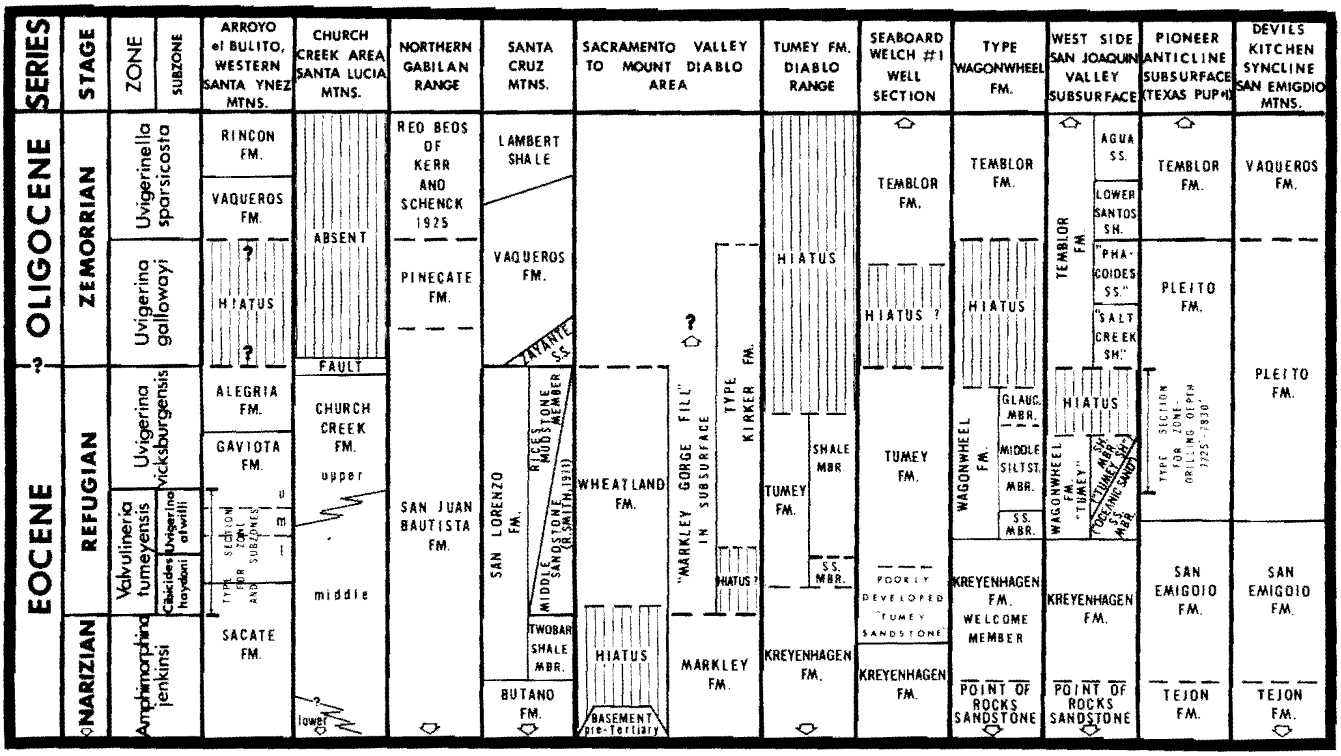


FIGURE 9
Correlation of selected Refugian marine sequences in California.

SUPERJACENT STAGE

The rare locations at which lower Zemorrian strata overlie the Refugian Stage conformably in outcrop have been enumerated in the discussion of the *Uvigerina vicksburgensis* Zone (see also Kleinpell, 1938, p. 108).

The faunal criteria for recognition of the base of the Zemorrian Stage include the lowermost occurrences of *Uvigerina gesteri* Barbat and von Estorff, *Siphogenerina* spp., *Buliminella curta* Cushman, *Buliminella subfusiformis* Cushman, *Planulina cushmani* (Barbat and von Estorff), *Epistomina ramonensis* Cushman and Kleinpell, *Cassidulina crassipunctata* Cushman and Hobson, and others as listed by Kleinpell (1938, pp. 110–111).

The present author disagrees, however, with Kleinpell's listing of *Uvigerina gesteri, Cassidulina crassipunctata*, and *Eponides frizzelli* as occurring as low as the Refugian, and with the listing of *Cibicides hodgei* s.s. as occurring in the Zemorrian Stage. The first three named are restricted to Zemorrian or younger strata, and the latter is restricted to Refugian and older horizons. R. M. Kleinpell concurs with these emendations (pers. comm., 1975).

RELATIONSHIP OF THE REFUGIAN STAGE TO ZONATIONS BASED ON PLANKTONIC ORGANISMS

Published and unpublished records of planktonic forminifera from the Refugian Stage in California include those of Sullivan (1962), Waters (1963), Lipps (1967), and Donnelly (1976). Schmidt (1970) and Bandy (1972) treat the correlation of the Stage with the standard planktonic foraminiferal zones of Bolli (1957, 1966) and Blow (1969), inferring the general equivalency of the Refugian with parts of P15 through P17 and with the *Globigerapsis semiinvoluta* or *Globorotalia cerroazulensis* Zones of Bolli.

Refugian nannoplankton have been studied in California by Brabb, Bukry, and Pierce (1971), and by Lipps and Kalisky (1972).

Warren and Newell (1976, 1980) have documented and greatly refined the correlation of the Refugian Stage with the chronologies based on planktonic organisms by studying continuous sequences where chronologically significant planktonic and benthonic microfossils occur together, e.g., the Sacate and Gaviota Formations at Arroyo el Bulito, the San Lorenzo Formation in the Santa Cruz Mountains, and the Bastendorff Formation in southern Oregon. They demonstrate the equivalency of the Refugian Stage with the *Globorotalia cerroazulensis* Zone (Bolli, 1957, 1966), P16 and P17 of Blow (1969), and with the *Isthmolithus recurvus* Subzone of the *Discoaster barbadiensis* calcareous nannoplankton Zone of Bukry (1973, 1975), NP19 and NP20 of Martini (1971). Warren and Newell show that the Narizian-Refugian boundary is correlative with the boundary between nannoplankton zones NP18 and NP19, and that the Refugian-Zemorrian boundary is approximately correlative with the boundary between NP20 and NP21.

GEOGRAPHIC LIMITS OF THE NEW ZONATION

The present zonation is believed to be applicable in all explored areas of California and the California borderland. South of southern California, scarcity of evidence prevents any precise delineation of the southern limits of applicability of the Refugian zonation for California. Refugian marine strata are apparently absent in Baja California. Certainly, correlative benthonic faunas of the Gulf Coast and Caribbean regions belong to a separate biogeographic province, for despite some elements in common with those of California they are distinctly more tropical in character.

To the north of California, the Refugian foraminiferal faunas of Oregon and Washington have become well known through studies by Rau (1948, 1951, 1958, 1964, 1966, 1975), Cushman and Schenck (1928), Detling (1946), Tipton (1975), Rooth (1974), McDougall (1975) and others. Donnelly (1976) summarized the evidence for correlations from California to each area of Refugian occurrence in the Pacific Northwest, and enumerated similarities and differences in the faunal sequences of the two regions.

The many similarities in Refugian faunal content from southern California to northern Washington led Donnelly (1976) to the conclusion that during Refugian time a single zoogeographic province for offshore benthic Foraminifera stretched from southern California at least as far north as the present Straits of Juan de Fuca. However, a few variations in actual faunal content and many variations in stratigraphic ranges of species from one region to the other imply that, for zonation, northern Oregon and Washington should be considered separately from California and southern Oregon. The present zonation is applicable to the southern biogeographic *subprovince*, while the zonation of Rau (1958, 1966) is applicable to the northern *subprovince* (see Fig. 10), which may also include Vancouver Island and southern Alaska. These conclusions are fully treated in Donnelly (1976).

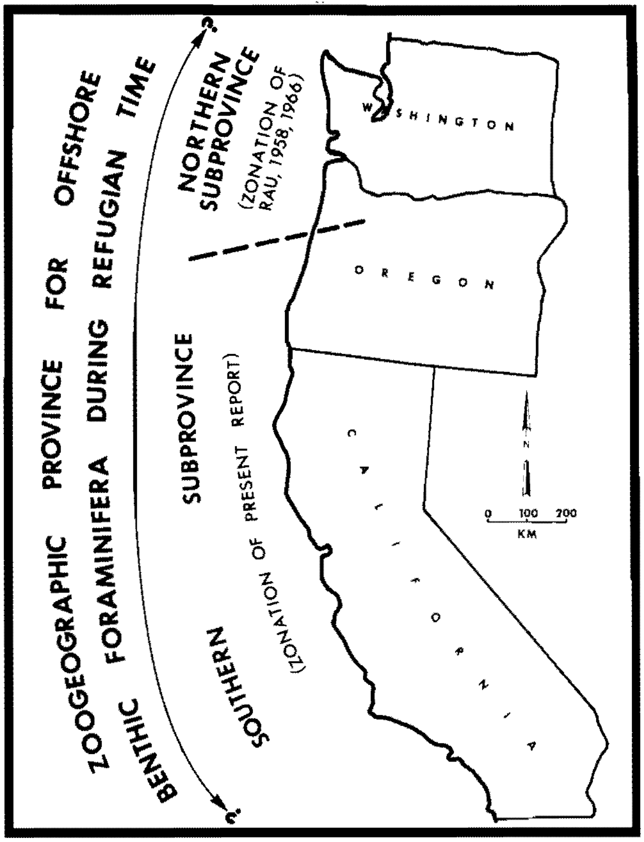


FIGURE 10

Approximate locations of northern and southern subprovinces of the West Coast zoogeographic province for offshore benthic foraminifera, Refugian Age.

ACKNOWLEDGMENTS

Generous contributions of ideas, information, and helpful criticism are gratefully acknowledged from the following persons and their institutions: R. M. Kleinpell (University of California, Berkeley); D. W. Weaver (University of California, Santa Barbara); Weldon W. Rau (Division of Mines and Geology, Olympia, Washington); A. D. Warren, James Newell, Daniel McKeel, and Richard Boettcher (Anderson, Warren and Associates); Martin Link (L. A. Harbor College); John Armentrout, Lloyd Edwards, E. R. Orwig (Mobil Oil Corporation); W. R. Dickinson and Steven Graham (Stanford University); Dean Milo (Consultant, San Diego); Kristin McDougall, Samuel Clarke, David Howell, Tor Nilsen, Warren Addicott, Carl Wentworth, Thomas Dibblee (U.S. Geological Survey); A.

A. Almgren, Lowell Redwine (Union Oil Company of California); Andrew Marianos (Exxon Co., U.S.A.); Gordon Hornaday and F. Jay Phillips (Museum of Paleontology, U. C. Berkeley); Archer Warne (Consultant, Bakersfield).

Thanks are also extended to the petroleum industry for vital cooperation and assistance, particularly Mobil Oil Corporation, Union Oil Co. of California, Texaco, Inc., Exxon Co., U.S.A., Occidental Exploration and Production Co., and Standard Oil Co. of California.

I am grateful for financial support of my research from the following institutions: Union Oil Co. of California, especially John Sherborne and Cortez Hoskins; Mobil Oil Corp., especially A. G. Alpha, Kingsley Nash, Charles Tranter, and E. R. Orwig; and the Department of Geological Sciences, University of California, Santa Barbara.

Michael F. Donnelly drafted the text figures and assisted in preparing the manuscript. David G. Howell drew the illustrations of foraminifera for Figure 8.

REFERENCES TO FORAMINIFERAL SPECIES AND VARIETIES

The following are references to representative illustrations of selected foraminiferal taxa discussed in the text. A formal systematic listing of all checklisted forms is found in Donnelly (1976).

Alabamina kernensis Smith, H. P., 1956, p. 99, pl. 15, figs. 3, 4.

Amphimorphina jenkinsi (Church), Mallory, 1959, pl. 18, p. 216, fig. 5.

Anomalina californiensis Cushman and Hobson, 1935, p. 64, pl. 9, fig. 8.

Bifarina eleganta (Plummer), Mallory, 1959, p. 204, pl. 17, fig. 2.

Bolivina basisenta Cushman and Stone, Cushman, Stewart, and Stewart, 1947b, p. 102, pl. 13, fig. 6.

Bolivina jacksonensis Cushman and Applin, Cushman and Simonson, 1944, pp. 198–199, pl. 32, fig. 15.

Bolivina jacksonensis var. *tumeyensis* Cushman and Simonson, 1944, p. 199, pl. 32, fig. 16.

Bolivina marginata Cushman, Sullivan, 1962, p. 276, pl. 15, fig. 9.

Bulimina corrugata Cushman and Siegfus, 1942, p. 411, pl. 16, fig. 38.

Bulimina microcostata Cushman and Parker, Tipton, Kleinpell, and Weaver, 1973, p. 53, pl. 5, fig. 9.

Bulimina schencki Beck, 1943, p. 605, pl. 107, figs. 28, 33.

Bulimina sculptilis Cushman, 1923, p. 23, pl. 3, fig. 3.

Bulimina sculptilis var. *laciniata* Cushman and Parker, Rau, 1951, p. 441, pl. 65, fig. 22.

Buliminella curta Cushman, Sullivan, 1962, p. 273, pl. 14, fig. 1.

Buliminella subfusiformis Cushman, Sullivan, 1962, p. 273, pl. 14, figs. 2, 3.

Cancris joaquinensis Smith, 1956, pp. 98–99, pl. 15, figs. 5, 6.

Cassidulina crassipunctata Cushman and Hobson, Sullivan, 1962, pp. 282–283, pl. 20, fig. 6.

Cassidulina galvinensis Cushman and Frizzell, Rau, 1948, p. 173, pl. 31, figs. 9–11.

Cibicides cushmani Nuttall, 1930, p. 296, pl. 25, figs. 3, 5, 6.

Cibicides elmaensis Rau, 1948, p. 173, pl. 31, figs. 18–26.

Cibicides haydoni (Cushman and Schenck), Kleinpell and Weaver, 1963, p. 181, pl. 14, fig. 3.

Cibicides hodgei Cushman and Schenck, 1928, p. 315, pl. 45, figs. 3–5.

Cibicides natlandi Beck, 1943, p. 612, pl. 109, figs. 1, 5, 13.

Cibicides pseudoungerianus var. *evolutus* Cushman and Hobson, 1935, p. 64, pl. 9, fig. 11.

Cibicidoides coalingensis (Cushman and Hanna), Mallory, 1959, pl. 38, fig. 11.

Dentalina consobrina d'Orbigny, Wilson, 1954, p. 135, pl. 14, fig. 7.

Dentalina pauperata d'Orbigny, Cushman and Laiming, 1931, p. 99, pl. 10, figs. 11, 12.

Eggerella elongata Blaisdell, Tipton, Kleinpell, and Weaver, 1973, p. 42, pl. 1, figs. 9, 10.

Eggerella subconica Parr, 1950, p. 281, pl. 5, fig. 22.

Elphidium cf. *E. californicum* Cook, Sullivan, 1962, p. 268, pl. 11, fig. 13.

Epistomina eocenica Cushman and Hanna, Cushman and Schenck, 1928, p. 313, pl. 44, fig. 9.

Epistomina ramonensis Cushman and Kleinpell, 1934, p. 15, pl. 3, fig. 1.

Eponides gaviotaensis Wilson, 1954, p. 143, pl. 16, figs. 11, 12.

Eponides kleinpelli Cushman and Frizzell, 1940, p. 42, pl. 8, fig. 11.

Eponides mansfieldi var. *oregonensis* Cushman, Stewart and Stewart, 1947a, p. 48, pl. 6, fig. 4.

Eponides yeguaensis Weinzierl and Applin, Beck, 1943, p. 608, pl. 108, figs. 1, 4.

Globocassidulina globosa (Hantken), Fairchild, Wesendunk, and Weaver, 1969, p. 69, pl. 22, fig. 15.

Globocassidulina margareta (Karrer), Tipton, Kleinpell, and Weaver, 1973, pl. 11, fig. 1.

Gyroidina condoni (Cushman and Schenck), Wilson, 1954, p. 142, pl. 16, fig. 10.

Guttulina irregularis d'Orbigny, Cushman and Simonson, 1944, p. 196, pl. 31, figs. 10–12.

Lenticulina chirana (Cushman and Stone), Tipton, Kleinpell, and Weaver, 1973, p. 44, pl. 2, fig. 2.

Lenticulina limbosa var. *hockleyensis* (Cushman and Applin), Fairchild, Wesendunk, and Weaver, 1969, p. 42, pl. 6, fig. 2.

Lenticulina welchi (Church), *Robulus welchi* of Cushman and Simonson, 1944, p. 195, pl. 30, fig. 11.

Nodogenerina sanctaecrucis Kleinpell, 1938, p. 246, pl. 4, fig. 22.

Nonion planatum Cushman and Thomas, Kleinpell and Weaver, 1963, p. 173, pl. 8, fig. 3.

Planularia tolmani Cushman and Simonson, 1944, p. 195, pl. 30, figs. 13, 14.

Planulina cushmani (Barbat and von Estorff), Tipton, Kleinpell, and Weaver, 1973, pl. 12, fig. 6.

Plectofrondicularia garzaensis Cushman and Siegfus, 1939, p. 26, pl. 6, fig. 9.

Plectofrondicularia packardi var. *multilineata* Cushman and Simonson, 1944, p. 197, pl. 32, figs. 2, 4.

Plectofrondicularia packardi var. *packardi* Cushman and Schenck, Kleinpell and Weaver, 1963, p. 174, pl. 8, figs. 5–7.

Plectofrondicularia packardi var. *robusta* Kleinpell and Weaver, 1963, p. 174, pl. 9, fig. 1.

Plectofrondicularia vokesi Cushman, Stewart, and Stewart, Kleinpell and Weaver, 1963, p. 174, pl. 9, fig. 2.

Plectofrondicularia vaughani Cushman, Kleinpell and Weaver, 1963, p. 174, pl. 8, fig. 12.

Pseudohastigerina micra (Cole), Tipton, Kleinpell, and Weaver, 1973, p. 63, pl. 12, fig. 2.

Spiroloculina wilcoxensis Cushman and Garrett, Cushman and Simonson, 1944, p. 194, pl. 30, figs. 4–6.

Tritaxilina colei Cushman and Siegfus, 1935, p. 92, pl. 14, fig. 5.

Uvigerina atwilli Cushman and Simonson, 1944, p. 200, pl. 33, figs. 2–4.

Uvigerina cocoaensis Cushman, Tipton, Kleinpell, and Weaver, 1973, p. 56, pl. 6, figs. 11, 12.

Uvigerina gallowayi Cushman, Fairchild, Wesendunk, and Weaver, 1969, p. 56, pl. 12, fig. 14.

Uvigerina gardnerae Cushman, Smith, 1957, p. 177, pl. 26, fig. 7.

Uvigerina garzaensis Cushman and Siegfus, 1939, pp. 28–29, pl. 6, fig. 15.

Uvigerina garzaensis var. *nudorobusta* Mallory, 1959, p. 208, pl. 17, figs. 11, 13.

Uvigerina gesteri Barbat and von Estorff, 1933, pp. 171–172, pl. 23, figs. 7, 18.

Uvigerina jacksonensis Cushman, Smith, 1956, pl. 12, fig. 12.

Uvigerina kernensis Barbat and von Estorff, 1933, p. 172, pl. 23, fig. 13.

Uvigerina vicksburgensis Cushman and Ellisor, Cushman and Simonson, 1944, p. 200, pl. 33, fig. 5.

Vaginulinopsis saundersi (Hanna and Hanna), Beck, 1943, p. 598, pl. 105, figs. 1, 2, 4, 5, 10.

Valvulineria jacksonensis var. *welcomensis* Mallory, 1959, p. 231, pl. 20, figs. 3, 5.

Valvulineria menloensis Rau, 1951, pp. 446–447, pl. 66, figs. 17–22.

Valvulineria tumeyensis Cushman and Simonson, 1944, p. 201, pl. 33, figs. 13, 14.

Vulvulina curta Cushman and Siegfus, 1935, p. 91, pl. 14, figs. 1, 2.

FOSSIL LOCALITIES

University of California Santa Barbara locality numbers 520 through 597 refer to foraminiferal assemblage slides of core samples from the Kreyenhagen (Loc. 520–522), Tumey, (Loc. 523–594), and Temblor (Loc. 595–597) Formations, from the Seaboard Oil Corp. Welch #1 Well, Sec 10/T16S/R13E, MDBM, 521 meters south and 621 meters west of the northeast corner of the section, Fresno County, California. The drilling depth of each locality is shown on the checklist of Foraminifera (Fig. 7), from Donnelly (1976).

The assemblage slides from the Seaboard Welch #1 are housed at the Micropaleontological Laboratories of Texaco, Inc., Los Angeles, California. This well section is also discussed in Cushman and Simonson (1944).

University of California Santa Barbara localities 603 through 668 were collected by the author and D. W. Weaver in February 1974, in roadcuts along a dirt road on the first major ridge to the east of Arroyo el Bulito, western Santa Ynez Mountains, Santa Barbara County, California (see Sacate 7 ½′ U.S.G.S Topographic Quadrangle, and geologic maps of Dibblee, 1950, and Kleinpell and Weaver, 1963). The samples were collected in numerical and stratigraphic order, at approximately six-meter stratigraphic intervals where exposures were adequate, from near the base of the Sacate Formation to the top of the Gaviota Formation. Figure 3 shows the geographic and geologic locations of the samples and Figure 4 shows their stratigraphic locations.

REFERENCES

ALMGREN, A. A., and SCHLAX, W. N., 1957, Post-Eocene age of Markley Gorge Fill, Sacramento Valley, California: Am. Assoc. Petroleum Geologists Bull., v. 41, p. 326–330.

ATWILL, E. R., 1935, Oligocene Tumey Formation of California: Am. Assoc. Petroleum Geologists Bull., v. 19, p. 1192–1204.

Bandy, O. L., 1972, Late Paleogene-Neogene planktonic biostratigraphy and its geological implications, California: Pacific Coast Miocene Biostratigraphic Symposium, Proc., Pacific Sec., Soc. Econ. Paleontologists and Mineralogists, Bakersfield, Calif., p. 37–51.

Barbat, W. F., and Von Estorff, F. E., 1933, Lower Miocene Foraminifera from the southern San Joaquin Valley, California: Jour. Paleontology, v. 7, p. 164–174.

Beck, R. S., 1943, Eocene Foraminifera from Cowlitz River, Lewis County, Washington: Jour. Paleontology, v. 17, p. 584–614.

Berry, W. B. N., 1966, Zones and zones—with exemplification from the Ordovician: Am. Assoc. Petroleum Geologists Bull., v. 50, p. 1487–1500.

———, 1968, Growth of a prehistoric time scale: San Francisco, W. H. Freeman and Co., p. 1–158.

Blow, W. H., 1969, Late middle Eocene to Recent planktonic foraminiferal biostratigraphy: *in* Bronnimann, P., and Renz, H. H., eds., *Proc. First Internat. Conf. on Planktonic Microfossils, Geneva.* Leiden, E. J. Brill, v. 1, p. 199–421.

Bolli, H., 1957, The genera *Globigerina* and *Globorotalia* in the Paleocene-Lower Eocene Lizard Springs Formation of Trinidad, British West Indies: U.S. Natl. Mus. Bull., v. 215, p. 61–81.

———, 1966, Zonation of Cretaceous to Pliocene marine sediments based on planktonic Foraminifera: Assoc. Venezolana Geología Mineria Petróleo Bol. Inf., v. 9, p. 3–32.

Brabb, E. E., Bukry, D., and Pierce, R. L., 1971, Eocene (Refugian) nannoplankton in the Church Creek Formation near Monterey, central California: U.S. Geol. Survey Prof. Paper 750-C, p. C44–C47.

Bukry, D., 1973, Low-latitude coccolith biostratigraphic zonation: *Deep Sea Drilling Proj.*, Initial Repts., v. 15, p. 685–703.

———, 1975, Coccolith and silicoflagellate stratigraphy, northwestern Pacific Ocean, Deep Sea Drilling Project Leg 32: *Deep Sea Drilling Proj.*, Initial Repts., v. 32, p. 677–701.

Castro, M. J., 1967, Geology and oil potential of the area westerly of San Juan Bautista, California: *in Gabilan Range and adjacent San Andreas fault.* Field Trip Guidebook, Pacific Sec., Am. Assoc. Petroleum Geologists, Soc. Econ. Paleontologists and Mineralogists, p. 81–86.

Clark, J. C., and Rietman, J. D., 1973, Oligocene stratigraphy, tectonics, and paleogeography southwest of the San Andreas fault, Santa Cruz Mountains and Gabilan Range, California Coast Ranges: U.S. Geol. Survey Prof. Paper 783, p. 1–18.

Cushman, J. A., 1923, The Foraminifera of the Vicksburg Group: U.S. Geol. Survey Prof. Paper 133, p. 11–67.

Cushman, J. A., and Frizzell, D. L., 1940, Two new species of foraminifera from the Oligocene Lincoln formation of Washington State: Cushman Lab. Foram. Research Contr., v. 16, no. 2, p. 42–43.

Cushman, J. A., and Hobson, H. D., 1935, A foraminiferal faunule from the type San Lorenzo formation, Santa Cruz County, California: Cushman Lab. Foram. Research Contr., v. 11, no. 3, p. 53–64.

Cushman, J. A., and Kleinpell, R. M., 1934, New and unrecorded Foraminifera from the California Miocene: Cushman Lab. Foram. Research Contr., v. 10, pt. 1, p. 1–23.

Cushman, J. A., and Laiming, B., 1931, Miocene Foraminifera from Los Sauces Creek, Ventura County, California: Jour. Paleontology, v. 5, p. 79–120.

Cushman, J. A., and Schenck, H. G., 1928, Two foraminiferal faunules from the Oregon Tertiary: California Univ. Pub. Dept. Geol. Sci. Bull., v. 17, p. 305–324.

Cushman, J. A., and Siegfus, S. S., 1935, New species of Foraminifera from the Kreyenhagen shale of Fresno County, California: Cushman Lab. Foram. Research Contr., v. 11, p. 90–95.

———, 1939, Some new and interesting Foraminifera from the Kreyenhagen shale of California: Cushman Lab. Foram. Research Contr., v. 15, p. 23–33.

———, 1942, Foraminifera from the type area of the Kreyenhagen shale of California: San Diego Soc. Nat. History Trans., v. 9, p. 385–426.

Cushman, J. A., and Simonson, R. R., 1944, Foraminifera from the Tumey formation, Fresno County, California: Jour. Paleontology, v. 18, p. 186–203.

Cushman, J. A., Stewart, R. E., and Stewart, K. C., 1947a, Astoria Miocene Foraminifera from Agate Beach, Lincoln County, Oregon: Oregon Dept. Geology and Mineral Industries Bull., v. 36, Pt. II, p. 43–55.

———, 1947b, Eocene Foraminifera from Helmick Hill, Polk County, Oregon: Oregon Dept. Geology and Mineral Industries Bull., v. 36, p. 94–110.

Delise, K. C., 1967, Biostratigraphy of the San Emigdio formation, Kern County, California: California Univ. Pub. Geol. Sci., v. 68, p. 1–66.

Detling, M. R., 1946, Foraminifera of the Coos Bay lower Tertiary, Coos County, Oregon: Jour. Paleontology, v. 20, p. 348–361.

Dibblee, T. W., Jr., 1950, Geology of the southwestern Santa Barbara County, California: California Div. Mines Bull. 150, p. 1–95.

Dickinson, W. R., 1965, Tertiary stratigraphy of the Church Creek area, Monterey County, California: Calif. Div. Mines and Geology, Spec. Rep. 86, p. 25–44.

Donnelly, A. Tipton, 1976, The upper Eocene Refugian Stage of California: Foraminiferal zonation, geologic history, and correlations to the Pacific northwest: unpub. Ph.D. dissertation, Calif. Univ., Santa Barbara.

Fairchild, W. W., Wesendunk, P. R., and Weaver, D. W., 1969, Eocene and Oligocene Foraminifera from the Santa Cruz Mountains, California: California Univ. Pub. Geol. Sci., v. 81, p. 1–144.

Fenton, C. L., and Fenton, M. A., 1928, Ecologic interpretation of some biostratigraphic terms: Am. Midland Naturalist, v. 11, p. 20–22.

Kleinpell, R. M., 1938, Miocene stratigraphy of California: Tulsa, Oklahoma, Am. Assoc. Petroleum Geolgoists, p. 1–450.

Kleinpell, R. M., and Weaver, D. W., 1963, Oligocene biostratigraphy of the Santa Barbara embayment, California: California Univ. Pub. Geol. Sci., Pt. I, v. 43, p. 1–77.

Lipps, J. H., 1967, Planktonic Foraminifera, intercontinental correlation and age of California mid-Cenozoic micro-faunal stages: Jour. Paleontology, v. 41, p. 994–999.

Lipps, J. H., and Kalisky, M., 1972, California Oligo-Miocene calcareous nannoplankton biostratigraphy and paleoecology: Pacific Coast Miocene Biostratigraphic Symposium Proc., Pacific Sec., Soc. Econ. Paleontologists and Mineralogists, Bakersfield, Calif., p. 239–254.

Mallory, V. S., 1959, Lower Tertiary biostratigraphy of the California Coast Ranges: Tulsa, Oklahoma, Am. Assoc. Petroleum Geologists, p. 1–416.

Martini, E., 1971, Standard Tertiary and Quaternary calcareous nannoplankton zonation: 2nd Planktonic Conf., Rome, 1970, Proc., v. 2, p. 739–785.

McDougall, K. A., 1975, The microfauna of the type section of the Keasey Formation, northwestern Oregon. *in* Paleogene Symposium and selected technical papers. Pacific Sec., Am. Assoc. Petroleum Geologists, Soc. Econ. Paleontologists and Mineralogists, Soc. Econ. Geophysicists, Joint Ann. Mtg., Long Beach, Calif., p. 343–359.

NUTTALL, W. L., 1930, Eocene Foraminifera from Mexico. Jour. Paleontology, v. 4, p. 271–293.

PARR, W. J., 1950, Foraminifera, British and New Zealand Antarctic Research Exped., 1929–1931. Repts. Adelaide, ser. B, v. 5, pt. 6.

PHILLIPS, F. J., TIPTON, A., and WATKINS, R., 1974, Outcrop studies of the Eo-Oligocene Tumey Formation, Monocline Ridge, Fresno County, California: *in Paleogene of the Panoche Creek–Cantua Creek area, California*. Pacific Sec. Soc. Econ. Paleontologists and Mineralogists, Field Trip Guidebook, p. 99–131.

PRIMMER, S. R., 1964, Preliminary report of the type Kirker Formation, California: *in Mount Diablo Field Trip*. Guidebook, Geol. Soc. Sacramento, p. 60–69.

RAU, W. W., 1948, Foraminifera from the Porter shale (Lincoln formation), Grays Harbor County, Washington: Jour. Paleontology, v. 22, p. 152–174.

———, 1951, Tertiary Foraminifera from the Willapa River Valley of southwest Washington. Jour. Paleontology, v. 25, p. 417–453.

———, 1958, Stratigraphy and foraminiferal zonation in some new Tertiary rocks of southwestern Washington: U.S. Geol. Survey Oil and Gas Inv. Chart OC 57.

———, 1964, Foraminifera from northern Olympic Peninsula, Washington: U.S. Geol. Survey Prof. Paper 374-G, p. 1–33.

———, 1966, Stratigraphy and Foraminifera of the Satsop River area, southern Olympic Peninsula, Washington: Washington Div. Mines and Geology Bull. 53, p. 1–66.

———, 1975, Foraminifera and biostratigraphy of the Alsea Formation of western Oregon. *in Paleogene symposium and selected technical papers*. Pacific Sec., Am. Assoc. Petroleum Geologists, Soc. Econ. Paleontologists and Mineralogists, Soc. Explor. Geophysicists, Joint Ann. Mtg., Long Beach, Calif., p. 409–416.

ROOTH, G. H., 1974, Biostratigraphy and paleoecology of the Coaledo and Bastendorff Formations, southwestern Oregon: Oregon State Univ., unpub. Ph.D. dissert., 1974.

SCHENCK, H. G., and Kleinpell, R. M., 1936, Refugian Stage of Pacific Coast Tertiary: Am. Assoc. Petroleum Geologists Bull., v. 20, p. 215–225.

SCHMIDT, R. R., 1970, Planktonic Foraminifera from the lower Tertiary of California: California Univ., Los Angeles, unpub. Ph.D. Dissert.

SMITH, B. Y., 1957, Lower Tertiary Foraminifera from Contra Costa County, California: California Univ. Pub. Geol. Sci., v. 32, p. 127–242.

SMITH, H. P., 1956, Foraminifera from the Wagonwheel formation, Devil's Den district, California: California Univ. Pub. Geol. Sci., v. 32, p. 65–126.

SMITH, R. K., 1971, Foraminiferal studies of the lower and middle Tertiary of Soquel Creek, Santa Cruz, California: California Univ. Pub. Geol. Sci., v. 91, p. 1–86.

SULLIVAN, F. R., 1962, Foraminifera from the type section of the San Lorenzo formation, Santa Cruz County, California: California Univ. Pub. Geol. Sci., v. 32, p. 233–353.

TIPTON, A., 1975, Foraminiferal biostratigraphy of the late Eocene to early Oligocene type Bastendorff Formation, near Coos Bay, Oregon. *in Paleogene Symposium and selected technical papers*. Pacific Sec., Am. Assoc. Petroleum Geologists, Soc. Econ. Paleontologists and Mineralogists, Soc. Explor. Geophysicists, Joint Ann. Mtg., Long Beach, Calif., p. 563–585.

TIPTON, A. KLEINPELL, R. M., and WEAVER, D. W., 1973, Oligocene biostratigraphy, San Joaquin Valley, California: California Univ. Pub. Geol. Sci., v. 105, p. 1–81.

WARREN, A. D., and NEWELL, J. H., 1976, Nannoplankton biostratigraphy of the Sacate and Gaviota formations, Arroyo el Bulito, Santa Barbara County, California: Abstract, Pacific Sec., Am. Assoc. Petroleum Geologists, Soc. Econ. Paleontologists and Mineralogists, Soc. Explor. Geophysicists, Ann. Mtg., San Francisco, Calif., April, 1976.

———, 1980, Plankton biostratigraphy of the Refugian and adjoining Stages of the Pacific Coast Tertiary: Cushman Found. Foram. Research Contr., Spec. Pub. No. 19, p. 233–251.

WATERS, J. N., 1963, Oligocene Foraminifera from Church Creek, Santa Lucia Mountains, California: California Univ., Berkeley, unpub. M.A. thesis, 1963.

WEAVER, D. W., and FRANTZ, J. D., 1967, Re-evaluation of the type Refugian Stage of the Pacific Coast Tertiary. Abstract, Geol. Soc. America Cordilleran Sec. Meeting, Santa Barbara, California, p. 69–70.

WEAVER, D. W., and KLEINPELL, R. M., 1963, Oligocene biostratigraphy of the Santa Barbara Embayment, California: California Univ. Pub. Geol. Sci., Pts. II, III, v. 43, p. 78–250.

WEAVER, D. W., and TIPTON, A. 1972, Formations and age-subdivisions of the West Coast middle Tertiary: Pacific Coast Miocene Biostratigraphic Symposium, Proc. Pacific Sec., Soc. Econ. Paleontologists and Mineralogists, p. 52–62.

WILSON, E. J., 1954, Foraminifera from the Gaviota formation east of Gaviota Creek, California. California Univ. Pub. Geol. Sci., v. 30, p. 103–170.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 278–286, 1980

EASTERN EQUATORIAL PACIFIC PLIOCENE-PLEISTOCENE BIOSTRATIGRAPHY

W. N. ORR[1] AND D. GRAHAM JENKINS[2]

ABSTRACT

Nine Planktonic foraminiferal datums proposed and utilized by Hays and others (1969) in their study of eastern equatorial Pacific Pliocene/Pleistocene sediments have been applied to the thick sections recovered in continuous coring of three Leg 9 Deep Sea Drilling Project (DSDP) sites in the same area. At best the datums based on dissolution susceptible foraminiferal species were found to be difficult to identify in the deep-water sediments. Datums based on coiling changes were found to be particularly reliable and easily recognized. Magnetostratigraphy within the Pliocene/Pleistocene interval presented by Hays and others (1969) was readily correlated with the DSDP cores by using foraminiferal datums. Average specimen size in assemblages of *Pulleniatina primalis* and *P. obliquiloculata* and faunal diversity of the planktonic foraminifera were both found to show relationships with coiling changes in these two species. Four new potentially reliable datums are proposed in the sequence and are based on coiling changes in *Pulleniatina*.

INTRODUCTION

Biostratigraphic analysis of deep-sea cores has become increasingly refined in the past two decades. The use of planktonic foraminifera in Cenozoic biostratigraphy has been particularly improved by the employment of species coiling changes as stratigraphic datums. Early work by Bandy (1963) of Tertiary rocks in the Philippines and Bandy and Wade (1967) of ocean sediment cores in the South Atlantic included coiling changes as part of their chronologies. Late Cenozoic planktonic foraminiferal zonations by Bolli and Bermudez (1965) and Bolli (1966a, b) corroborate results presented by Bandy and Wade (1967). The above papers and several others on late Cenozoic ocean sediment stratigraphy are reviewed in detail by Hays and others (1969).

Hays and others (1969) studied a large suite of piston cores from the eastern equatorial Pacific wherein they were able to relate carbonate, paleomagnetic, and biostratigraphic chronologies within the Pliocene/Pleistocene interval. The detailed paleontological study was carried out on four of the cores which measured 11 to 13 meters in length. From this study emerged a proposed sequence of nine foraminiferal datums.

In the course of operations for Leg 9 of the Deep Sea Drilling Project (DSDP), Hays and others (1972) were able to continuously core the same late Tertiary stratigraphic interval at three of the nine sites. The intervals were cored at DSDP Sites 77, 83, and 84 (Fig. 1), and penetrated thick carbonate-rich Pleistocene sections measuring from a minimum of 80 meters in Site 77 to over 200 meters in Site 84. Foraminiferal faunas from these sequences were described by Jenkins and Orr (*In* Hays and others, 1972, p. 1059–1193). Our study here is an attempt to relate the datums proposed by Hays and others (1969) to the DSDP Leg 9 cores in order to evaluate the datums in expanded stratigraphic sections.

Details of the lithology, the techniques of sampling, sample processing, and sample frequency in the DSDP

---

[1] Department of Geology, University of Oregon, Eugene, Oregon.
[2] Department of Geology, The Open University, Milton Keynes, England.

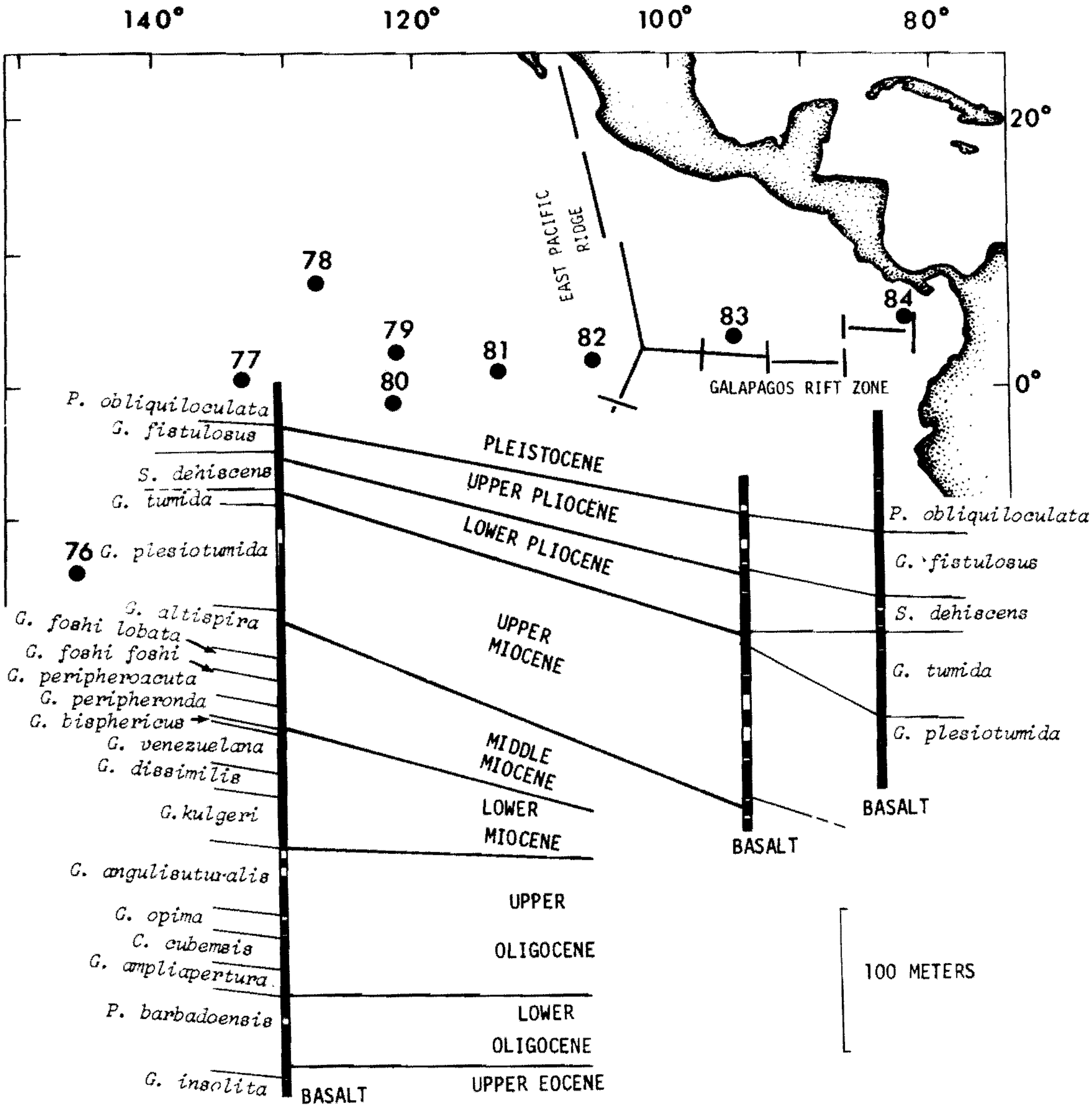


FIGURE 1

Locality map of sites drilled in the eastern equatorial Pacific on DSDP Leg 9. Cored intervals and epoch/zone correlations indicated for Sites 77, 83, and 84 (after Hays and others, 1972).

cores from Sites 77, 83, and 84 have been omitted here because of the detailed documentation in the Leg 9 Initial Core Description (Hays and others, 1972. Site 77, p. 43–208; Site 83, p. 537–614; Site 84, p. 615–706).

The zonation proposed by Banner and Blow (1965) was intended as a standard for DSDP legs. On Leg 9 we soon found this zonation to be difficult to apply due primarily to the problem of destructive solution of the calcareous foraminiferal tests. Our remedy for this (Jenkins and Orr, 1971) was to establish and use a revised zonation in which the zonal species were of a solution resistant type (Fig. 2). Hays and others (1969) experienced similar difficulties with the zonation of Banner and Blow (1965) with its revision by Blow (1969).

PLANKTONIC FORAMINIFERAL DATUMS

Hays and others (1969) carried out studies on foraminiferal and radiolarian faunas as well as on discoas-

	LEG 9 D.S.D.P.			
SERIES SUBSERIES	PLANKTONIC FORAMINIFERAL ZONES	DEFINITION OF ZONAL BOUNDARIES IA = APPEARANCE E = EXTINCTION	BOLLI 1957 a,b,c 1966, 1970 IN PRESS BOLLI & BERMUDEZ 1966	BANNER & BLOW (1965) PARKER (1967) BLOW (1969)
PLEISTOCENE	*Pulleniatina obliquiloculata*	*G. fistulosus* (E)	*G. truncatulinoides truncatulinoides*	N-22-23
UPPER PLIOCENE	*Globigerinoides fistulosus*	*G. fistulosus* (IA)	*G. truncatulinoides tosaensis*	N-21
LOWER PLIOCENE	*Sphaeroidinella dehiscens*	*S. dehiscens (IA)*	*G. exilis/ G. miocenica*	N-19-20
UPPER MIOCENE	*Globorotalia tumida*	*G. tumida* (IA)	*G. margaritae*	N-18
	Globorotalia plesiotumida	*G. plesiotumida (IA)*	*G. dutertrei – G. obliquus extremus*	N-17
MIDDLE MIOCENE	*Globoquadrina altispira*	*G. fohsi lobata* (E)	*G. acostaensis G. fohsi lobata*	N-12-16
	Globorotalia fohsi lobata	*G. foshi lobata* (IA)	*G. fohsi lobata*	N-10-11
	Globorotalia fohsi fohsi – Globorotalia peripheroacuta	*G. peripheroacuta* (IA)	*G. fohsi fohsi G. fohsi barisanensis*	
	Globorotalia peripheroronda	*P. glomerosa curva* (IA)		N-9
	Praeorbulina glomerosa curva subzone	*P. glomerosa curva* (IA)	*G. insueta*	N-8
LOWER MIOCENE	*Globigerinoides bisphericus subzone*	*P. glomerosa curva* (IA)		N-7
	Globoquadrina Venezualana		*G. dissimilis (E) C. dissimilis*	N-5-6
	Globigerinita dissimilis	*G. kugleri* (E)		
	Globorotalia kugleri	*G. kugleri* (IA)	*G. kugleri*	N-4
UPPER OLIGOCENE	*Globigerina angulisuturalis*	*G. opima* (E)	*G. ciperoensis ciperoensis*	N-3
	Globorotalia opima	*C. cubensis* (E)	*G. opima opima*	N-2
	Chiloguembelina cubensis	*G. opima* (IA)		
	Globigerina ampliapertura	*P. barbadoensis* (E)	*G. ampliapertura*	N-1
LOWER OLIGOCENE	*Pseudohastigerina barbadoensis*	*G. insolita* (E)	*C. chipolensis H. micra*	P-18-19
UPPER EOCENE	*Globorotalia insolita*		*G. cerroazulensis*	P-17

FIGURE 2

Zonal scheme for eastern equatorial Pacific deep-sea Tertiary sediments based on solution-resistant species of foraminifera (Jenkins and Orr, 1972).

TABLE 1

Equatorial Pacific Datums Proposed by Hays and others (1969, p. 1498).

Datum I. A marked upward decrease in abundance of *Sphaeroidinella dehiscens* at the Brunhes-Matuyama boundary.
**Datum II.* The first evolutionary appearance of *Pulleniatina finalis* from *P. obliquiloculata* midway between the Jaramillo and Olduvai Events.
Datum III. The upper limit of *Globigerinoides fistulosus* near the top of the Olduvai Event.
**Datum IV.* The first evolutionary appearance of *Globorotalia truncatulinoides* near the lower boundary of the Olduvai Event.
Datum V. The extinction of all species of *Sphaeroidinellopsis* coincident with increased upward abundance of *Sphaeroidinella dehiscens* at the top of the Mammoth Event.
**Datum VI.* The extinction of *Globorotalia margaritae* at the Gauss-Gilbert boundary.
Datum VII. A sharp left to right coiling change in *Pulleniatina*, primarily of *P. primalis*, just above the Gilbert "a" Event.
**Datum VIII.* The extinction of *Globigerina nepenthes* at the top of the Gilbert "a" Event.
**Datum IX.* The first evolutionary appearance of *Pulleniatina spectabilis* from *P. primalis* near the top of the Gilbert "c" Event.

* Datum recognized only with some difficulty in one or more DSDP cores due to dissolution.

ter, diatom, and silicoflagellate floras. The nine datums they proposed were based on planktonic foraminiferal parameters (Table 1). We were able to recognize most of their datums in the cores from DSDP Sites 77, 83, and 84 and correlate the paleomagnetic events documented by Hays and others (1969). The following summary is an evaluation of each of their datums in descending stratigraphic order in the light of our research.

Datum I. The upward decrease in the number of specimens of *Sphaeroidinella dehiscens* was found by us to be a consistent marker in all three of the Leg 9 sites (Figs. 3, 4). Hays and others (1969) reported Datum I to be a particularly reliable intercore marker because of the resistivity to solution of the species and positioned the datum at the boundary between the Brunhes Normal and Matuyama Reversed Magnetic Epochs.

Datum II. The evolutionary appearance of *Pulleniatina finalis* from *Pulleniatina obliquiloculata* midway between the Jaramillo and Olduvai Events was not recognized by us in the Leg 9 cores. We experienced considerable difficulty in attempting to distinguish all of the various transition members between *Pulleniatina primalis* and *Pulleniatina finalis* noted by Blow (1969). Nevertheless, it was possible to consistently distinguish *Pulleniatina primalis* from *Pulleniatina obliquiloculata*. In doing this we followed Parker's (1967) taxonomic treatment where she included "*Pulleniatina praecursor*" in synonymy with *Pulleniatina primalis*. In a similar way *Pulleniatina finalis* is here considered to be synonymous with *Pulleniatina obliquiloculata*.

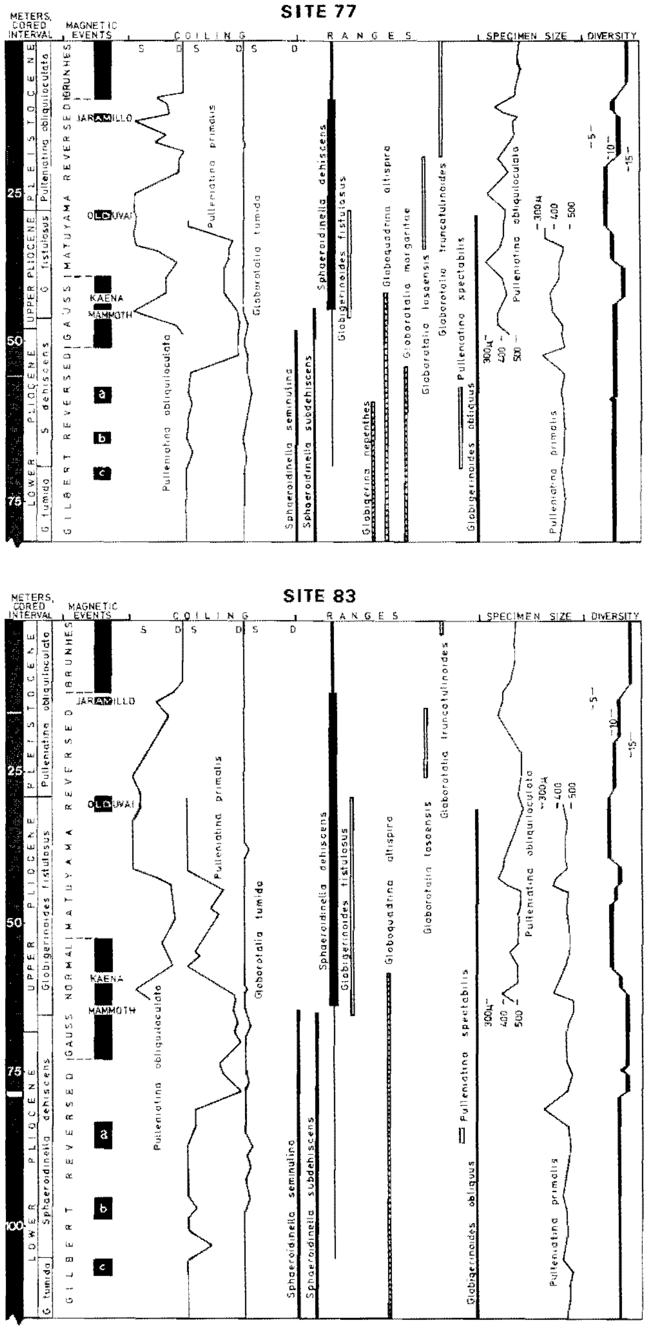


FIGURE 3

Coiling, stratigraphic ranges, specimen size, and diversity changes of planktonic foraminifera from Leg 9 Sites 77 and 83. Magnetic data from Hays and others (1969) by direct correlation of phylogenetic events of the planktonic foraminifera.

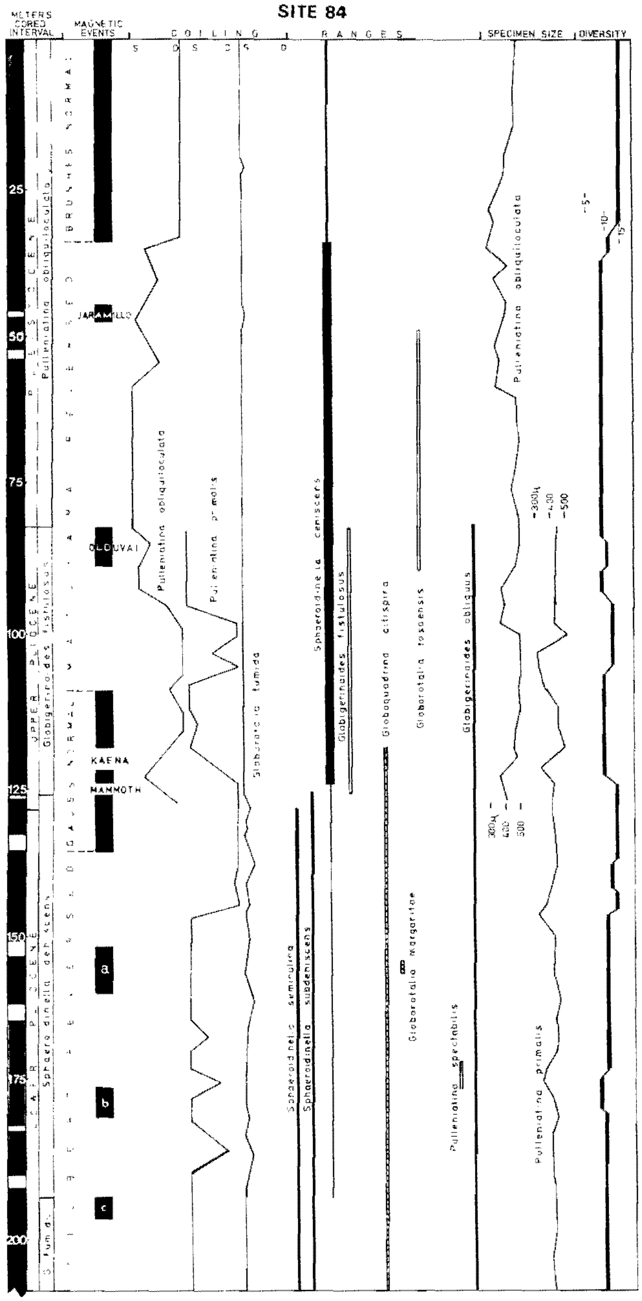


FIGURE 4

Coiling, stratigraphic ranges, specimen size, and diversity of Leg 9 Site 84 foraminifera. Magnetic data from Hays and others (1969) by direct correlation of phylogenetic events of the planktonic foraminifera.

In addition to the evolutionary first appearance of "*Pulleniatina finalis*," Hays and others (1969) also recorded at this datum a coiling change in species of *Pulleniatina* from sinistral to dextral. This coiling change was easily recognized in the DSDP sites, but the upward transition from sinistral to dextral populations occurred over an extended stratigraphic interval in Site 83 and therefore was of only limited use (Fig. 3).

Datum III. The extinction of *Globigerinoides fistulosus* at or near the top of the Olduvai Event was found to be a particularly reliable marker at the three sites. Although species of *Globigerinoides* are normally regarded as solution susceptible (Ruddiman and Heezen, 1967; Berger, 1970), *Globigerinoides fistulosus* was consistent within its stratigraphic range in all of the Leg 9 cores to such a degree that its local range zone was used as a new zone in the eastern equatorial Pacific (Jenkins and Orr, 1972; p. 1066; Fig. 2). Other events corresponding to the same horizon were the simultaneous extinction of *Pulleniatina primalis* and *Globigerinoides obliquus*. Again, here, a species of the "solution-susceptible" genus *Globigerinoides* was found to be reliable as a horizon indicator in deep-sea sediments. Hays and others (1969) recorded a similar range termination for *Pulleniatina primalis*, but their species "*Pulleniatina praecursor*" has a range extending well up above the Olduvai almost to the Jaramillo Event.

Datum IV. The first evolutionary appearance of *Globorotalia truncatulinoides* near the lower boundary of the Olduvai Event was not recognized by us. Hays and others (1969) noted that the datum is poorly developed in the tropics due to the paucity there of temperate species. They showed an intermittent first appearance (dotted range) for the species, and its first occurrence did not correspond to the base of the Olduvai Event in any of the Leg 9 cores. We regard the scarcity of *Globorotalia truncatulinoides* here to be due to the solution susceptibility of this species. At Site 77 *Globorotalia truncatulinoides* first appeared midway between the Olduvai and Jaramillo Events, but at Site 83 it appeared only in a few samples near the top of the Brunhes Epoch (Fig. 3). *Globorotalia tosaensis*, the apparent ancestor of *Globorotalia truncatulinoides*, is evidently more solution resistant. The inconsistency of the stratigraphic occurrence of the former species in the Matuyama Reversed-Gauss Normal interval, readily apparent in the Leg 9 cores, was also recognized and noted by Hays and others (1969). Another possibility is that *Globorotalia tosaensis* was not a tropical species in the Late Cenozoic.

Datum V. The extinction of all species of *Sphaeroidinellopsis* (*Sphaeroidinella*) coincident with the increased upward abundance of *Sphaeroidinella dehiscens* at the top of the Mammoth Event was found to represent as many as three separate horizons in one of our cores (Site 84). At the other Sites, 77 and 83, the extinctions of *Sphaeroidinellopsis* were also at different levels. The upward increase in abundance of *Sphaeroidinella dehiscens* was, on the other hand, very consistent in Leg 9 cores with respect to other species ranges and coiling changes in this part of the stratigraphic column. The increased abundance of *Sphaeroidinella dehiscens* occurred in all of the examined Leg 9 cores just above the initial appearance of *Globigerinoides fistulosus* and just below a sharp coiling change in *Pulleniatina obliquiloculata* from dextral to sinistral. Hays and others (1969) did not record this brief sinistral peak for *Pulleniatina obliquiloculata*, but their coiling tabulation is a composite of all species of *Pulleniatina*. The coiling variation may have been thus "averaged out" between *Pulleniatina obliquiloculata* and *Pulleniatina primalis* because the two taxa exhibit different coiling within this interval.

Hays and others (1969) regarded Datum V as correlative with Bandy's (1963) "*Sphaeroidinella dehiscens* datum." It should be noted that Bandy (1963) also recorded at this interval a pronounced but brief coiling change from dextral to sinistral in populations of *Pulleniatina obliquiloculata* in the Philippines. At about the same level we found that *Pulleniatina primalis* underwent a coiling change from dextral to sinistral. This latter change is not as ephemeral as that found in *Pulleniatina obliquiloculata*, and at Site 77 does not represent a complete change to sinistral coiling (Fig. 3).

Datum VI. The extinction of *Globorotalia margaritae* at the Gauss/Gilbert boundary was not a consistent horizon in the Leg 9 cores. The species has a partial stratigraphic range at Site 77 (Fig. 3) but is rare or absent in the remaining sites. We regard the species as solution susceptible as many specimens at Site 77 showed considerable evidence of solution. Hays and others (1969) also noted the relatively high solution susceptibility of the *Globorotalia margaritae*.

Datum VII. A sharp sinistral to dextral coiling change in *Pulleniatina* just above the Gilbert "a" Event was easily and consistently recognized at all three sites. This coiling change applies only to *Pulleniatina primalis* as the initial appearance of *Pulleniatina obliquiloculata* is well above this horizon. A similar coiling change at about the same stratigraphic level has been recorded by 1) Bandy (1963) in the Philippines, 2) Bandy and Wade (1967) in the South Atlantic, and 3) Bolli (1966a) in Java.

Datum VIII. The extinction of *Globigerina nepenthes* at the top of the Gilbert "a" Event was of limited use in the Leg 9 cores due to the apparent solution susceptibility of the species. Hays and others (1969) noted that the extinction of *Globigerina nepenthes* corresponded closely to the extinction of *Pulleniatina spectabilis*. This latter species is also apparently solution susceptible, but since it occurred in all of the three DSDP sites it was regarded as a more reliable marker than *Globigerina nepenthes* at this level. *Globigerina nepenthes* was only found by us in the lower Pliocene section at one site (77). At Sites 83 and 84 the species disappeared well down below the Gilbert Reversed Epoch in the *Globorotalia plesiotumida* zone of upper Miocene. At about the same horizon (Datum VIII) Hays and others (1969) and Bolli (1966) record a partial coiling change for the species *Globorotalia tumida* from sinistral to dextral. Our cores showed only minor fluctuations in the dominant sinistral coiling pattern of *Globorotalia tumida* at this horizon. These coiling variations in *Globorotalia tumida* seldom involve more than five percent of the total population and extended over much of the Gilbert/Gauss interval. Slight variations in coiling of *Globorotalia tumida* also occur above the Gauss, but we were unable to distinguish any definite correlative horizons from core to core (see Figs. 3, 4).

Datum IX. The first evolutionary appearance of *Pulleniatina spectabilis* from its ancestor *Pulleniatina primalis* near the top of the Gilbert "c" Event was also a difficult datum to recognize in DSDP cores. *Pulleniatina spectabilis* was recorded at the three sites, but only in Site 77 was the occurrence consistent enough to regard its total stratigraphic range with confidence. *Pulleniatina spectabilis* may be the only species of *Pulleniatina* which is solution susceptible. Its stratigraphic range as reported by Parker (1967) is short, and Hays and others (1969) noted that this datum may only be useful in the Indo-Pacific area as the species is apparently restricted to that region.

Datum IX corresponds to the base of the *Sphaeroidinella dehiscens* zone (Fig. 2) which was recognized by the initial appearance of the zonal marker. A similar first occurrence for *Sphaeroidinella dehiscens* was reported by Parker (1967), Banner and Blow (1967), and Blow (1969). Hays and others (1969) extend the range downward slightly to below the base of the Gilbert "c" Event. Just above Datum IX we recorded a brief but distinct fluctuation to dextral in the dominantly sinistrally coiled populations of *Pulleniatina primalis*. Similar minor fluctuations were recorded from this horizon up to the pronounced coiling change in *Pulleniatina primalis* from sinistral to dextral just above the Gilbert "a" Event (Datum VII).

PROPOSED ADDITIONAL DATUMS

In addition to Hays and others (1969) Datums I–IX, we were able to recognize four other distinct datums based on coiling changes in species of *Pulleniatina*. Of the several types of datums used, we found the highest degree of reproductibility in coiling changes. The most important factor affecting the other biostratigraphic parameters (first appearances, extinctions, and abundance changes) is the dissolution of calcium carbonate in the deep sea below the compensation depth. Four new datums are:

1. A short peak of dominantly sinistrally coiled individuals of *Pulleniatina obliquiloculata* near the base of the Jaramillo Event. This datum is coincident with the disappearance of *Globorotalia tosaensis* at Sites 83 and 84 and is located between Datums I and II (Hays and others, 1969). Hays and others (1969) recorded this brief change in coiling and the terminal range of *Globorotalia tosaensis* as synchronous on their summary chart, but in their graph of core V23-59 (p. 1488) they extend the range of *Globorotalia tosaensis* well up into the Brunhes Normal Epoch. Bandy and Wade (1967) also noted a sinistral peak for *Pulleniatina obliquiloculata* at about this interval, and a similar terminal range for *Globorotalia tosaensis* was recorded by Banner and Blow (1967).

2. A pronounced coiling change from dextral to sinistral of both *Pulleniatina primalis* and *Pulleniatina obliquiloculata* occurs between the Gauss Normal Epoch and the base of the Olduvai Event. This event was recorded by Hays and others (1969) between Datums IV and V but does not seem to be as pronounced in the piston cores they examined. No other biostratigraphic events correspond to this datum, but the fact that it involves both species of *Pulleniatina* made it an easily recognized horizon in the Leg 9 cores. At Site 77, the coiling change in *Pulleniatina obliquiloculata* occurs slightly before *Pulleniatina primalis*, whereas in the remaining more eastern Sites 83 and 84 the event appears to be synchronous.

3. Pronounced coiling changes in both species of *Pulleniatina* occur between the top of the Mammoth Event and the Matuyama Epoch. The change is from sinistral to dextral for *Pulleniatina obliquiloculata* and dextral to sinistral for *Pulleniatina primalis*. The advantage of separating the coiling histories of the two species is again illustrated. This event occurs just above Datum V of Hays and others (1969) and is recorded by them as a gradual coiling change of the combined data on both species from dextral to sinistral. Their combined coiling tabulation corresponds to the actual coiling change for *Pulleniatina primalis* and is due to the numerical predominance of *Pulleniatina primalis* in this interval. The event is close to the top of the range of *Globoquadrina altispira* near the top of the Kaena Event as recorded by Hays and others (1969).

4. A short coiling change in *Pulleniatina primalis* from 100 percent sinistral to around 30–50 percent dextral at a maximum occurs just above the Gilbert "c" Event. This datum is just above Hays and others (1969) Datum IX at the top of the Gilbert "c" Event, and they recorded only a minor coiling fluctuation at this point for *Pulleniatina primalis*. At Site 77 only about 10 percent of the population responded to the change, but at the more easterly Sites 83 and 84 the change was pronounced (Figs. 3, 4). At all three sites the event occurred just above the first evolutionary appearance of *Sphaeroidinella dehiscens*.

SIZE DISTRIBUTION

In addition to recording coiling changes, specimen frequency, and stratigraphic ranges, we noted changes in specimen size in certain of the foraminiferal species assemblages. Up to 200 specimens of *Pulleniatina* per sample were measured by micrometer for the maximum diameter of each specimen, and an average specimen size for each of the two species was tabulated for each sample. In order to ascertain any possible connection between size and coiling preference, the samples were originally counted separately for each of the sinistral and dextral groups of *Pulleniatina obliquiloculata* and *Pulleniatina primalis*. There appeared to be no such correlation, and all members of the same species are plotted together on Figures 3, 4.

Comparing the specimen size and the coiling graphs of the two taxa (Figs. 3, 4) it is evident that each of the major coiling changes either corresponds to or is just preceded by a marked reduction in average specimen size. Nevertheless, the average specimen size recovers to normal size rapidly in each case, and the coiling changes correspond to the size graph as a series of sharp dips. This reduction in specimen size may be interpreted in a number of ways, and the distributional pattern certainly merits further study before reasonable conclusions as to its significance may be drawn. If a coiling change is itself the manifestation of an environmental change for a given foraminiferal population, the failure of these individuals to reach mature size is consistent. The impetus for the coiling change may conversely stimulate increased reproductivity in foraminiferal populations to trigger crowding and competition in the populations. It has been demonstrated elsewhere (Orr, 1967, 1969) that the average specimen size in sediment samples may be increased by secondary *post mortem* dissolution removing the juveniles. We doubt that any secondary process would similarly reduce average adult specimen size; thus, we regard this as a primary feature of the original populations. We were able to find no morphological features to distinguish the smaller specimens in the coiling change interval from other small specimens in adjacent intervals. Thus, it appears that coiling changes and the drop in average specimen size are related phenomena in *Pulleniatina primalis* and *Pulleniatina obliquiloculata*.

DIVERSITY

Considerable fluctuations in simple species diversity were recorded in the Pliocene-Pleistocene at Sites 77, 83, and 84 by Jenkins and Orr (1972; p. 1080–1081). More detailed planktonic foraminiferal diversity for original and additional samples counted shows interesting correlations with coiling changes. These fluctuations have been averaged in the present work over intervals much like coiling data (Figs. 3, 4). Although considerable diversity variation from site to site is apparent in the Miocene and older sections (Jenkins and Orr, 1972; p. 1080–1081), the diversity patterns between Sites 77, 83, and 84 in the Pliocene/ Pleistocene interval correspond well with each other. Diversity of Pliocene and Pleistocene faunas may run as high as 30 species or more in a single sample, but the average diversity for any given interval over five meters in thickness almost never exceeds 15 species.

The most significant pattern that emerged was a relationship between coiling and diversity. Major changes in diversity tend to be coincident with major coiling changes in *Pulleniatina obliquiloculata* and *Pulleniatina primalis*. Almost without exception, where the populations were dextrally coiled, the average diversity is on the order of five species or more greater than the adjacent sinistral coiled populations of *Pullenitina*. The only exception to this pattern is in the interval where the coiling of *Pulleniatina primalis* and *Pulleniatina obliquiloculata* was dextral for one population and sinistral for the other between the Mammoth Event and Matuyama Epoch and just above Gilbert "b" Event, Site 84. Because the dips in average size correspond to coiling change events, these changes in the size also correspond to changes in the diversity.

Bandy (1960) recorded coiling changes in planktonic foraminiferal populations of *Neogloboquadrina pachyderma* corresponding geographically to major surface isotherms. The species diversity decrease noted in all of our cores below the base of the Brunhes and corresponding to the coiling change from sinistrally coiled *Pulleniatina obliquiloculata* may represent the end of cool conditions in the eastern equatorial Pacific. This may be further supported by the disappearance at about this interval of cool-water species *Globorotalia inflata* at Sites 77 and 83 and of *Neogloboquadrina pachyderma* at Site 84 (Jenkins and Orr, 1972, p. 1089).

Hays and others (1969) were able to relate carbonate cycles to climatic phases. These agreed with the suggestion by Arrhenius (1952) that the cool glacial phases were periods of increased biologic productivity and consequent increase in calcium carbonate in the stratigraphic record was due to increased intensity of tradewinds and subsequent stronger equatorial current. Carbonate data on DSDP Leg 9 recorded by Hays and others (1972) was not from sufficiently close intervals to compare in detail to findings by Arrhenius (1952) or Hays and others (1969), but the overall $CaCO_3$ curve produced corresponded inasmuch as glacial phases tend to be rich in $CaCO_3$.

CONCLUSIONS

1. Most of the datums proposed by Hays and others (1969) were recognized in the DSDP Leg 9 cores from Sites 77, 83, and 84 through thick Pliocene/Pleistocene sections. We found the most reliable of their datums to be Datums I, III, V, and VII. The datums we had difficulty with were for the most part based on extinctions of species, and the difficulty could be directly attributed to the dissolution of the tests of the foraminifera.

2. The most reliable datums recorded by Hays and others (1969) were coiling changes, and four additional datums based on coiling changes of *Pulleniatina* are proposed. These latter coiling changes are recognized by the separate counting and tabulation of coiling *Pulleniatina obliquiloculata* and *Pulleniatina primalis*.

3. In addition to coiling changes we also found significant variations of the average specimen size in successive populations of *Pulleniatina primalis* and *Pulleniatina obliquiloculata*. The reduction in average specimen size of populations is related to coiling changes such that coiling changes are either accompanied by or just preceded by a marked reduction in the average specimen size of the population undergoing the coiling change.

4. Considerable fluctuation of diversity in Leg 9 cores is apparent, but, like the size variation, major changes in diversity apparently correspond to coiling changes. When coiling in populations of *Pulleniatina*

obliquiloculata changes from sinistral to dextral, the average diversity figures almost invariably increase on the order of five additional species per sample. The coiling change and concurrent diversity increase is interpreted as corresponding to an increase in paleotemperature. Similar interpretations of diversity and paleotemperature changes have been made for the New Zealand Cenozoic planktonic foraminifera (Jenkins, 1968, 1973).

ACKNOWLEDGMENTS

The directors of the Deep Sea Drilling Project are thanked for permission to use DSDP cores for this study. Illustrations are by DSDP personnel and Mr. A. J. Norris-Rogers of the University of Natal.

REFERENCES

Arrhenius, G., 1952, Sediment cores from the East Pacific: Swedish Deep-Sea Exped. (1947–1948) Repts., v. 5, fasc. 1, 89 p.

Bandy, O. L., 1960, The geologic significance of coiling ratios in the foraminifera *Globigerina pachyderma* (Ehrenberg): Jour. Paleontology, v. 34, (4), p. 671–681.

———, 1963, Miocene-Pliocene boundary in the Philippines as related to late Tertiary stratigraphy of deep-sea sediments: Science, v. 142, p. 1290–1292.

Bandy, O. L., and Wade, M. E., 1967, Miocene-Pliocene-Pleistocene boundaries in deep-water environments: Progress in Oceanography, Pergamon Press, v. 4, p. 51–66.

Banner, F. T., and Blow, W. H., 1965, Progress in the planktonic foraminiferal biostratigraphy of the Neogene: Nature, v. 208, p. 1164–1166.

———, 1967, The origin, evolution and taxonomy of the foraminiferal genus *Pulleniatina* Cushman, 1927: Micropaleontology, v. 13, p. 133–162.

Berger, W. H., 1970, Planktonic foraminifera: selective solution and the lysocline: Marine Geology, v. 8, p. 111–138.

Blow, H. M., 1969, Late middle-Eocene to Recent planktonic foraminiferal biostratigraphy: Int. Conference Planktonic Microfossils, 1st (Geneva), p. 199–422.

Bolli, H. M., 1957a, The Genera *Globigerina* and *Globorotalia* in the Paleocene-Eocene Lizard Springs Formation of Trinidad, B.W.I.: U.S. Natl. Mus. Bull., v. 215, p. 61–81.

———, 1957b, Planktonic foraminifera from the Oligocene-Miocene Cipero and Lengua formations of Trinidad, B.W.I.: U.S. Natl. Mus. Bull., v. 215, p. 97–123.

———, 1957c, Planktonic foraminifera from the Eocene Navet and San Fernando Formations of Trinidad, B.W.I.: U.S. Natl. Mus. Bull., v. 215, p. 155–172.

———, 1966a, The planktonic foraminifera in Well Bodjonegoro I of Java: Java: Ecologae Geol. Helvetiae, v. 59, p. 449–465.

———, 1966b, Zonation of Cretaceous to Pliocene marine sediments based on planktonic foraminifera: Asoc. Venezolana Geología, Minería y Petróleo, Bol. Inf., v. 9, p. 3–32.

———, 1970, The foraminifera of sites 23–31: Deep Sea Drilling Proj. Initial Repts., v. 4, p. 577–644.

Bolli, H. M., and Bermudez, P. J., 1965, Zonation based on planktonic foraminifera of middle Miocene to Pliocene warm-water sediments: Asoc. Venezolana Geología, Minería y Petróleo Bol. Inf., v. 8, p. 121–149.

Hays, J. D., Saito, T., Opdyke, N. D., and Burckle, L. H., 1969, Pliocene-Pleistocene sediments of the Equatorial Pacific: their paleomagnetic, biostratigraphic, and climatic record: Geol. Soc. America, Bull., v. 80, p. 1481.

Hays, J. D., Cook, H. E., Jenkins, D. G., Cook, F. M., Fuller, J., Goll, R., Milow, E. D., and Orr, W. N., 1972, Deep Sea Drilling Proj. Initial Repts., v. 9, p. 1205.

Jenkins, D. G., 1968, Variations in the numbers of species and sub-species of planktonic Foraminiferida as an indicator of New Zealand Cenozoic paleotemperatures: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 5, p. 309–313.

———, 1973, Diversity changes in the New Zealand Cenozoic planktonic foraminifera. Jour. Foram. Research, v. 3, (2), p. 78–88.

Jenkins, D. G., and Orr, W. N., 1971, Cenozoic planktonic foraminiferal zonation and the problem of test solution. Rev. Española Micropaleontologia, v. 3, p. 301–304.

———, 1972, Planktonic foraminiferal biostratigraphy of the eastern equatorial Pacific: Deep Sea Drilling Proj. Initial Repts., v. 9, p. 1059–1193.

Orr, W. N., 1967, Secondary calcification in the foraminiferal genus *Globorotalia*: Science, v. 157, p. 1554–1555.

———, 1969, Variation and distribution of *Globigerinoides ruber* in the Gulf of Mexico: Micropaleontology, v. 15, (3), p. 373.

Parker, F. L., 1967, Late Tertiary biostratigraphy (planktonic foraminifera) of tropical Indo-Pacific deep-sea cores: Am. Paleontology Bull., v. 52 (235), p. 115–203.

Ruddiman, W. F., and Heezen, B. C., 1967, Differential solution of planktonic foraminifera: Deep-Sea Research, v. 14, p. 801–808.

Cushman Foundation Special Publication No. 19
Memorial to Orville L. Bandy
p. 287–300, pls. 1–2, 1980

LATE NEOGENE RADIOLARIAN BIOSTRATIGRAPHY RELATED TO MAGNETOSTRATIGRAPHY AND PALEOCEANOGRAPHY WITH SUGGESTED COSMOPOLITAN RADIOLARIAN DATUMS[1]

RICHARD E. CASEY AND RICHARD A. REYNOLDS
Department of Geology, Rice University, Houston, Texas 77001

ABSTRACT

Most radiolarian biostratigraphic datums and zonations currently used (as well as other microfossil datums, and zonations) appear to be time transgressive due to their being based upon warm-water shallow living radiolarians with disjunct distributions whose geographic ranges and local first and last occurrences are controlled mainly by paleoclimatic conditions. The Miocene-Pliocene transition appears to be a time of worldwide cooling (including a cooling in the type locality) and this has probably led to elevations and depressions of the paleontologically recognized boundary in many areas.

In an equatorial Pacific core studied (V24-59) Nigrini's (1971) equatorial Pacific radiolarian Zones 1, 2, and most of 3 occur within the Brunhes Magnetic Epoch, and Zone 4 extends from the Jaramillo Event to the Gilsa or Olduvai Event. Riedel and Sanfilippo's *Pterocanium prismatium* Zone (Riedel and Sanfilippo, 1970, 1977 and 1978) from the Gilsa or Olduvai event into the upper Gauss, the *Spongaster pentas* Zone extends from the upper Gauss to around Gilbert *b*, and their *Stichocorys peregrina* Zone begins around Gilbert *b*. These "warm-water" datums, when compared to radiolarians believed to have been tropical submergent or deep living suggest that tropical submergent or deep living forms may be very useful for establishing "cosmopolitan" datum planes. Two such datums approximating the Miocene-Pliocene boundary are the first occurrences of *Lamprocyclas heteroporos* and *Sphaeropyle langii* at about 4.2 and 5 m.y.a. respectively.

INTRODUCTION

The four main objectives of this paper are: (a) to relate the magnetic stratigraphy of equatorial Pacific core V24-59 to the radiolarian datums and zones of Riedel and Sanfilippo (1970, 1977 and 1978) and Nigrini (1971); (b) to compare these datums and zonation to the Antarctic radiolarian zonation of Hays (1965) and Bandy and others (1971); (c) to relate these datums and zonations to paleoceanographic phenomena; and (d) to give examples of and suggest that radiolarian datums and radiolarian zonation based on inferred and/or known tropical submergent or deep living radiolarians may be the closest approximation to a cosmopolitan zonation.

This paper is especially appropriate for this memorial volume because Dr. Bandy and the senior author originally initiated this project together. Here, we will try to bring in some of Dr. Bandy's thoughts from the conversations the senior author and Dr. Bandy had in the early stages of this project. Dr. Bandy had begun work on specific aspects of this project, including counts of foraminifers from core V24-59. Attempts to

---

[1] Acknowledgment is made to the donors of the Petroleum Research Fund, administered by the American Chemical Society, for the partial support of this research.

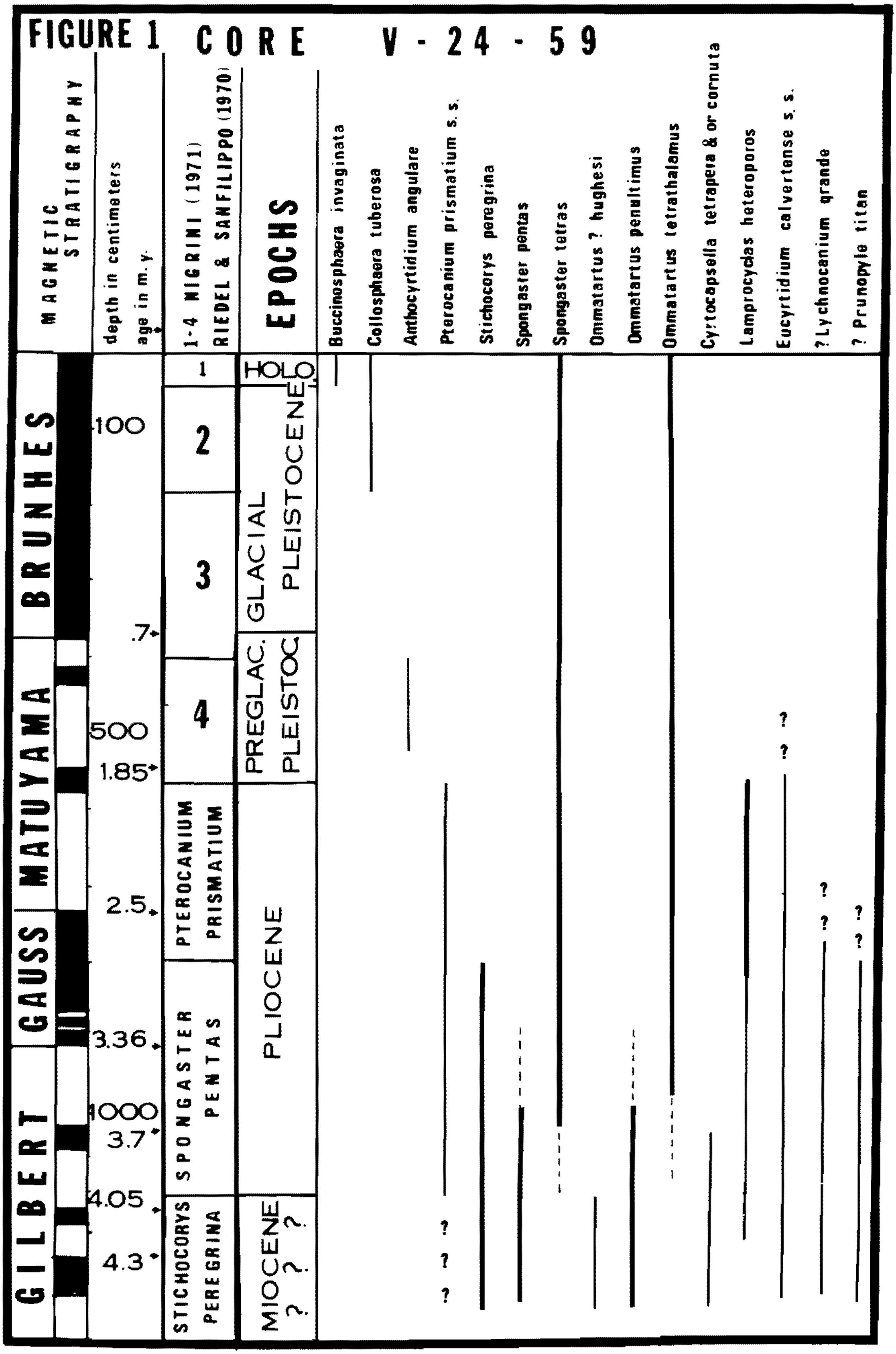


FIGURE 1 CORE V-24-59

relate some of his preliminary work will be mentioned in the appropriate sections.

The works of Hays (1965) and Hays and Opdyke (1967) have been outstanding contributions in developing and relating an Antarctic radiolarian zonation to magnetostratigraphy. Further, Hays and others (1969) presented a classic paper that related a combined paleontologic and paleomagnetic stratigraphy for the late Neogene of the equatorial Pacific. These works are of such significance that the senior author of this paper re-evaluated and added to the radiolarian biostratigraphy of some of Hay's Antarctic cores (Bandy and others, 1971) and we herein re-evaluate the radiolarian biostratigraphy of core V24-59, one of the equatorial Pacific cores studied by Hays and others (1969), and compare them to one another and to other sections.

ANTARCTIC RADIOLARIAN PLANKTONIC DATUM PLANES AND MAGNETOSTRATIGRAPHY

The Antarctic radiolarian zonation of Hays consists of six zones in which the upper limits of occurrence in cores are employed (Hays, 1965, 1967; and Hays and Opdyke, 1967). Three of the Antarctic cores studied by Hays and Opdyke were restudied for additional information (Bandy and others, 1971). One of these cores, E14-8, which is used in this paper, was taken from the western flank of the Albatross Cordillera in the South Pacific Ocean (latitude 59°40′S, longitude 160°17′W).

Prior to the restudy of these Antarctic cores, Bandy (1967) had noted that the widespread occurrence of the radiolarian referred to as *Prunopyle titan* Campbell and Clark in the lower portions of many Antarctic cores might be taken as the upper limit of the Miocene in view of the restriction of this species to the upper Miocene in California (Campbell and Clark, 1944; Ingle, 1967). Upon restudy of these three cores, a number of radiolarians believed to be restricted to the Miocene were found in the deeper portions of these cores (Bandy and others, 1971). Paleotemperatures were reconstructed from these cores using the ratio of "cold" to "warm" radiolarians (Bandy and others, 1971). The *Prunopyle titan* Datum consistently occurred in the upper Gauss. This datum occurred within a cold interval which had been preceded by a warm interval. Warm-water radiolarians such as *Cyrtocapsella tetrapera* Haeckel, and *Ommatocampe hughesi* Campbell and Clark (now *Ommatartus*) suggested that the lower portions of these latter cores were of Miocene age. However, it is now believed by us (and was also believed by Dr. Bandy) that the Miocene-Pliocene boundary is somewhat lower than the *Prunopyle titan* Datum, and is perhaps close to or bounded by the first occurrences of *Lamprocyclas heteroporos* Hays (also *Lamprocyrtis*), and *Sphaeropyle langii* Dreyer in the sense of Foreman (1975).

EQUATORIAL PACIFIC RADIOLARIAN DATUM PLANES AND MAGNETOSTRATIGRAPHY

Core V24-59 from the equatorial Pacific (latitude 2°34′N, longitude 145°22′W) was used for this study because previous work had been done on the radiolarians, foraminifers, diatoms, silicoflagellates, and calcareous nannofossils (Hays and others, 1969; Gartner, 1973) making this core extremely significant in correlating one microfossil zonation with another. This core also had a good magnetic signature with which to compare these datum planes and zonations.

Figure 1 shows the ranges of radiolarians in core V24-59 related to the radiolarian zonations of Nigrini (1971) and Riedel and Sanfilippo (1970), and also related to the paleomagnetic scale of V24-59 from Hays and others (1969). Plates 1 and 2 figure some radiolarians from core V24-59.

Nigrini (1971) developed radiolarian zones for the Quaternary of the equatorial Pacific Ocean. Nigrini's diagnostic taxa are present in core V24-59 and are used to define Nigrini's zones as represented on Figure 1. The *Buccinosphaera invaginata* Range Zone (Zone 1; uppermost Quaternary) is defined by the range of *Buccinosphaera invaginata* Haeckel in accordance with the American Commission on Stratigraphic Nomenclature (1961). This zone is present in about the upper 50 cm of core V24-59. The top of the *Collosphaera*

←

FIGURE 1

Radiolarian ranges from core V24-59 related to the magnetic stratigraphy of that core (magnetic stratigraphy from Hays and others, 1969), the radiolarian zonations of Nigrini (1971) and Riedel and Sanfilippo (1970) and the late Neogene time scale. Thin lines represent rare specimens and/or sporadic occurrences, thick lines represent common occurrences and question marks represent questionable occurrences as discussed in the text. The dashed lines above or below the thick lines represent specimens of those species before or after their evolutionary transition in the sense of Riedel and Sanfilippo (1977). The correlation of the Holocene with Nigrini's Zone 1 is due to chance.

tuberosa Concurrent Range Zone (Zone 2) is defined by the earliest appearance of *B. invaginata*, and the bottom by the earliest appearance of *Collosphaera tuberosa* Haeckel. Within this zone *C. tuberosa*, *Amphirhopalum ypsilon* Haeckel, and *Theocorythium trachelium trachelium* (Ehrenberg) have concurrent ranges. This zone is found within core V24-59 extending from about 50 cm to about 190 cm. The *Amphirhopalum ypsilon* Assemblage Zone (Zone 3) occurs in core V24-59 from about 190 cm to about 390 cm. The top of this zone is defined by the earliest appearance of *C. tuberosa*, and the bottom by the latest appearance of *Anthocyrtidium angulare* Nigrini. The top of the *Anthocyrtidium angulare* Concurrent Range Zone (Zone 4; lowermost Quaternary) is defined by by the latest appearance of *A. angulare*, and the bottom by the latest appearance of *Pterocanium prismatium* Riedel. This zone extends from about 390 cm to about 560 cm in core V24-59. Zones 1 and 2 and almost all of 3 occur within the Brunhes. In fact, the Zone 3–4 boundary is between the Brunhes-Matuyama boundary and the Jaramillo Event. Zone 4 extends to the Gilsa or Olduvai Event. Plates 1 and 2 figure some of the aforementioned species.

Riedel and Sanfilippo (1970 and 1977) developed a Cenozoic radiolarian zonation exclusive of the Quaternary, and later modified this zonation and included the Quaternary (Riedel and Sanfilippo, 1978). The upper two zones and the top of the third are found in core V24-59. The base of the uppermost zone (the *Pterocanium prismatium* Zone) is defined by the last occurrence of *Stichocorys peregrina* (Riedel) (Riedel and Sanfilippo, 1970, 1977 and 1978) and the top by the latest evolutionary occurrence of *P. prismatium* (Riedel and Sanfilippo, 1970 and 1977) (the top is now defined by the evolutionary transition of *Lamprocyrtis neoheteroporos* Kling to *L. haysi* Kling (Riedel and Sanfilippo, 1978)). This zone is represented in core V24-59 by the interval from about 560 cm to about 800 cm. The base of the *Spongaster pentas* Zone was originally defined by the earliest appearance of *P. prismatium* (Riedel and Sanfilippo, 1970 and 1977), and later by the evolutionary transition of *Spongaster berminghami* (Campbell and Clark) to *S. pentas* (Riedel and Sanfilippo) (Riedel and Sanfilippo, 1978). Herein, the base of the *Spongaster pentas* Zone is delineated by the earliest appearance of *P. prismatium* s.s. and the latest occurrence of *Ommatartus hughesi* both of which appear to be near the evolutionary transition of *S. berminghami* in core V24-59. The specimens of *Ommatartus hughesi* in core V24-59 usually do not bear more than one chamber distal of the polar cap such as Figure 5 on Plate 1, but a few are more typical of the type species such as Figure 1 on Plate 2. On Figure 1, question marks are drawn below the solid line depicting the range of *Pterocanium prismatium* s.s. to indicate the range of the possible ancestor to that form. This ancestor differs in having less straight sides, a shorter thorax, and less well-developed thorns on the ribs than does *P. prismatium* s.s. (Pl. 1, Figs. 7 and 8). Riedel and Sanfilippo (1970) in discussing *Pterocanium prismatium* stated, ". . . the original description of this species admitted specimens without thorns on the three thoracic ribs, but such forms are now excluded," and later (Riedel and Sanfilippo, 1978) state, ". . . the use of the lower morphotypic limit of *Pterocanium prismatium* to define the lower limit of this zone was rather unsatisfactory—the use of the evolutionary transition from *Spongaster berminghami* to *S. pentas* will, it is hoped, permit recognition of the lower limit of this zone with greater ease." The *Spongaster pentas* Zone extends from about 800 cm to about 1,100 cm in core V24-59. The top of the *Stichocorys peregrina* Zone is coincident with the base of the *Spongaster pentas* Zone.

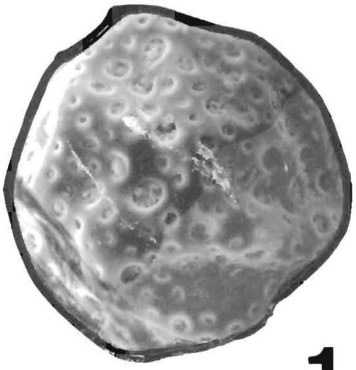
In relating to the zones of Riedel and Sanfilippo (1970, 1977, and 1978) to the magnestostratigraphy of core V24-59, the *Pterocanium prismatium* Zone extends from the Gilsa or Olduvai Event to within the upper Gauss, the *Spongaster pentas* Zone extends

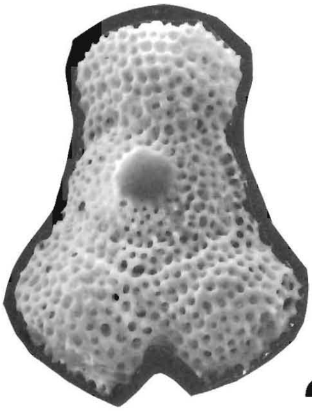
→

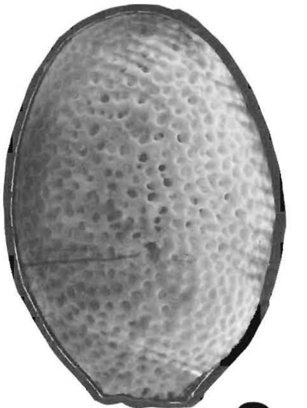
PLATE 1

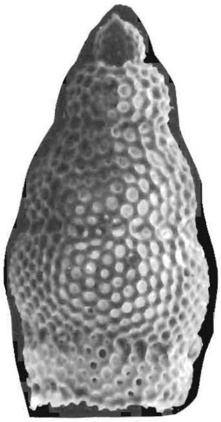
Selected radiolarians from core V24-59, their occurrence given as the depth from top of core, and the approximate length of maximum dimension.

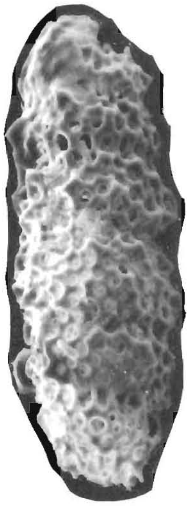
1 *Collosphaera tuberosa* Haeckel. From about 10 cm, 120 μm.
2 *Amphirhopalum ypsilon* Haeckel. Stratigraphic position unknown, 200 μm.
3 ? *Prunopyle titan* Campbell and Clark. 809 cm, 130 μm.
4 *Stichocorys peregrina* (Riedel). 1,008 cm, 200 μm.
5 *Ommatartus* ? *hughesi* (Campell and Clark). 1,191 cm, 220 μm.
6 *Ommatartus penultimus* (Riedel). 1,241 cm, 300 μm.
7 *Pterocanium prismatium* Riedel (in the strict sense). 1,111 cm, 205 μm.
8 Ancestor of *Pterocanium prismatium*. 1,191 cm, 200 μm.
9 *Lamprocyclas heteroporos* Hays. 809 cm, 200 μm.

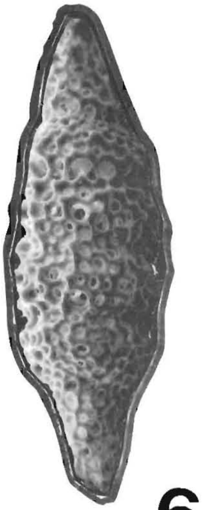

1


2

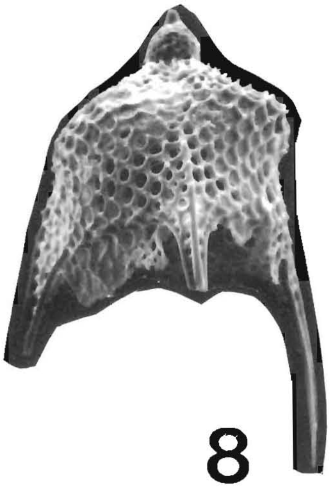

3

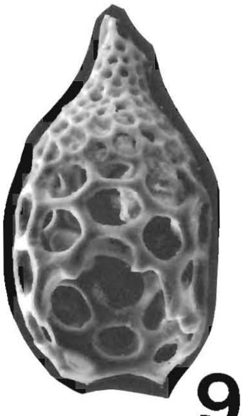

4


5

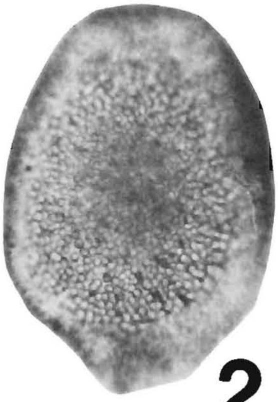

6

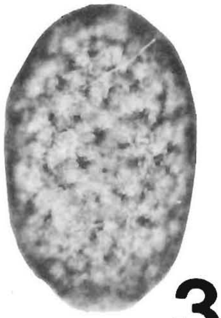

7

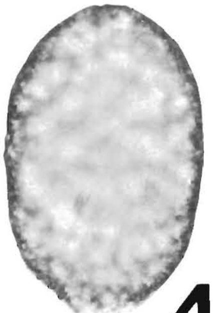

8


9

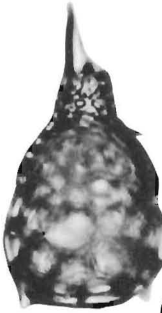

1

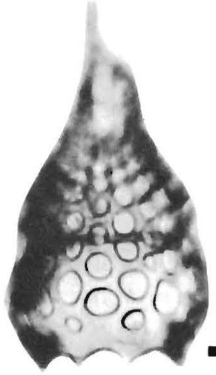

2

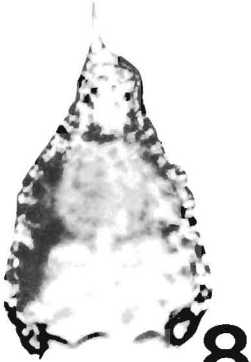

3

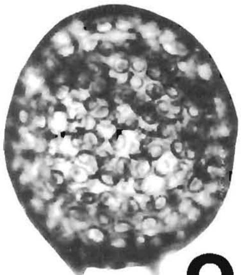

4

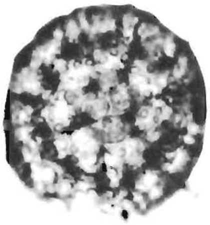

5

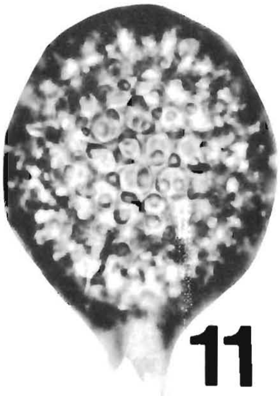

6

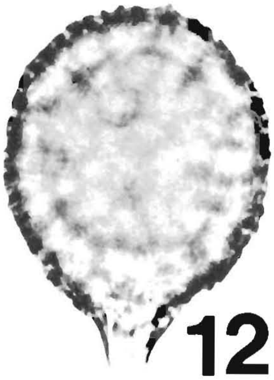

7

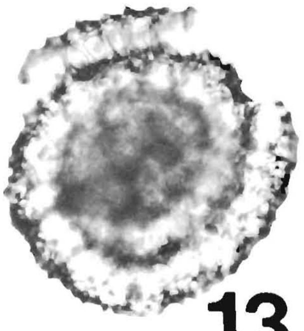

8

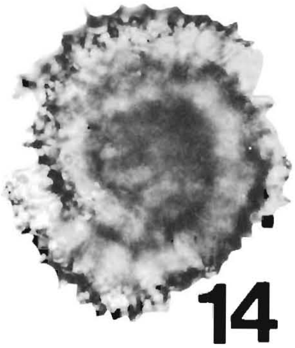

9

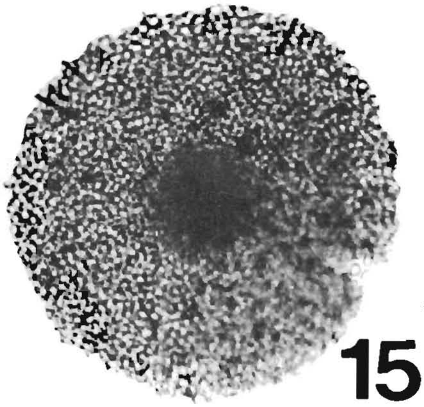

10


11


12


13


14


15

from the upper Gauss to just above Gilbert *b*, and the *Stichocorys peregrina* Zone starts just above Gilbert *b* and extends to the bottom of the core.

Aside from the diagnostic taxa that define the zones of Nigrini (1971) and Riedel and Sanfilippo (1970, 1977, and 1978) other important radiolarian datum planes were studied in core V24-59. At about Gilbert *b* a number of datums occur. These include the first appearance of *P. prismatium* and *Lamprocyclas heteroporos* and the latest occurrence of *Ommatartus ? hughesi. Lamprocyclas heteroporos* is rare in the region represented by the thin line on Figure 1. The species does not become well represented in the core until the base of the *Pterocanium prismatium* Zone indicated by the thicker line. Specimens of this species noted by the thin-lined region do not have as well-developed large pores on their abdomens, or as well-developed abdomens (Pl. 2, Figs. 7 and 8) as the thick-lined region (Pl. 1, Fig. 9; Pl. 2, Figs. 5 and 6).

Other important datums are clustered just above Gilbert *a*. *Spongaster pentas* evolved into *S. tetras* Ehrenberg at this level making it the easiest recognizable paleontological event in the core. The transition from *Ommatartus penultimus* (Riedel) (Pl. 1, Fig. 6) to *Ommatartus tetrathalamus* (Haeckel) also occurs at this level. The last occurrence of *Cyrtocapsella tetrapera* Haeckel (counts of *Cyrtocapsella cornuta* Haeckel were included with *C. tetrapera*) lies just below these other datums.

The next clustering of datum planes occurs within the upper Gauss. At this horizon the last occurrence of *Stichocorys peregrina* delineates the top of the *Spongaster pentas* Zone (Riedel and Sanfilippo, 1978). At about this same horizon, very sparse and sporadic occurrences of what appear to be forms of *Prunopyle titan* (Pl. 1, Fig. 3; Pl. 2, Figs. 2–4) and *Lychnocanium grande* Campbell and Clark last occur. From paleomagnetic evidence, these two forms last occur in the Antarctic at about the same horizons. At this same level in core V24-59, *L. heteroporos* becomes more abundant and more like the type specimen with large irregular abdominal pores and a well-developed abdomen.

The last clustering of datums occurs at the Tertiary-Quaternary boundary with the last occurrences of *P. prismatium*, *L. heteroporos*, and *Eucyrtidium calvertense* Martin s.s. The last occurrence of *E. calvertense* at this level is questionable. *Eucyrtidium calvertense* last occurs in Antarctic cores consistently at the Olduvai or Gilsa Event. Casey (1972) considered the last occurrence of *E. calvertense* as a local extinction in the North Pacific within the pre-glacial Pleistocene. However, Casey's samples produced few specimens, and both Hays (1970) and Kling (1971) found *E. calvertense* in the *Eucyrtidium tumidulum* Zone of Hays (1970) in the North Pacific. There are some specimens that somewhat resemble *E. calvertense* occurring above the Gilsa or Olduvai Event in core V24-59 and *E. calvertense* appears to live in the intermediate waters of the Atlantic today (McMillen and Casey, 1978).

Since the first submission of this paper, in 1974, Johnson and Knoll (1975) compared two cores from the same geographical region to Nigrini's zonation (Nigrini, 1971). Their suggested correlation to the magnetostratigraphy (Johnson and Knoll, 1975) and ours agree fairly well with our Nigrini Zone 1 being somewhat shorter, our Zone 3–Zone 4 boundary being above the Jaramillo Event and their below, and their Nigrini Zone 4–*Pterocanium prismatium* Zone boundary being slightly higher than ours. However, these differences may well be academic, for Johnson and

---

←

PLATE 2

Selected radiolarians from cores V24-59 and E13-17 (their occurrence given as the depth from top of cores), and the Messinian samples mentioned in the text, and the approximate length of maximum dimension.

1 *Ommatartus ? hughesi* (Campbell and Clark). Core V24-59, 1,241 cm, 250 μm.

2 ? *Prunopyle titan* Campbell and Clark. Core V24-59, 1,181 cm, 150 μm (showing mesh).

3, 4 ? *Prunopyle titan* (Campbell and Clark). Core V24-59, 977 cm, 150 μm (3 = mesh, 4 = outline of same specimen).

5, 6 *Lamprocyclas heteroporos* Hays. Core V24-59, 759 cm, 150 μm (regular form), (5 = lattice, 6 = outline of same).

7, 8 *Lamprocyclas heteroporos* Hays. Core V24-59, 1,150 cm, 160 μm (primitive form), (7 = lattice, 8 = outline of same).

9 *Sphaeropyle langii* Dreyer. Core E13-17, 140 μm.

10 *Sphaeropyle langii* Dreyer. Core E13-17, 150 μm.

11, 12 *Sphaeropyle langii* Dreyer. DSDP Hole 77B, core 7, section 1, 24–27 cm, 120 μm (11 shows pores of both outermost shells as do Figures 9 and 10, 12 = outline of same).

13 *Lithelius nautiloides* Popofsky. Messinian sample, 180 μm.

14 *Lithelius nautiloides* Popofsky. Messinian sample, 200 μm.

15 *Spongotrochus glacialis* Popofsky. Messinian sample, 250 μm.

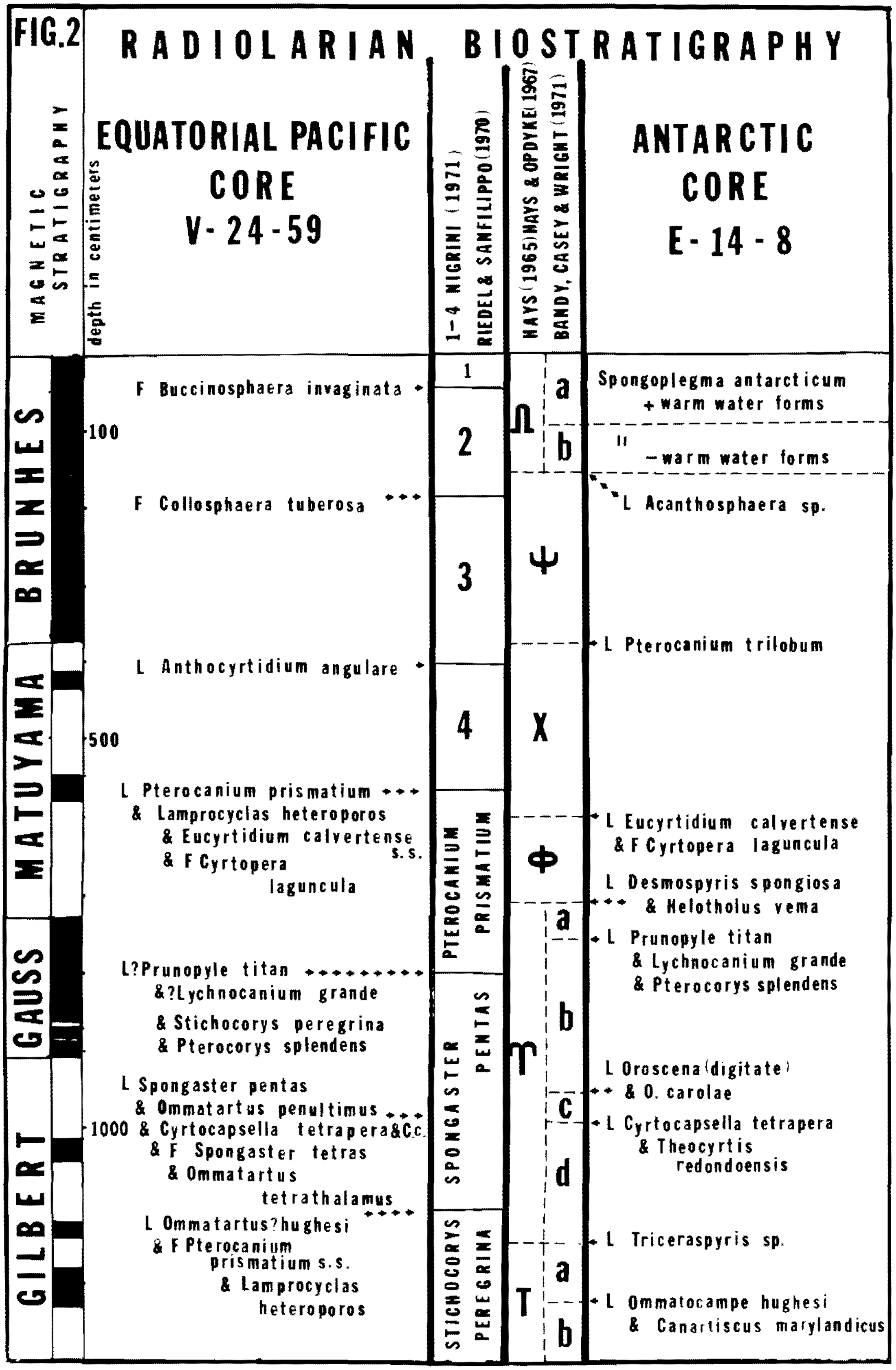


FIG.2 RADIOLARIAN BIOSTRATIGRAPHY

Knoll point out a significant diachroneity (time-transgressive nature) in their cores. We again suggest that during times of major climatic change warm-water (shallow tropical and perhaps temperate) radiolarian datums are time transgressive. This has prompted our search for a more cosmopolitan and less time-transgressive radiolarian zonation.

Dr. Bandy left a hand-tabulated range chart of the foraminifers found in core V24-59. We feel that it is especially appropriate that mention of this be made in this paper and especially in this volume. However, the authors want to make it clear that this document was probably in a preliminary stage and some interpretation was needed to decipher it. Therefore, any inaccuracies are accepted by us. On this range chart, Bandy designated the following datums: the first occurrence of *Sphaeroidinella dehiscens immatura* (Cushman) at 952 cm, the first question-marked occurrence on his range chart shows *Sphaeroidinella dehiscens* (Parker and Jones) (with flange) at 750 cm, the first occurrence of *Globorotalia tosaensis* Takayamagi and Saito at 730 cm, and the only recognition of *Globorotalia truncatulinoides* (d'Orbigny) in a sample at 680 cm. If our interpretations of Bandy's chart are correct the Miocene-Pliocene boundary (assuming the first occurrence of *S. dehiscens immatura* to be the datum marking this boundary) would be at 952 cm in the core or about 3.5 million years ago (which is almost correlative with the last occurrences of *Spongaster pentas* (evolutionary) and *Cyrtocapsella tetrapera-cornuta* and the first evolutionary occurrence of *Spongaster tetras* Ehrenberg and *Ommatartus tetrathalamus* (Haeckel). The only occurrences recorded for *Globorotalia truncatalinoides* occurred between the Gilsa or Olduvai Event and the Gauss. Bandy also recorded sinistral *Neogloboquadrina pachyderma* (Ehrenberg) within Gilbert *a* and sporadic occurrences of its dextral form in the Matuyama.

In working on core V24-59, care was used to distinguish between the "rind" and the "center" of the sediment samples from the core. Dr. Bandy suspected that some of the down core occurrences of foraminiferal species plotted by Hays and others (1969) may have been contaminates due to the dragging down of sediments along the sides of the core barrel. Therefore, samples from both the sides and centers of the cores were processed separately. Dr. Bandy's notes indicate that the oldest *Sphaeroidinella dehiscens* from the center of the core was found near Gilbert *a*, however, he did find some further down in the rind. We did not look extensively into this problem but did note that *Pterocanium prismatium* s.s. did occur in the rind further down core than in samples from the center. Bandy (1973) suggested the Miocene-Pliocene boundary to be at about 3.5 m.y. based on evidence from deep-sea cores and the upper Miocene-lower Pliocene Italian type sections.

A COMPARISON OF AN EQUATORIAL PACIFIC RADIOLARIAN ZONATION TO OTHER MICROFOSSIL DATUM PLANES AND ZONATIONS FOR THE EQUATORIAL PACIFIC AND TO AN ANTARCTIC RADIOLARIAN ZONATION

Figure 2 compares the radiolarian biostratigraphies of the equatorial Pacific (core V24-59) and Antarctic (core E14-8). Both are correlated to the magnetic stratigraphy of core V24-59 (taken from Hays and others, 1969). It is suggested that the last occurrences of *Eucyrtidium calvertense* s.s., *Prunopyle titan,* and *Lychnocanium grande* and perhaps the first occurrence of *Cyrtopera laguncula* Haeckel and the last occurrence of *Pterocorys splendens* (Campbell and Clark) actually occur at the same horizons in V24-59 and E14-8 and represent "cosmopolitan" datums because they are tropical submergent forms. Whereas, the last occurrences of *Ommatartus hughesi* and *Cyrtocapsella tetrapera* are most likely environmentally controlled because they are shallow-water forms. Therefore, their "extinctions" or last occurrences are time transgressive.

Figure 3 compares the radiolarian biostratigraphy herein derived from core V24-59 with Hays and others (1969) zonation form the same core with Berggren and Van Couvering's (1973 and 1974) and Theyer and Hammond's (1974) radiolarian zonations from other sources. All of these zonations are plotted against the magnetostratigraphy for core V24-59 (Fig. 3) assuming all of the Gilbert *c* Event is present. On Figure 3, the foraminiferal, diatom and silicoflagellate datums from Hays and others (1969) are plotted, as are the calcar-

←

FIGURE 2

Radiolarian datum planes and zonations of cores V24-59 and E14-8 are related to one another and to the paleomagnetic signature of core V24-59 (magnetostratigraphy from Hays and others, 1969).

eous nannofossil datums for this core (Gartner, 1973). The acme beginning of *Ceratolithus rugosus* Bukry and Bramlette and the last occurrence of *Ceratolithus tricorniculatus* Gartner (now considered *Amaurolithus tricorniculatus*) are both considered indicative of the earliest Pliocene (Bukry, 1978) and lend support to our contention that the first occurrence of *Lamprocyclas heteroporos* (about 50 cm and 100 cm above these datums respectively) is near the Miocene-Pliocene transition (Fig. 3).

RADIOLARIANS IN THE MESSINIAN AND THEIR BIOSTRATIGRAPHIC AND PALEOCLIMATIC INFERENCES FOR THE MIOCENE-PLIOCENE BOUNDARY

In Messinian samples examined by the authors to date, the last radiolarian zone encountered before the evaporites are encountered, appears to be the *Stichocorys peregrina* Zone. However, this age assignment is questionable. These samples contain few specimens of *Stichocorys peregrina*: and common occurrences of *Lithelius nautiloides* Popofsky (Pl. 2, Figs. 13 and 14) and *Spongotrochus glacialis* Popofsky (Pl. 2, Fig. 15). We believe that the Mediterranean region at that time was perhaps temperate enough for *Stichocorys peregrina* (the forms seen are similar to those "cold forms" from California) but too "cold" for members of the genus *Spongaster*, or the species *Pterocanium prismatium*. Petrushevskaya (1972) shows *P. prismatium* to be more restricted to low-latitude waters through time than was *S. peregrina*, and she also shows a general trend of an equatorial-ward contraction (time transgressive) prior to the extinction of many forms. Whatever the zone, our radiolarian investigation suggests that the Mediterranean region underwent a severe cooling (indicated by the abundance of *L. nautiloides* and *Spongotrochus glacialis*) just prior to the deposition of the evaporite beds. This cooling may help explain the formation of the evaporites if a cooling (glaciation) can be associated with eustatic drop in the sea level that helped or served to isolate the Mediterranean Basin from the Atlantic. A similar cooling and eustatic drop in sea level for the Messinian has been suggested by Bandy (1973). Bandy's chart herein referred to recorded sinistral *Neogloboquadrina pachyderma* within Gilbert *a* which also suggests cooling. The paleotemperatures from the Antarctic (Bandy and others, 1971) show a dramatic cooling between about Gilbert *b* and *c* and this may well reflect the same worldwide cooling and eustatic sea level drop. We believe that one of the main problems with recognizing the Miocene-Pliocene boundary in many regions is that the actual boundary at the type locality (and worldwide) was synchronous with a time of glaciation or at least a cold interval. In the type locality the shallow or shoaling sill at Gibraltar may have blocked the entrance of tropical submergent species such as *Sphaeropyle langii* and *Lamprocyclas heteroporos* which appear to be cosmopolitan species whose first appearances approximates the boundary. Many coeval last occurrences of certain diagnostic species may then appear either below or above the actual boundary in many parts of the world or would be time transgressive as Petrushevskaya (1972) showed for the last occurrence of a number of radiolarians. This is because these diagnostic species are "warm-," shallow-water species that exhibit time-transgressive last occurrences at different latitudes and/or different paleotemperatures, and also because their distributions are disjunct or provincial since about the middle Miocene (Casey and McMillen, 1977).

LAMPROCYCLAS HETEROPOROS AND *SPHAEROPYLE LANGII* AS COSMOPOLITAN INDICATORS APPROXIMATING THE MIOCENE-PLIOCENE BOUNDARY

We suggest that *Lamprocyclas heteroporos* is a tropical submergent radiolarian with a cosmopolitan distribution. Theyer (1973) found *L. heteroporos* to first occur within Gilbert *b*. Hays (1970) shows *L. heteroporos* extending slightly below Gilbert *b*, and Boellstorff and Steineck (1975) state that their fission track ages for the Malga Cove section confirm that *L. heteroporos* evolved at about 4.2 m.y.a.

Sphaeropyle langii Dreyer (Pl. 2, Figs. 9–12) in the sense of Foreman (Foreman, 1975) is also herein considered a tropical submergent species that is biostratigraphically useful. Foreman (1975) defined the *Sphaeropyle langii* Zone (the base is defined by the

→

FIGURE 3

Radiolarian zonation from this paper related to the zones for this core of Hays and others (1969), the zonations of Berggren and Van Couvering (1973 and 1974) and Theyer and Hammond (1974), the microfossil datum planes other than radiolarian for core V24-59 from Hays and others (1969) and Gartner (1973). All are correlated to the magnetic stratigraphy of core V24-59 from Hays and others (1969).

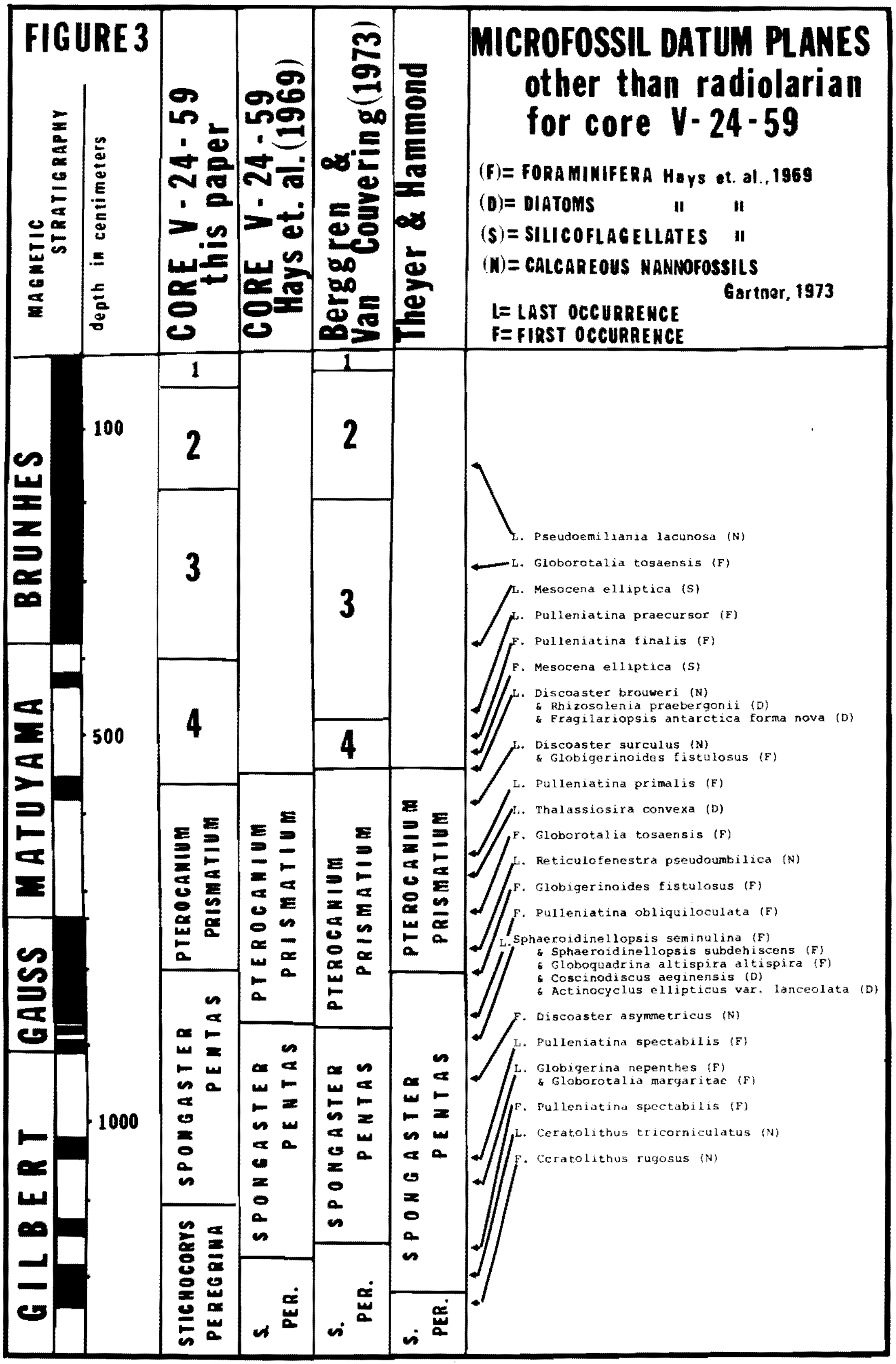


FIGURE 3

MICROFOSSIL DATUM PLANES other than radiolarian for core V-24-59
(F)= FORAMINIFERA Hays et. al., 1969
(D)= DIATOMS " "
(S)= SILICOFLAGELLATES "
(N)= CALCAREOUS NANNOFOSSILS Gartner, 1973
L= LAST OCCURRENCE
F= FIRST OCCURRENCE
MAGNETIC STRATIGRAPHY
depth in centimeters
100
500
1000
BRUNHES
MATUYAMA
GAUSS
GILBERT
CORE V-24-59 this paper
CORE V-24-59 Hays et. al. (1969)
Berggren & Van Couvering (1973)
Theyer & Hammond
1
2
3
4
PTEROCANIUM PRISMATIUM
SPONGASTER PENTAS
STICHOCORYS PEREGRINA
S. PER.
L. Pseudoemiliania lacunosa (N)
L. Globorotalia tosaensis (F)
L. Mesocena elliptica (S)
L. Pulleniatina praecursor (F)
F. Pulleniatina finalis (F)
F. Mesocena elliptica (S)
L. Discoaster brouweri (N) & Rhizosolenia praebergonii (D) & Fragilariopsis antarctica forma nova (D)
L. Discoaster surculus (N) & Globigerinoides fistulosus (F)
L. Pulleniatina primalis (F)
L. Thalassiosira convexa (D)
F. Globorotalia tosaensis (F)
L. Reticulofenestra pseudoumbilica (N)
F. Globigerinoides fistulosus (F)
F. Pulleniatina obliquiloculata (F)
L. Sphaeroidinellopsis seminulina (F) & Sphaeroidinellopsis subdehiscens (F) & Globoquadrina altispira altispira (F) & Coscinodiscus aeginensis (D) & Actinocyclus ellipticus var. lanceolata (D)
F. Discoaster asymmetricus (N)
L. Pulleniatina spectabilis (F)
L. Globigerina nepenthes (F) & Globorotalia margaritae (F)
F. Pulleniatina spectabilis (F)
L. Ceratolithus tricorniculatus (N)
F. Ceratolithus rugosus (N)

first occurrence of *S. langii* and the top by the last occurrence of *Stichocorys peregrina*) and placed its lower limit just below the Miocene-Pliocene boundary.

The junior author used the first occurrence of *S. langii* in the same sense as Foreman (1975) to delineate the Miocene-Pliocene boundary in Deep Sea Drilling Project samples off Japan (Reynolds, in press). *Sphaeropyle langii* extends to the bottom of core V24-59. The magnetic stratigraphy below 1,650 cm on core E14-8 is not reliable (Hays and Opdyke, 1967), however, Antarctic core E13-17 (latitude 65°14′S, longitude 123°06′W) penetrates magnetic Epoch 5 with the Gilbert-Epoch 5 boundary at 2,200 cm. In this core (E13-17) *S. langii* was found to a depth of 2,126 cm which by extrapolation would be about 5 m.y.a. In Deep Sea Drilling Project Hole 77B (equatorial Pacific) the oldest *S. langii* we have found is in core 8, section 1 at 25 to 27 cm yielding a similar absolute age assignment (approximately 5 m.y.a., van Andel and others, 1975). In the Malaga Cove section of southern California the oldest *S. langii* occurs in Casey's sample C-20-2 stratigraphically below the first occurrence of *Lamprocyclas heteroporos* (Casey and others, 1972). Therefore, it seems that the first occurrence of *S. langii* is a cosmopolitan datum, and occurs at or near the commonly accepted age of the Miocene-Pliocene boundary or about 5 m.y.a. However, it appears that *S. langii* is somewhat susceptible to dissolution, at least more so than *L. heteroporos* which appears to be very solution resistant.

SUGGESTED COSMOPOLITAN RADIOLARIAN DATUM PLANES USING INFERRED TROPICAL SUBMERGENT AND/OR DEEP LIVING RADIOLARIANS AND CONCLUSIONS

Many radiolarian datum planes and zonations are either provincial, such as Riedel and Sanfilippo's "warm-water" Cenozoic, and Nigrini's equatorial Quaternary zonations (Casey and McMillen, 1977), or are time transgressive, such as has been shown by Petrushevskaya (1972). Studies herein suggest that at least some radiolarians might exhibit fairly consistent datum planes of a more or less cosmopolitan nature. These were apparently shallow-living polar and/or temperate forms that were "endemic" to descending water masses (intermediate and central) and exhibit tropical submergence, or are deep living cosmopolitan forms (of deep or bottom water). Living radiolarians exhibiting this type of distribution have been described by Casey (1971 and 1977), Casey and McMillen (1977), and McMillen and Casey (1978). These include *Cyrtopera laguncula* Haeckel endemic to the intermediate water masses, *Peripyramis circumtexta* Haeckel in both central and intermediate water masses and probably *Sphaeropyle langii* although we have not observed this species in the plankton to date, *Cornutella profunda* Ehrenberg endemic to intermediate and deeper waters, and *Clathrocyclas bicornis* Hays endemic to intermediate and North Atlantic Deep Water (J. Spaw of Rice University has recently found radiolarians perhaps indicative of Antarctic Bottom Water). Fossil radiolarians believed to have possibly exhibited this type of distribution include: (1) *Lamprocyclas heteroporos* probably endemic to the diving Central Water Masses as it does not occur in sediments south of the Antarctic Convergence (Hays, 1965) but does occur in sediments south of the Subtropical Convergence (Hays, 1965 and Theyer, 1972), (2) *Prunopyle titan* and *Lychnocanium grande* probably endemic to the descending Intermediate Water Masses as they were found by Weaver (1973) to occur as far south as 65 and 63 degrees respectively in his cores, well south of the present day Antarctic Convergence where the Intermediate Water descends, and (3) *Eucyrtidium calvertense* s.s. which appears to have occurred in both central and intermediate water masses due to its relatively common occurrence in V24-59 and its occurrence as far south as *P. titan* in Weaver's cores (1973). *Eucyrtidium calvertense* appears to live in intermediate waters in the Atlantic today (McMillen and Casey, 1978). These fossil forms may well prove to exhibit "cosmopolitan" datum planes (from poleward of sub-tropical convergence to poleward of sub-tropical convergence or from poleward of polar convergence to poleward of polar convergence), and a biostratigraphic zonation based on radiolarians of this type may be used to develop a "cosmopolitan" biostratigraphic zonation. These fossil species are considered to exhibit this tropical submergent pattern of distribution because their occurrence in fossil sediments mirrors the occurrences of the living tropical submergent forms in recent sediments (being dominant in high latitudes and rare in tropical sediments). Their occurrence in core V24-59 is shown in Figure 1. Their consistency as useful datum planes is suggested by comparing their extinctions and evolutions in high (core E14-8) and low (core V24-59 latitudes with magnetostratigraphy as shown on Figure 2. *Lamprocyclas heteroporos* last occurs near The Olduvai or Gilsa Event, and *Lynchnocanium grande* and *Prunopyle titan* (and their submergent counterparts ?*L. grande* and ?*P. titan*) consistently last occur within the upper Gauss; whereas *Lamprocyclas heteroporos* apparently first occurs in a primitive form just below Gilbert *b*. Using this same line of reasoning, it is possible to suggest that *Theocyrtis redondoensis* s.s. Campbell and Clark exhibited a bipolar pattern of distribution instead of a tropical submergent pattern for it appears at high and mid latitudes during the late Neogene but not at low latitudes (such as core V24-59), we have also found it in the Messinian samples suggesting it is a shallow- and cold-water form. Another line of evidence, which can be cited in support of these forms being endemic to descending waters, is their slower or lack of response to small climatic variations when compared with tropical surface living forms (Reynolds, 1978).

These ideas are still preliminary and will need to be tested in future studies. For example, Weaver (1973) has shown that in extreme high latitudes in the Southern Ocean some of these "cosmopolitan" species such as *Prunopyle titan* and *Lychnocanium grande* are time transgressive. This might be expected for at these latitudes we are observing fluctuations in the shallow-water terminal range of these species which should fluctuate with time and paleoceanographic changes similar to the aforementioned ranged of *Lamprocyclas heteroporos* poleward of the Subtropical Convergences.

Lamprocyclas heteroporos and *Sphaeropyle langii* are the only preserved species we know of whose first occurrences are cosmopolitan in nature and approximate the Miocene-Pliocene boundary. The absolute age assignments for these two first occurrences of species are as follows: *L. heteroporos* may be used as a datum approximating 4.2 m.y.a. and *S. langii* may be used as a datum approximating 5 m.y.a.

To further develop such a cosmopolitan radiolarian zonation a number of parallel investigations should take place and to some extent are taking place such as: Casey and McMillen's (1977) and McMillen and Casey's (1978) work on living radiolarians to determine which of the living species are deep living and cosmopolitan, to gain information on their morphologic characteristics and distributions in present day sediments, and to infer a deep living niche for extinct forms; detailed radiolarian biostratigraphic work in high latitudes such as the work of Hays and Opdyke (1967), Foreman (1975), and Kling (1973) and Reynolds (in press) and the relation of such work to low latitude radiolarian biozonations and the magnetic scale if possible because many high-latitude radiolarians are tropical submergent and therefore, their datums may not be time transgressive; and develop a zonation based on these forms as herein started or as Reynolds (1978) knowingly did for the cornutellids and as Friend and Riedel (1967) and Nigrini (1977) unknowingly started by their first attempts at using orosphaerids and artostrobids (from our recent plankton work these forms appear to be mainly deep living) in zonation schemes.

ACKNOWLEDGMENTS

Acknowledgment is made to the Donors of The Petroleum Research Fund, administered by the American Chemical Society, for the partial support of this research. Additional support came through the Oceanography Section, National Science Foundation, NSF Grants DES74-21805 and OCE74-21805 A01.

The senior author most gratefully acknowledges the help in obtaining samples, cooperative analysis, and the years of friendship of the late Orville L. Bandy. Dr. Bandy was instrumental in obtaining many of the samples used for this study and for many of the ideas for this and many other studies of the senior author. Thanks also go to the National Science Foundation for making available core E14-8 and samples from the Deep Sea Drilling Project. Samples of core V24-59 were provided by the Lamont-Doherty Geological Observatory, through Dr. James D. Hays and Mr. Roy R. Capro, for which we are most grateful. Grants from ONR (N00014-67-A-0108-0004) and NSF (GA-29460) helped to maintain the core storage facilities at Lamont-Doherty. The Messinian samples referred to in the text were supplied by Dr. Walter W. Wornardt, Jr., of the Redlands University. Thanks also to Dr. Benjamin N. Powell and Mr. Steve Schafersman, both of Rice University, for taking the SEM photographs at the Carey Corneis Electron Microprobe-Scanning Electron Microscope Facility, Rice University. The editorial and typing assistance were provided by Gail Sandle, Rebecca Lindig, and the late Barbara Hawkins, all of the Geology Department of Rice University.

REFERENCES

American Commission on Stratigraphic Nomenclature, 1961, Code of stratigraphic nomenclature: Am. Assoc. Petroleum Geologists Bull., v. 45, p. 645–665.

Bandy, O. L., 1967, Problems of Tertiary foraminiferal and radiolarian zonation, circum-Pacific area: Pacific Sci. Cong., 11th Tokyo, Japan, August, 1966, Symposium 25, *Tertiary Correlations and Climatic Changes in the Pacific*, Sasaki Sendai, Japan, p. 95–102.

———, 1973, Chronology and paleoenvironmental trends, Late Miocene-Early Pliocene, western Mediterranean, *in* Drooger, E. W., ed., *Messinian Events in the Mediterranean:* Koninkl. Nederlandse Akad. Wetensch., Amsterdam, p. 21–25.

BANDY, O. L., CASEY, R. E., and WRIGHT, R. C., 1971, Late Neogene planktonic zonation, magnetic reversals, and radiometric dates, Antarctic to the tropics, *in* Reid, J. L., ed., *Antarctic Oceanology I:* Antarctic Research Series, 15, p. 1–26.

BERGGREN, W. A., and VAN COUVERING, J., 1973, *Late Neogene chronostratigraphy, biostratigraphy, biochronology and paleoclimatology.* Technical report, prepared for the National Science Foundation, p. 1–275, unpublished manuscript.

———, 1974, The Late Neogene, biostratigraphy, geochronology and paleoclimatology of the last 15 million years in marine and continental sequences: Elsevier, p. 216.

BOELLSTORFF, J. D., and STEINECK, P. L., 1975, The stratigraphic significance of fission-track ages on volcanic ashes in the marine late Cenozoic of southern California: Earth and Planetary Sci. Letters, v. 27, p. 143–154.

CAMPBELL, A. S., and CLARK, R. L., 1944, Miocene radiolarian faunas from southern California: Geol. Soc. America Spec. Paper 51, p. 1–76.

CASEY, R. E., 1971, Radiolarians as indicators of past and present water-masses, *in* Funnell, B. M., and Riedel, W. R., eds., *Micropaleontology of Oceans:* Cambridge Univ. Press. p. 331–341.

———, 1972, Neogene radiolarian biostratigraphy and paleotemperatures: southern California, the experimental Mohole, Antarctic core E14-8: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 12, p. 115–130.

———, 1977, The ecology and distribution of recent Radiolaria, *in* Ramsay, A. T. S., ed., *Oceanic Micropaleontology:* Cambridge Univ. Press, p. 809–843.

CASEY, R. E., and MCMILLEN, K. J., 1977, Cenozoic radiolarians of the Atlantic basin and Margins, *in* Swain, F. M., ed., *Stratigraphic Micropaleontology of Atlantic Basin and Borderlands:* Elsevier, Amsterdam, p. 521–544.

CASEY, R. E., PRICE, A. B., and SWIFT, C. A., 1972, Radiolarian definition and paleoecology of the late Miocene to early Pliocene in southern California, *in* Stinemeyer, E. H., and Church, C. C., eds., *Proc. of the Pacific Coast Miocene Biostratigraphic Symposium*: Pacific Section S.E.P.M., p. 226–238.

FOREMAN, H. P., 1975, Radiolaria from the North Pacific, Deep Sea Drilling Project, Leg 32, *in* Larson, R. L., Moberly, R., and others, Initial Reports of the Deep Sea Drilling Project: U.S. Govt. Printing Office, v. 32, p. 579–676.

FRIEND, J. K., and RIEDEL, W. R., 1967, Cenozoic orosphaerid radiolarians from tropical Pacific sediments: Micropaleontology, v. 13, p. 217–232.

GARTNER, S., 1973, Absolute chronology of the late Neogene calcareous nannofossil succession in the equatorial Pacific: Geol. Soc. America Bull., v. 84, p. 2021–2034.

HAYS, J. D., 1965, Radiolaria and late Tertiary and Quaternary history of Antarctic seas, *in Biology of Antarctic Seas II*: Am. Geophys. Union, Antarctic Research Series, v. 5, p. 125–184.

———, 1967, Quaternary sediments of the Antarctic Ocean, *in* Sears, M., ed., *Progress in Oceanography*: Pergamon, v. 4, p. 117–131.

———, 1970, The stratigraphy and evolutionary trends of radiolaria in north Pacific deep-sea sediments: Geol. Soc. America Mem. 126, p. 185–218.

HAYS, J. D., and OPDYKE, N. D., 1967, Antarctic Radiolaria, magnetic reversals, and climatic change: Science, 158, p. 1001–1011.

HAYS, J. D., SAITO, T., OPDYKE, N. D., and BURCKLE, L. H., 1969, Pliocene-Pleistocene sediments of the equatorial Pacific: their paleomagnetic, biostratigraphic, and climatic record: Geol. Soc. America Bull., v. 80, p. 1481–1514.

INGLE, J. C., JR., 1967, Foraminiferal biofacies variation and the Miocene-Pliocene boundary in southern California: Bull. Am. Paleontology, v. 52, p. 217–394.

JOHNSON, D. A., and KNOLL, A. H., 1975, Absolute Ages of Quaternary Radiolarian Datum Levels in the Equatorial Pacific: Quaternary Research, v. 5, p. 99–110.

KLING, S. A., 1971, Radiolaria, Leg 6 of the Deep Sea Drilling Project: Deep Sea Drilling Proj. Initial Repts., v. 6, p. 1069–1117.

———, 1973, Radiolaria from the eastern North Pacific, Deep Sea Drilling Project, Leg 18: Deep Sea Drilling Proj. Initial Repts., v. 18, p. 617–671.

MCMILLEN, K. J., and CASEY, R. E., 1978, Distribution of living polycystine radiolarians in the Gulf of Mexico and Caribbean Sea, and comparison with the sedimentary record: Marine Micropaleontology, v. 3, p. 121–145.

NIGRINI, C., 1971, Radiolarian zones in the Quaternary of the equatorial Pacific Ocean, *in* Funnell, B. M., and Riedel, W. R., eds., *Micropalaeontology of Oceans*: Cambridge Univ. Press, p. 443–461.

———, 1977, Tropical Cenozoic Artostrobiidae (Radiolaria): Micropaleontology, v. 23, p. 241–269.

PETRUSHEVSKAYA, M. G., 1972, Biostratigraphy of deep-water Quaternary deposits from radiolarian analysis: Oceanology, v. 12, p. 57–70.

REYNOLDS, R. A., 1978, Cosmopolitan biozonation for Late Cenozoic radiolarians and paleoceanography from Deep Sea Drilling Project Hole 77B of Leg 9: Gulf Coast Assoc. Geol. Soc. Trans., v. 28, p. 423–431.

———, in press, Radiolarians from DSDP Leg 57, Japan Trench: *in* Nasu, N., and Von Huene, R. S., Initial Reports of the Deep Sea Drilling Project, v. 57, U.S. Govt. Printing Office.

RIEDEL, W. R., and SANFILIPPO, A., 1970, Radiolaria, Leg 4, Deep Sea Drilling Project: Deep Sea Drilling Proj. Initial Repts., v. 4, p. 502–575.

———, 1977, Cainozoic Radiolaria *in* Ramsay, A. T. S., ed., *Oceanic Micropaleontology*: Cambridge Univ. Press., p. 847–912.

———, 1978, Stratigraphy and evolution of tropical Cenozoic radiolarians: Micropaleontology, v. 23, p. 61–96.

THEYER, F., 1972, Late Neogene paleomagnetic and planktonic zonation, southeast Indian Ocean-Tasman Basin: Univ. of Southern California, unpublished doctoral thesis.

———, 1973, Globorotalia truncatulinoides Datum Plane: Evidence for a Gauss (Pliocene) Age in Subantarctic cores: Nature Phys. Sci., v. 241, p. 142–145.

THEYER, F., and HAMMOND, S. R., 1974, Paleomagnetic polarity sequence and radiolarian zones, Brunhes to Polarity Epoch 20. Earth and Planetary Sci. Letters, v. 22, p. 207–319.

THEYER, F., MATO, C. Y., and HAMMOND, S. R., 1978, Paleomagnetic and geochronologic calibration of latest Oligocene to Pliocene radiolarian events, equatorial Pacific: Marine Micropaleontology, v. 3, p. 377–395.

VAN ANDEL, T. H., HEATH, G. R., and MOORE, T. G., 1975, *Cenozoic History and Paleoceanography of the Central Equatorial Pacific Ocean*: Geol. Soc. America Mem. 143, 134 pp.

WEAVER, F. M., 1973, Pliocene paleoclimatic and paleoglacial history of east Antarctica recorded in deep sea piston cores: Florida State Univ., unpublished masters thesis.