Modern Foraminifera
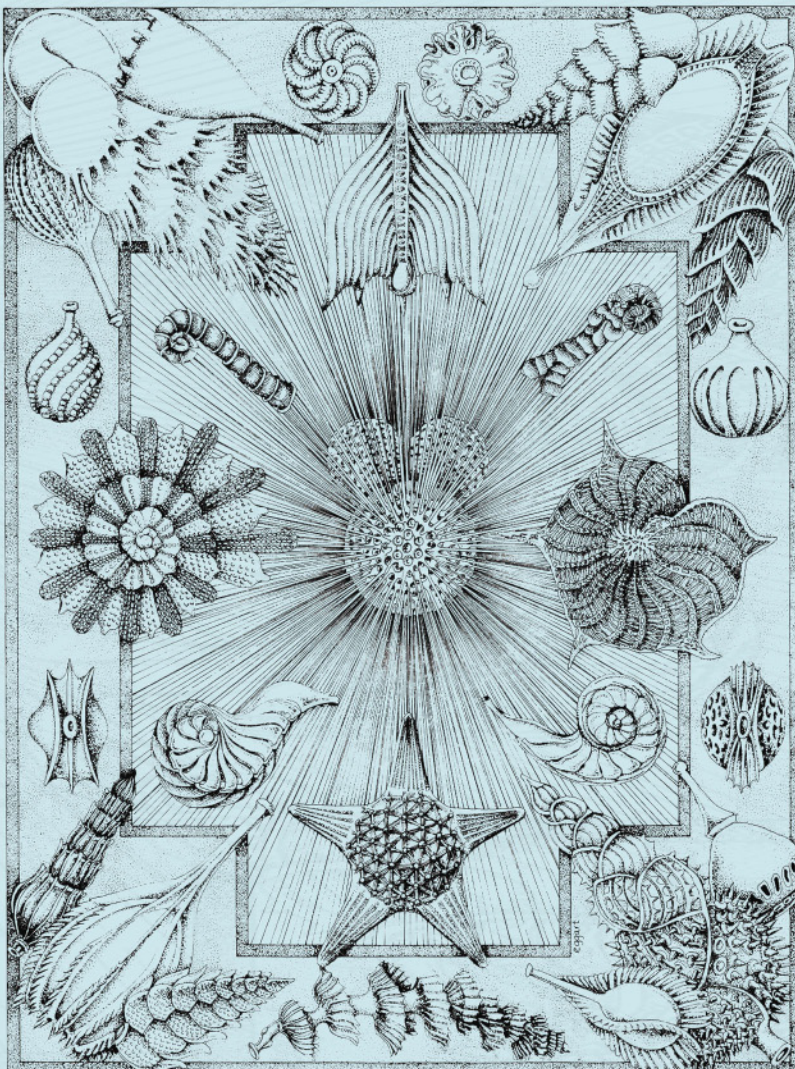
Barun K. Sen Gupta (Editor)

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edited by

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Nous disons qu'elle est à la portée de tout le monde, en ce sens que, placé n'importe où, sur les côtes des diverses portions du globe terrestre ou sur les parties des continents recouvertes par des terrains tertiares, crétacés ou oolithiques, partout disons-nous, l'observateur trouve sous ses pieds, et dans une seule pincée de sable, une grande quantité de Foraminifères qu'il peut étudier avec le seul secours d'une loupe. Pour l'importance réelle de leur étude, nous croyons qu'il n'est pas de série animale offrant plus de facilités et d'avantages au géologue et au zoologiste: au premier, pour déterminer la température des lieux où vivaent les espéces perdues, par la comparaison avec ce que nous voyons maintenant dans les mers, et pour expliquer la formation des couches (questions de la plus haute importance dans l'histoire de notre planète); au second, par leur admirable diversité, par l'élégance de leurs formes, par la singularité de leur organisation, et enfin en ce qu'ils constituent une classe des plus nombreuses du règne animal, et jouent, malgré leur petitesse, un rôle immense dans la nature.

Alcide d'Orbigny, 1839, in Ramon de la Sagra, *Histoire Physique, Politique et Naturelle de l'Ile de Cuba*

Love the organisms for themselves first, then strain for general explanations, and, with good fortune, discoveries will follow. If they don't, the love and pleasure will have been enough.

Edward O. Wilson, 1994, *Naturalist.*

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Preface
and Acknowledgments

Modern Foraminifera started with a simple idea: to write an advanced text for university students that would also serve as a reference book for professionals. Being keenly aware of the boundaries of my competence, I invited fourteen colleagues to write most of the chapters. The chapters were designed to be balanced reviews, but, with the lone exception of chapter two, they had to be written under a rather stringent space limitation. Thus, although the list of references is long, it surely does not include every single significant article on every topic covered in the book. Both the subject matters of the chapters and the selection of authors were entirely my responsibility, and no other author can be accused of a personal bias in the structure of the book. I have assumed that the reader will have an elementary knowledge of foraminiferal shell morphology, as found in undergraduate paleontology texts.

I am deeply indebted to the reviewers who helped shape the chapters into their final form. They are: Paul Aharon, Elisabeth Alve, Laurie Anderson, Anthony Arnold, William Berggren, Joan Bernhard, Samuel Bowser, Kevin Carman, Robert Carney, Lui-Heung Chan, Bruce Corliss, Robert Douglas, Thomas Gibson, Susan Goldstein, Andrew Gooday, Pamela Hallock, Jeffrey Hanor, John Haynes, Johann Hohenegger, Scott Ishman, Frans Jorissen, Susan Kidwell, Martin Langer, David Lea, Richard Norris, William Parker, Nancy Rabalais, Charles Ramcharan, Charles Schafer, Scott Snyder, Kenneth Towe, Bert van der Zwaan, and two others who chose to remain anonymous. Jessica Schreyer assisted in editorial tasks. In the final stages of putting the book together, my burden was lightened by the cheerful cooperation of Petra van Steenbergen, our publishing editor at Kluwer. In addition, I was helped by Ian Francis at the planning stage of the book.

Two people deserve special acknowledgment. I am grateful to Mary Lee Eggart for the art on the cover and in several chapters, and to Poree Sen Gupta, my wife, for her tolerance of my obsessive preoccupation with the book for the past two years.

Finally, I thank the Cushman Foundation for its very special role in publishing and promoting foraminiferal research. In appreciation of this service, the royalty for the book has been transferred to this organization.

Baton Rouge   Barun K. Sen Gupta
December, 1998

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PART I:
BASIC
CONSIDERATIONS

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1

Introduction to modern Foraminifera

Barun K. Sen Gupta

'These minute animals are interesting objects of study, geologically and biologically as well as esthetically. As objects of beauty they arrest the attention of even the casual observer by the delicacy of their structure as well as the symmetry and variety of their forms. Geologically they are of interest because they are among the most ancient and abundant of fossils and also the most efficient of rock builders. Biologically they are instructive examples of the powers and possibilities of an individualized bit of protoplasm.'

James M. Flint, 1899, *Recent Foraminifera: A Descriptive Catalogue of Specimens Dredged by the U.S. Fish Commission Steamer Albatross.*

Foraminifers are better known for their spectacular fossil record than for their variety or abundance in modern marine environments. They, however, constitute the most diverse group of shelled microorganisms in modern oceans. In 1846, Alcide d'Orbigny counted 68 modern foraminiferal genera, and estimated that there are 1,000 modern species. In the latest taxonomic *magnum opus* on the class, Alfred R. Loeblich and Helen Tappan (1987) described 878 modern genera. The number of extant foraminiferal species is now estimated to be about 10,000 (Vickerman, 1992), that is, about one-eighth of the estimated number of modern species within the Kingdom Protoctista (Hammond *et al.,*

1995). The overwhelming majority of modern Foraminifera are benthic; there are only about 40–50 planktonic species. In addition to their much greater diversity, the benthic species have a much longer geological record. Their oldest fossils are Cambrian in age, whereas those of the planktonic species are Jurassic.

Shells (usually called 'tests') of extant Foraminifera have been noticed in shore sands since the 17th century (see Cifelli, 1990). An unusual early find was by the great microscopist Antonie van Leeuwenhoek, who, in 1700, wrote about foraminifer shells 'no bigger than a coarse sand grain' in stomachs of shrimps, and described the specimens as 'very little snail shells, which

because of their roundness, I called little cockles' (Dobell, 1932). Leeuwenhoek's drawing of one of these shells (Fig. 1.1) is detailed enough to be recognized as that of an *Elphidium*. It is an interesting but not a surprising coincidence that after foraminifers were identified as shelled protists (chapters 2, 3), the early studies of their life cycle were focused on *Elphidium* (e.g. Lister, 1895; chapter 3). This genus is easily collected from nearshore environments, where large populations are common (chapter 9). Overall, a relative ease of collection is reflected in the much greater body of literature that exists on continental-shelf foraminifers, compared to that on deeper-water species.

The biology of foraminifers has not been examined as intensively as that of some protoctistan cousins (e.g. ciliates); apparently, the shell has been somewhat of a problem in cellular studies. The biological feature that has drawn the most attention is the alternation between a sexual and an asexual generation (and the variations of this cycle; chapter 3), because this explains the distinct morphological dimorphism that is seen in the shells of many species, including, especially, some relatively large fossil forms. In addition, from the very beginning of biological studies of foraminifers in the 19th century, the reticulate pseudopodia ('reticulopodia') have

been regarded as a special feature of this group, and recent studies have shed light on their diverse functions (chapter 3). To most students and researchers, however, the most significant aspect of foraminiferal biology is the production of an amazing variety of shells (chapter 2), matched in no other class of organisms. On the basis of the morphology of these shells, one can recognize 15 extant foraminiferal orders. In seven orders, the shell is made of secreted calcite; in others, the species secrete aragonite or opaline silica, or make their shells with organic matter or foreign particles (chapter 2). The mechanics of chamber formation in some calcareous species has been studied in great detail (chapters 3, 4), and used in the recognition of suprageneric taxa (chapter 2). Genetic research on Foraminifera is a new and sparsely populated field, but judging by the effect of this research on species-level taxonomy (e.g. Pawlowski *et al.,* 1995), a major impact on foraminiferal systematics is expected in the future.

The ecology of Foraminifera became a major area of study in the second half of the 20th century, and the first text on this subject was by Fred B Phleger (1960a). In the the past 30 years, research in this field has increased greatly, mainly because of the realization that modern foraminiferal distributions are likely to provide reliable clues ('analogs') for the understanding of marine environmental changes in the geological (and, in some cases, historical) past. The advantage of using foraminifers in paleoecology lies in their significant numerical density in diverse marine sediments and in the excellent preservation of their shells. Both of these factors are partly related to their small size. Some species, however, are better preserved than others, causing a taphonomic bias even in relatively recent sedimentary records (chapter 16).

Traditionally, the focus of foraminiferal distribution studies has been on water depth (relevant to paleodepth research on sedimentary rocks), except for marginal marine species, which are strongly influenced by salinity changes (chapter 9). In waters of normal marine salinity, placing a foraminiferal zone boundary at the shelf-slope break is common practice. Furthermore,
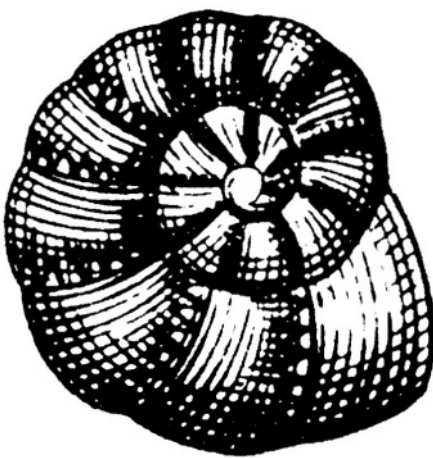

Figure 1.1 Leeuwenhoek's drawing of *Elphidium* in a letter dated June 2, 1700. From Dobell (1932), where the genus is reported as *Polystomella*.

numerous investigators have followed Phleger (e.g. 1964a) in recognizing distinctive foraminiferal assemblages on the 'inner continental shelf, outer continental shelf, upper continental slope, lower continental slope and deep sea.' Application of numerical techniques of data analysis (chapter 5) to relative abundances of species has led to finer groupings in many areas. With a different perspective, latitudinally extensive biogeographic provinces of benthic Foraminifera have been recognized on various continental shelves and slopes. In many of these provinces, the proportion of endemic species in the foraminiferal community is very high (chapter 6).

Recognition of patterns (and their causes) in the distribution of deep-sea benthic Foraminifera has remained a problem since the *Challenger* report of 1884, because many species of this 'cold-water sphere' are ubiquitous. They, however, are not equally abundant everywhere, and the dominance of certain species seems to be connected with particular deep-bathyal or abyssal water masses, although invariant associations are hard to establish. Two associations that have been verified in multiple deep basins relate to well-oxygenated waters: *Cibicides wuellerstorfi* is a dominant species in North Atlantic Deep Water (or its remnant in Caribbean basins), and *Nuttallides umbonifera* in Antarctic Bottom Water (e.g. Streeter, 1973; Schnitker, 1974b; Douglas and Woodruff, 1981; Sen Gupta, 1988). In many correlations between a benthic foraminiferal species or assemblage and a water mass (defined by the combination of temperature and salinity), causality is elusive. On the other hand, there is compelling evidence that the variable input of labile organic matter (a reflection of surface-ocean productivity) affects abundances of deep-sea foraminiferal species (chapter 11). Thus, *Epistominella exigua,* once thought to be a foraminiferal marker of some deep-water masses, is now known to be a species whose population density is dependent on phytodetritus falls (e.g. Gooday, 1993). In bathyal depths, the correlation between a benthic foraminiferal association and the oxygen-minimum water has been clearly demonstrated (e.g. Hermelin and Shimmield, 1990; Denne and Sen

Gupta, 1993), but the controlling factor may be the organic-rich sediment on the seafloor (Hermelin and Shimmield, 1990). This book does not include a chapter on the connection between water masses and foraminiferal assemblages on the deep-sea floor, but the point of view that there is a connection is expressed succinctly by Schnitker (1994): 'Benthic foraminifers are unequivocal indicators of productivity in areas where productivity is high. In areas of low or very uniform productivity the composition of the benthic fauna clearly carries the imprint of deep water mass structure as the dominant feature.' An additional difficulty is posed by the probability that all species in the same deep-sea assemblage may not be equally dependent on food falls. A recent study in eastern South Atlantic Ocean provides an illustration. Schmiedl and Mackensen (1997) studied the variations in the Quaternary benthic foraminiferal record of two cores taken from the same depth (about 3,000 m), but under surface waters of sharply different productivities. They concluded that fluctuations in the abundances of *Cibicides wuellerstorfi* and *Bulimina alazanensis* are related to temporal changes in the advection of North Atlantic Deep Water, whereas those of *Cassidulina laevigata, Melonis barleeanus,* and *M. zaandami* are linked to shifts in productivity.

At the sediment-water interface, many Foraminifera are neither obligate epibenthos (living *on* the sediment) nor obligate endobenthos (living *within* the sediment), because they can move up or down the sediment column in search of food, and thus have variable microhabitats (Linke and Lutze, 1993). Some truly epibenthic species (free or attached) live on substrates *above* the sediment surface, whereas some truly endobenthic species live several centimeters down in the sediment (chapter 10). Such deep endobenthic species may have to cope with a severe shortage of oxygen in the sediment pore water, but as recent research has shown, many foraminiferal species can live in extremely oxygen-poor water in varying depths of the sea (chapter 12). Because of the paucity of observations on the preferred depths of living individuals within the substrate, microhabitats of most sedi-

ment-dwelling species are unknown. Some researchers use the shell shape ('morphotype') to infer the microhabitat, but this practice has an inherent uncertainty (chapter 10).

In many coastal areas, especially in industrialized countries, pollution has severely affected foraminiferal microhabitats. Studies on the effects of various forms of pollution on Foraminifera show that many species can serve as indicators in pollution monitoring programs (chapter 13). Many foraminiferal species have adapted to extreme natural environments, such as habitats of very high salinity (chapter 9), areas near hydrothermal vents (e.g. Jonasson *et al.*, 1995), bacterial mats at hydrocarbon vents (e.g. Sen Gupta *et al.,* 1997) or in silled basins (e.g. Bernhard *et al.,* 1997), and pack ice (planktonic species, chapter 7). These are not exotic species, however; they are recruited from the surrounding areas where the environment is 'normal' for the water depth and distance from the shore.

Modern planktonic Foraminifera, because of their enormous population sizes, produce a significant amount of oceanic carbonate. There is a much larger proportion of taxa with algal symbionts within this group than within the benthic group (chapter 8). The environmental controls on planktonic species are much better understood than those on benthic species, because the only major variables are the temperature, salinity, and productivity of the surface layer of seawater (mainly in the upper 100 m). The species are distributed in a few large latitu-dinal provinces, with some showing bipolar distributions; many species can be used as tracers of ocean currents (e.g. Oberhänsli, 1992). The present-day temperature limits of the biogeographic provinces have been of great use in estimating Quaternary sea-surface paleo-temperatures from the fossil record of extant species (chapter 7).

The extraordinary progress of foraminiferal shell geochemistry in recent years has been in the context of major questions of paleoceanography that relate to the nature and movement of past water masses, at the sea surface and in the water column. The principles behind these inquiries have to be established by analyses of modern foraminiferal shells – both planktonic and benthic. Culturing studies have become especially significant in this research, because of the necessity of understanding the species-specific 'vital effect' in the incorporation of trace elements and the acquiring of the oxygen and carbon isotope signatures in the shell (chapters 14 and 15).

In summary, much of this book is about patterns of foraminiferal distribution in seafloor sediments and in seawater, and about the processes that govern this distribution. In spite of prolific research since Phleger's days, many questions about processes remain unresolved. On matters of speculative interpretation, there may be disagreement even among authors of this book. We hope such issues will generate thought and discussion, not frustration.

2

Systematics of modern Foraminifera

Barun K. Sen Gupta

2.1 INTRODUCTION: THE EARLY PHASE OF SUPRAGENERIC TAXONOMY

As J.J. Lister wrote, 'the Foraminifera received their name before their nature was understood' (Lister, 1903). In fact, numerous foraminiferal species had been described under a linnaean binomial before this understanding. In the latter half of the 18th century, most foraminifers were described as cephalopods, particularly as *Nautilus*. The original descriptions of about 140 such false nautiluses named between 1758 and 1819 are given in the *Catalogue of Foraminifera* (Ellis and Messina, 1940 and later). Many of the species and varieties were well illustrated by their authors, and it is possible to place them under currently accepted generic labels. The best known example of this phase of foraminiferal taxonomy is the *Testacea Microscopica* of Fichtel and Moll (1798) in which 47 extant and fossil taxa (putatively, distinct species or varieties) were given linnaean names under the single generic heading of *Nautilus*; 18 separate genera (Fig. 2.1), all extant, are now recognized within this group (Rögl and Hansen, 1984).

The identification and separation of foraminiferal species, genera, and higher taxa solely by aspects of test morphology, especially chamber arrangement, did not change with the recognition by Felix Dujardin (1835a–c; spelt 'Desjardins' in 1835a) that the foraminiferal body was simply a jelly-like mass ('sarcode') with pseudopodia (Fig. 2.2; see also chapter 3). The classification in vogue at this time (d'Orbigny, 1826) underwent only minor modifications after d'Orbigny's acceptance of Dujardin's conclusion that foraminifers were unicellular organisms, and not cephalopods. In d'Orbigny's 1826 classification, the Foraminifera, as a foramina-bearing (as opposed to siphon-bearing) class of cephalopods, was split into five orders; his 1852 classification of the Foraminifera (as sarcodines), included all of these orders, plus an order for single-chambered forms (Monostègues) and one in which chambers were arranged in annuli (Cyclostègues; Fig. 2.3). At this stage, d'Orbigny had recognized a total of 72 foraminiferal genera. Although wall characters were considered a significant criterion in generic taxonomy, d'Orbigny (1852) placed both calcareous and agglutinated genera in the same family, because of some similarity in chamber arrangement. For example, the agglutinated form *Clavulina* and the calcareous forms *Bulimina* and *Globigerina*
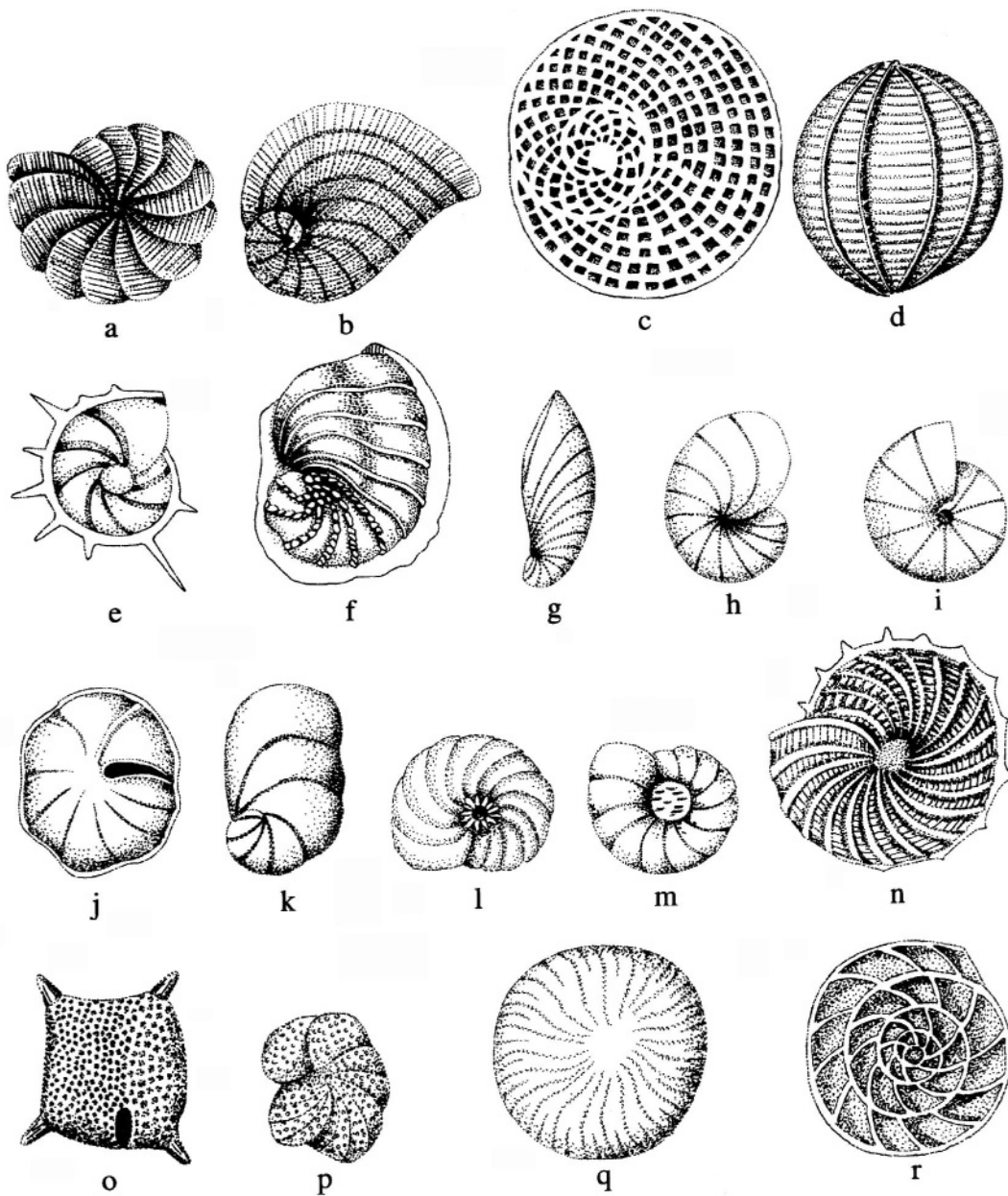
Figure 2.1 Foraminiferal genera (all extant) considered as micromolluscs and placed under *Nautilus* by Leopold von Fichtel and Johann Paul Carl von Moll (1798). Redrawn from Fichtel and Moll (plates in Rögl and Hansen, 1984); j, l, m, p, ventral views; q, dorsal view; c, r, sectional views. Currently accepted generic nomenclature (Rögl and Hansen, 1984) and ordinal and superfamilial affiliations (Loeblich and Tappan, 1987, 1992) are as follows: a, *Dendritina* (Miliolida, Soritacea); b, *Peneroplis* (Miliolida, Soritacea); c, *Archaias* (Miliolida, Soritacea); d, *Borelis* (Miliolida, Soritacea); e, *Lenticulina* (Lagenida, Nodosariacea); f, *Planularia* (Lagenida, Nodosariacea); g, *Astacolus* (Lagenida, Nodosariacea); h, *Nonion* (Lagenida, Nonionacea); i, *Melonis* (Lagenida, Nonionacea); j, *Eponides* (Rotaliida, Discorbacea); k, *Cancris* (Rotaliida, Discorbacea); l, *Hanzawaia* (Rotaliida, Chilostomellacea); m, *Anomalinoides* (Rotaliida, Chilostomellacea); n, *Elphidium* (Rotaliida, Rotaliacea); o, *Calcarina* (*Rotaliida, Rotaliacea*); p, *Cibicides* (Rotaliida, Planorbulinacea); q, *Amphistegina* (Rotaliida, Asterigerinacea); r, *Nummulites* (Rotaliida, Nummulitacea); a–d are porcelaneous genera, e–r hyaline.

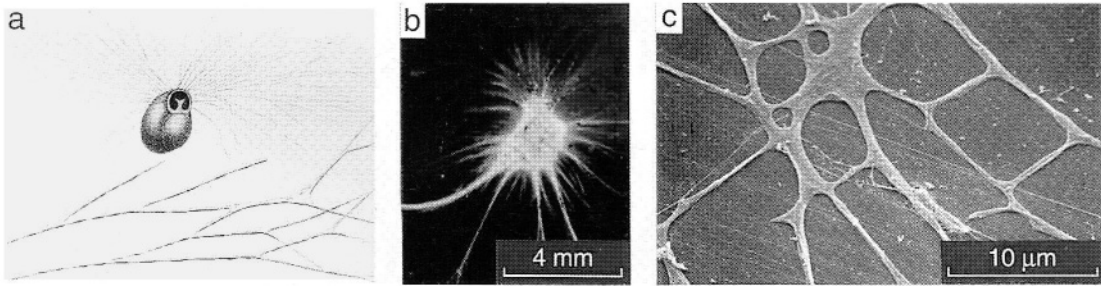**Figure 2.2** Pseudopodial network (reticulopodia) in Foraminifera; a, top (8 ×) and bottom (250 ×), miliolaceans (reduced from drawings in Dujardin, 1835c); b and c, *Astrammina rara*, an astrorhizacean (scanning electron micrographs by Samuel Bowser, reprinted with permission).
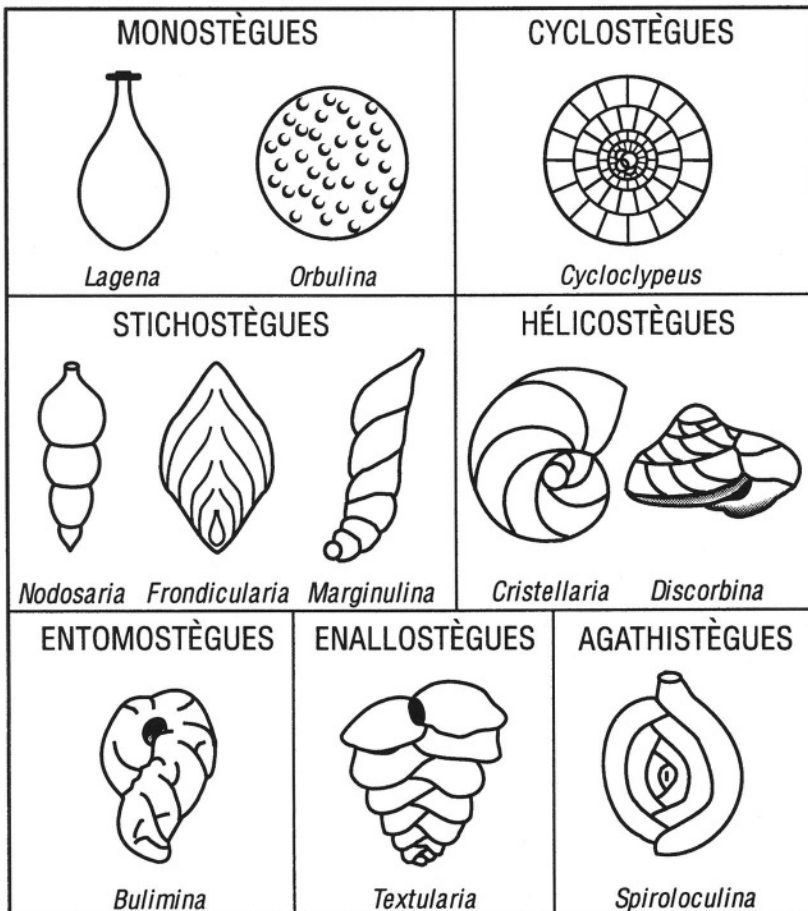

Figure 2.3 The seven foraminiferal orders of Alcide d'Orbigny (1852). Redrawn from Chapman (1902).

were all placed under Tubinoidaea (Order Heli-costègues). This practice of placing agglutinated and calcareous genera (especially those with serial chamber arrangements) within one family continued well into the 20th century. At the highest level of taxonomic discrimination, how-ever, the shift in the primary emphasis from chamber arrangement to wall characters is clear in many schemes of foraminiferal classification developed in Europe and the U.S. (see, e.g. Gal-loway, 1933; Glaessner, 1945; Loeblich and Tappan, 1964a, b). The most significant trans-itions are discussed below. An elegant summary of all major classifications from d'Orbigny (1826) to Galloway (1933), their philosophical bases, and their relevance in an evolutionary context are given in Cifelli (1990).

The hierarchical base of d'Orbigny's classifi-cation was severely criticized by a number of researchers in Great Britain in the 1850s and 1860s (W.K. Parker, T.R. Jones, W.C. William-son, W.B. Carpenter, and H.B. Brady; see Cifelli, 1990), because they concluded that these unicel-lular organisms are so variable that clear distinc-tions, whether among species or among orders, are unattainable (Carpenter *et al*., 1862). Never-theless, attempts at classification, by these critics and others, continued, culminating in two hier-archical schemes of great significance (Reuss, 1861; Carpenter *et al*., 1862). Although they were considerably different in details, wall struc-ture was used as the feature of primary impor-tance in both of these schemes, and two major divisions were recognized, one with perforate families, the other with imperforate families. The scheme was significantly modified by Jones (1876) when he separated the porcelaneous group from the arenaceous, thus recognizing three major divisions.

One of the greatest works on modern Fora-minifera was H.B. Brady's magnificent mono-graph (1884) on the material collected during the *Challenger* expedition of 1873–1876. Brady's illustrations are still used extensively for species identifications; names may have changed because of questions of priority, but by and large, the internal consistency of nomenclature is impressive (see Barker, 1960; Jones, 1994).

Brady's views on foraminiferal systematics, forcefully expressed in the *Challenger* mono-graph, strongly influenced researchers in the next five decades. Brady included both modern and ancient (including Paleozoic) genera in his 10 families and 29 subfamilies, but placed no importance on stratigraphic distributions, occa-sionally grouping Paleozoic genera together with very different Cenozoic ones. In Brady's view, even the largest taxa within the Foramini-fera (to him, an order) had to be recognized on the basis of multiple characters, and no single character (e.g. wall composition or texture) could be used as the sole basis for the separation of these taxa. Thus, he kept all known genera with serially arranged chambers within a single family, the Textularidae (Textulariidae of later workers), because he considered the wall com-position to span the range between agglutinated or calcareous, warranting no more than a recognition of two subfamilies, Textularinae (Textulariinae of later workers) for the former, and Bulimininae for the latter. On the whole, however, the value of wall structure is reflected in Brady's classification. Of the other nine fami-lies, the largest taxonomic groups in his scheme, one (Gromidae) is characterized by organic walls, two (Astrorhizidae and Lituolidae) by agglutinated walls, one (Miliolidae) by calcare-ous imperforate walls, and five (Chilostomelli-dae, Lagenidae, Globigerinidae, Rotaliidae, Nummulinidae) by calcareous perforate walls. Furthermore, the practice of placing all plank-tonic foraminifers into a distinct major taxon was firmly established with Brady's classifica-tion, although currently this group has the status of an order (Globigerinida as in Loeblich and Tappan, 1992) rather than that of a family (Globigerinidae as in Brady, 1884). About two decades later, Lister (1903), while keeping the basic hierarchy of Brady, elevated his 10 fora-miniferal families to superfamilies (with a suffix change from -idae to -idea), and the order Fora-minifera to a class. Lister categorically rejected Carpenter's extreme view (Carpenter *et al.,* 1862) that morphological variability and intergrada-tion among foraminifers are so strong that the separation of species is impossible. He clarified

the issue by stating that the question 'appears to be not whether all intermediate forms do or do not exist between dissimilar forms, but whether the whole body of forms, as they occur in nature, tend to group themselves or are aggregated about certain centres. ... In a very large number of cases, ... such centres do exist among the Foraminifera, as among other organised beings, and the characters of the middle individuals of them are those of the species' (Lister, 1903).

2.2 THE AGE OF CUSHMAN

Joseph A. Cushman, the most notable foraminiferal taxonomist in the first half of the 20th century, was strongly influenced by Brady's view of suprageneric groupings. Cushman's first classification (1925) was simply an adaptation of Brady's 10 families with some changes in the naming of subfamilies. Although he argued against keeping genera with the same chamber arrangement but different wall structures (e.g. the coiled-tubular *Ammodiscus, Cornuspira,* and *Spirillina*) within one family, he retained Brady's concept of the Textulariidae, with both agglutinated and calcareous genera. The big expansion came with his 1927 and 1928 classifications, in which he increased the number of families to 45, without proposing superfamilies or orders. Apart from test morphology, Cushman's new classification was 'based upon the known geological history of the genera, upon the phylogenetic characters through a study of very much fossil material from all the continents, and finally by a study of the ontogeny in very many microspheric specimens, which show the relationships much more definitely than do megalospheric specimens of the same species' (Cushman, 1933; see Fig. 2.4). In the final version of this classification (Cushman, 1948), the number of families (without any suprafamilial groupings) was 50. Galloway's classification, apparently ready in 1927, and the cause of a private and public dispute between Galloway and Cushman regarding claims to priority (see Cifelli, 1990), was published in 1933. As in Cushman (1927),

(1) the number of families was greatly expanded (to 35, from Brady's 10), without the recognition of superfamilies or suborders, and (2) the agglutinated textulariids were separated from the calcareous-hyaline buliminids, but the phylogenetic concepts of Cushman and Galloway and their family and subfamily groupings were substantially different. With Cushman's expanded classification of 1927, the role of wall structure was firmly established as the primary basis for first-level splitting. Although Cushman did not propose any suprafamilial taxon within the Order Foraminifera, he arranged the families in a wall-structure sequence, beginning with membranous and single-chambered agglutinated families, which he considererd the most primitive, and ending with calcareous, perforate, trochospiral families, which he considered the most advanced. The morphological separation of families and genera was unambiguous, permitting Cushman to produce identification keys (1928, 1933, 1940, 1948). An abbreviated version of his last identification key to foraminiferal families (1948) is given below (Table 2.1). Cushman did not identify any suprafamilial, subordinal taxa, but the identities of several of the morphological groups in his key match the orders proposed in the most widely accepted classification of later decades (Loeblich and Tappan, 1964a).

Within about twenty years after its publication, Cushman's 1927 classification became the standard classification, 'adopted by workers on the Foraminifera throughout the world' (Cushman, 1948). A contributing factor was Cushman's reputation as the foremost specialist in the use of fossil Foraminifera in petroleum exploration. Biological research on the Foraminifera, however, had not progressed much beyond what it was at the beginning of the 20th century. Thus, according to a distinguished protozoologist, not enough information was available on living organisms to warrant a complete revision of the classification, and Cushman's monumental work was subject to some derision because it was 'plain that some of Cushman's splitting of groups' was not 'biologically sound.' An allowance was made that such a classification, based purely on shell morphology, 'may
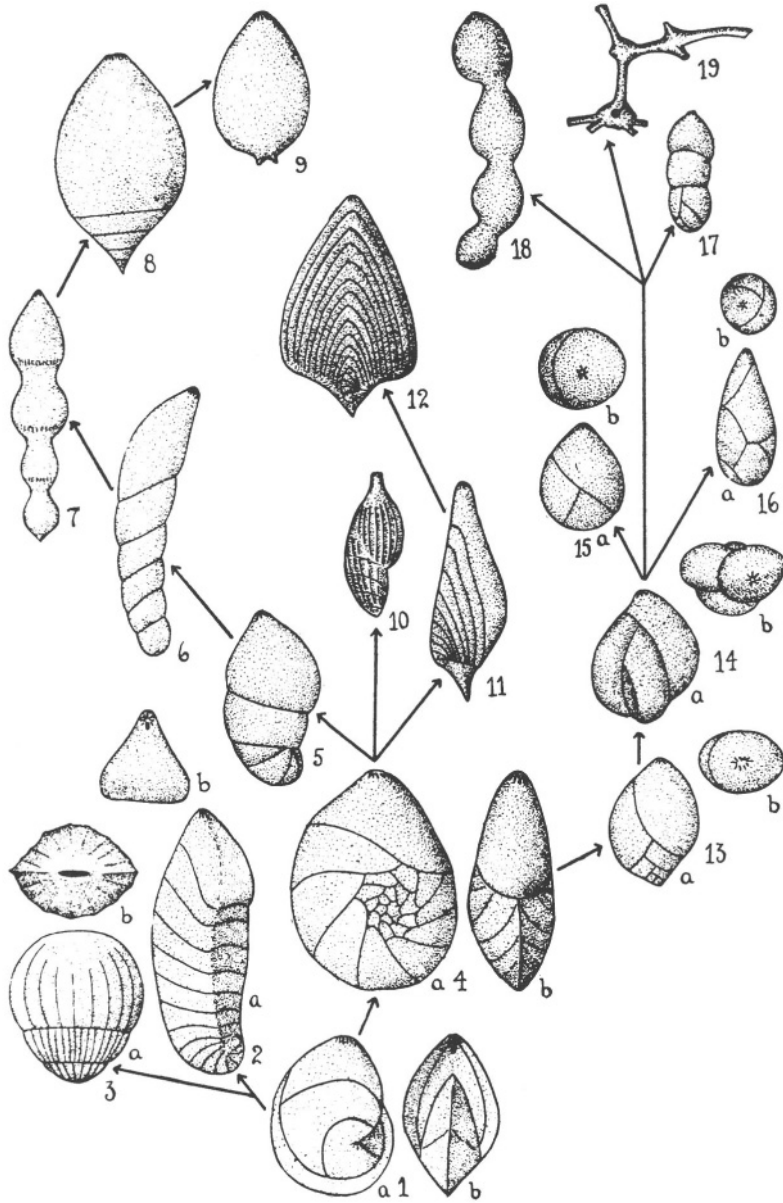
Figure 2.4 Evolutionary relationships envisaged by Cushman (1927) among the genera he placed in the Lagenidae and Polymorphinidae. 1, *Robulus*; 2, *Saracenaria*; 3, *Lingulina*; 4, *Cristellaria*; 5, *Marginulina*; 6, *Dentalina*; 7, *Nodosaria*; 8, *Glandulina*; 9, *Lagena*; 10, *Amphicoryne*; 11, *Vaginulina*; 12, *Frondicularia*; 13, *Polymorphina*; 14, *Guttulina*; 15, *Globulina*; 16, *Pyrulina*; 17, *Dimorphina*; 18, *Vitrewebbina*; 19, *Ramulina*. From Cushman (1927), with the generic names used by him.

serve the commercial purpose for which it was in fact designed,' but zoologists were admonished to 'adhere to Brady's simpler classification' (Jepps, 1956). A reticence still exists among some biologists in accepting shell morphology, especially wall structure, as a basis for elaborate, hierarchical, foraminiferal classifications (e.g. Cavalier-Smith, 1993, discussed later).

Several classifications developed in the two decades following Cushman's last major taxo-

Table 2.1 Outline of Cushman's identification key (1948) to foraminiferal families. The complete version includes a key to each family, followed by keys to the genera. The informal morphological group and subgroup numbers and the family numbers are from Cushman. Asterisks indicate extinct families. The Paleozoic families Fusulinidae and Neoschwagerinidae are misplaced in the key. Their calcareous wall is correctly noted in the text descriptions of the families (written by C.O. Dunbar).

Group	Wall structure	Subgroup	Chamber arrangement and other key characters	Families	
I	Membranous			1.	Allogromiidae
II	Agglutinated	II A	Single chamber or irregular cluster	2.	Astrorhizidae
				3.	Rhizamminidae
				4.	Saccamminidae
		II B	Two chambered, coiled	5.	Hyperamminidae
				7.	Ammodiscidae
				16.	Silicinidae
		II C	Multichambered	6.	Reophacidae
				8.	Lituolidae
				12.	Fusulinidae*
				13.	Neoschwagerinidae*
				14.	Loftusiidae*
				9.	Textulariidae
				10.	Verneuilinidae
				11.	Valvulinidae
				15.	Neusinidae
				20.	Trochamminidae
				21.	Placopsilinidae
				22.	Orbitolinidae*
III	Calcareous imperforate	III A	Coiled in multiple planes	17.	Miliolidae
		III B	Trochospiral	19.	Fischerinidae
		III C	Planispiral, at least in early part	18.	Ophthalmidiidae
				27.	Peneroplidae
				28.	Alveolinellidae
		III D	Globular test	29.	Keramosphaeridae
IV	Calcareous perforate	IV A	Not trochospiral; vitreous lustre; radiate aperture	23.	Lagenidae
				24.	Polymorphinidae
		IV B (Types 1–6)	Planispiral, serial, or crudely trochospiral; no vitreous lustre; no radiate aperture	25.	Nonionidae
				26.	Camerinidae
				30.	Heterohelicidae
				41.	Hantkeninidae*
				31.	Buliminidae
				32.	Ellipsodinidae
				34.	Pegidiidae
		IV B (Type 7)	Trochospiral, at least in early stage; no vitreous lustre; no radiate aperture	33.	Rotaliidae
				35.	Amphisteginidae
				36.	Calcarinidae
				37.	Cymbaloporidae
				38.	Cassidulinidae
				39.	Chilostomellidae
				40.	Globigerinidae
				42.	Globorotaliidae
				43.	Anomalinidae
				44.	Planorbulinidae
				45.	Rupertiidae
				46.	Victoriellidae*
				47.	Homotremidae
				48.	Orbitoididae*
				49.	Discocyclinidae*
				50.	Miogypsinidae*

nomic work (1948) introduced a suprafamilial hierarchy within the order Foraminifera, but other than a scheme developed in the Soviet Union (Rauzer-Chernousova and Fursenko, 1959, 1962; Grigelis, 1978; see later), none received a wide acceptance. This scene changed with the appearance of Loeblich and Tappan's first book on foraminiferal systematics (1964a). Meanwhile, a landmark paper on foraminiferal wall structure (Wood, 1949) focused attention on optical characters of calcitic foraminiferal walls that had been more or less ignored until this time.

2.3   CRYSTAL ORIENTATION IN CALCAREOUS WALLS

As already explained, the wall structure had been considered as a basis for foraminiferal taxonomy since its early days. However, little attention had been paid to the details of the wall characters of calcareous taxa, other than the simple distinction between perforate and imperforate groups, and the related hyaline and porcelaneous surface textures observed in reflected light under the microscope. Although several studies of the optical phenomena observed in calcareous walls of Foraminifera had been published in late 19th and early 20th centuries, and the presence of an extinction cross had been reported in polarized-light studies of certain species (e.g. Ehrenberg, 1854; Sollas, 1921), the careful documentation by Wood (1949) demonstrated clearly the difference between two interference patterns produced by polarized light when viewed between crossed nicols: (1) a 'radial' pattern, in which a black cross and concentric color bands are observed in single chambers or fragments of chambers (Fig. 2.5, 2.6a) and (2) a 'granular' pattern, characterized by randomly distributed flecks of color (Fig. 2.6b). The radial pattern, a mimic of the uniaxial negative interference figure, is caused by the perpendicular orientation of the c-axis of calcite crystals in relation to the curvature of the test wall. The granular pattern reflects the lack of any such preferred orientation. The extensive
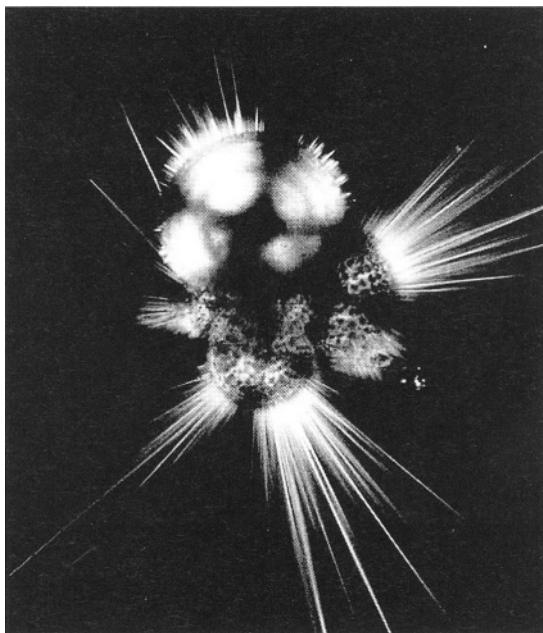

Figure 2.5 Black-and-white image of pseudoextinction cross and concentric color bands in a radial-walled foraminiferal test (*Globigerina*), 150 ×. Original color photograph by Manfred Kage, 1980 Zeiss calendar (reprinted with permission).
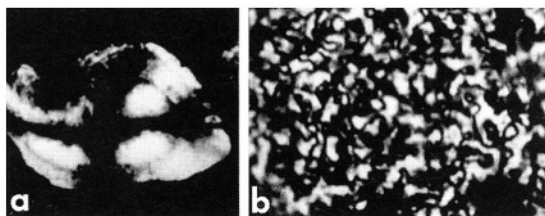

Figure 2.6 Optically radial wall of *Islandiella algida* (a, 290 ×) and granular wall of *Cassidulina crassa* (b, 470 ×). From French (1979, reprinted with permission).

documentation of the optical characters of numerous calcareous hyaline genera by Wood made it possible for Loeblich and Tappan (1964a) to place a new emphasis on crystal orientation in their first suprageneric classification (see next section). Electron-microscopic studies of crystal orientation (e.g. Towe and Cifelli, 1967; Stapleton, 1973; Bellemo, 1974a, 1976) later showed that calcite crystals in optically granular walls are not randomly put together but arranged in oblique orientation or in bundles of several preferred orientations, but the optical

distinction between radial and granular walls has been retained as a taxonomic guide at some level, especially in the schemes proposed by Alfred R. Loeblich and Helen Tappan.

2.4   EARLIER CLASSIFICATIONS OF LOEBLICH AND TAPPAN

New suprafamilial taxonomic entities were proposed within the Foraminifera by several workers in the 1950s (see Loeblich and Tappan, 1964a), including one in which the nature of lamellae in the foraminiferal wall was used as the basis for the recognition of superfamilies (Reiss, 1958). The most elaborate of these post-Cushman classifications was organized by a team of Soviet paleontologists (Rauzer-Chernousova and Fursenko, 1959; 1962). It contained 13 orders (within the subclass Foraminifera), 14 superfamilies, and 72 families. In contrast, Loeblich and Tappan's 1964 classification, which soon became the most widely used taxonomic guide to the Foraminifera, included 5 suborders (within the order Foraminiferida), 17 superfamilies, and 94 families (see Grigelis, 1978, for a comparison of the two systems). Loeblich and Tappan (1964a) recognized about 1200 extant and extinct genera as valid, about a three-fold increase since the last revision of Cushman's taxonomy (1948), but still the outcome of a conservative approach (Berggren, 1965).

Following Galloway (1933) and Cushman (1945), Loeblich and Tappan (1964a) argued that 'the same chamber arrangement and form of test may have developed in independent lineages by parallel evolution, without indicating interrelationship of the similarly shaped shells.' Thus, in the descending hierarchy of classification, the starting point was the nature of the test wall. The wall composition and texture formed the basis for the separation of the live suborders: (1) organic wall for the Allogromiina, (2) agglutinated wall for the Textulariina, (3) calcareous microgranular wall for the extinct Fusulinina, (4) calcareous, porcelaneous wall for the Miliolina, and (5) calcareous, hyaline wall for the Rotaliina.

Within the Rotaliina, the suborder with the most variety (10 superfamilies), eight superfamilies were partially or completely segregated on the basis of various combinations of wall layering (monolamellar, bilamellar with primarily doubled septa, and bilamellar with secondarily doubled septa; see chapter 4) and optical orientation of crystals (single crystal, radial arrangement, and granular crystal arrangement). These distinctions sufficed for the Discorbacea, Spirillinacea, Rotaliacea, and Cassidulinacea. Additional features were needed for distinguishing superfamilies that could not be segregated on the basis of the observed wall characters: (a) apertural characteristics (terminal radiate vs. loop-shaped aperture with internal toothplate) for Nodosariacea and Buliminacea; and (b) environmental adaptation (benthic vs. planktonic) for Orbitoidacea and Globigerinacea. Apparently, the optical properties were considered more significant in superfamily distinctions than the wall layering. Cassidulinacea, the only superfamily with granular test wall, included both monolamellar and bilamellar taxa. Single properties were used to distinguish Carterinacea and Robertinacea: a wall with secreted calcite spicules for the former, an aragonitic wall for the latter. Within the suborders Textulariina and Fusulinina ('lower groups'), the number of chambers was used for the separation of superfamilies. Thus, in the Textulariina, an essentially non-septate test was considered typical of the Ammodiscacea, whereas multiple-chambered forms were placed within the Lituolacea.

Several modifications to their 1964 classification were proposed by Loeblich and Tappan in later years (e.g. Loeblich and Tappan, 1974, 1984; Tappan and Loeblich, 1982), culminating in a large compendium (Loeblich and Tappan, 1987; not 1988, as in some citations in the literature; see Loeblich and Tappan, 1989) with descriptions of 2,446 genera (Haman, 1988), including 878 extant genera (Tappan and Loeblich, 1988). A brief, but significant, revision of the taxonomic hierarchy (orders to subfamilies) was published in 1992. The 1987 classifica-

tion included 12 suborders (Fig. 2.7). In the 1992 revision, 10 of these were changed to orders, 4 new orders were recognized, and the taxon Foraminifera (labeled 'Foraminiferea' after Lee, 1990a) was raised to the rank of class.

2.5   PRESENT CLASSIFICATION

2.5.1

The classification adapted in this chapter is a modified version of Loeblich and Tappan (1992), with morphological criteria taken from Loeblich and Tappan (1987), and, for one order (Globigerinida), also from Simmons *et al.* (1997). The 1987 monograph of Loeblich and Tappan does not include a hierarchical summary of the classification, but outlines are given in Ross and Haman (1989) and Decrouez (1989). At infraordinal levels, there are many inconsistencies and inadequate explanations; these have been noted and discussed in an illuminating review by Haynes (1990). Loeblich and Tappan (1992) includes some discussion of the wall structure, as used in that final revision of the 1964 classification, but not all new taxonomic groups are defined. Perhaps the most serious lag is in the non-definition of the new order, Buliminida (Fursenko, 1958). In the modified version of Loeblich and Tappan's 1992 classification proposed in this chapter, the distinction between Rotaliida and Buliminida (split from Rotaliina of Loeblich and Tappan, 1987) is partly taken from Grigelis (1978) and

Figure 2.7 Foraminiferal suborders in Loeblich and Tappan (1987) and their envisaged phylogeny. Redrawn from Tappan and Loeblich (1988). Among the suborders in this scheme, only the Fusulinina is extinct.

Haynes (1981), but since the inclusion of infraordinal taxa in either Buliminida or Rotaliida follows the practice in Loeblich and Tappan (1992), the distinction is equivocal. The separation, based on multiple characters, is easy in typical cases, for instance between a high-trochospiral test with a loop-shaped aperture that projects internally as a toothplate (Buliminida) and a low-trochospiral test with a slit-like aperture and no toothplate (Rotaliida), but there are many taxa whose placement in one of these two orders (using the 1992 scheme for suprageneric taxa, and the 1987 scheme for genera) appears to be highly subjective. The term 'toothplate' has been used by various authors for several internal structures that differ in detail (Revets, 1993); a restricted definition (an internal structure descending from an apertural lip and 'composed of a single piece of inner lining,' Revets, 1993) would apply to the Buliminida. In Loeblich and Tappan (1992), however, this order includes taxa such as Loxostomatacea that possess no toothplate. Clearly, a major taxonomic and phylogenetic study is needed to resolve the ambiguities and contradictions in this part of the foraminiferal classification.

Table 2.2 gives a comparison of the orders in the present classification with those in two relatively recent classifications in which the Foraminifera are considered a class (Haynes, 1981; Lee, 1990a). The total number of orders in the present classification is 16, and it differs from Loeblich and Tappan (1992) in the status of two orders.

(1) Order Silicoloculinida. The primary character for the separation of the orders in the 1992 classification is the shell composition, including mineralogy. However, Silicoloculinina, separated from Miliolina in 1987, was made part of the Miliolida, the new porcelaneous order. Loeblich and Tappan (1992) did not clearly explain this shift, except to say that 'mineralized particles of the wall in the abyssal-dwelling suborder Silicoloculinina also are randomly oriented rodlike crystals, although consisting of silica rather than calcite' (as is the case with typical Miliolida). Although not articulated, the
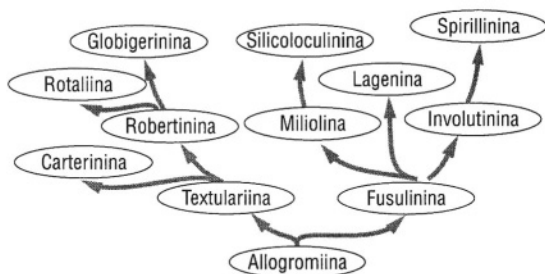
Table 2.2 Comparison of the ordinal nomenclature in the present adaptation of Loeblich and Tappan (1992) with those in Lee (1990a) and Haynes (1981), showing approximate matches. Unless indicated otherwise, the named orders are extant.

Loeblich and Tappan (1992), present adaptation, Class Foraminifera	Lee (1990a), Class Foraminiferea	Haynes (1981), Class Foraminifera
Allogromiida	Allogromiida	Allogromiida
Textulariida	Textulariida, part	Textulariida, part
Astrorhizida	Textulariida, part	Astrorhizida
Lituolida	Textulariida, part	Lituolida
Trochamminida	Textulariida, part	Textulariida, part
Fusulinida (*Paleozoic*)	Fusulinida (*Paleozoic*)	Fusulinida (*Paleozoic*)
Spirillinida	Spirillinida	Rotaliida, part
Involutinida	Involutinida (*only Mesozoic*)	Rotaliida, part
Carterinida	Carterinida	None
Miliolida	Miliolida	Miliolida
Silicoloculinida	Silicoloculinida	None
Lagenida	Lagenida	Nodosariida
Robertinida	Robertinida	Robertinida
Globigerinida	Globigerinida	Globigerinida
Buliminida	Rotaliida, part	Buliminida
Rotaliida	Rotaliida, part	Rotaliida, part

milioline chamber arrangement of *Miliammellus,* the single genus within the silicic group, was probably a factor in this taxonomic placement. In the present adaptation, the Silicoloculinida (silicic wall) is retained as a distinct entity and not placed under the Miliolida (calcitic wall). The available information on the wall structure (Resig *et al.*, 1980) shows that the opaline silica is secreted, not agglutinated. Furthermore, the interpretable phylogeny of Miliolida is unaffected by the recognition of silicic foraminifers as a separate suborder or a separate order. Thus, in spite of test isomorphism with miliolids, the placement of silicic foraminifers in a separate major taxon, the order Silicoloculinida (as in Lee, 1990a), is justified.

(2) Order Involutinida. In Loeblich and Tappan (1992), the calcite-aragonite distinction was not used as an invariant basis for ordinal separation among calcareous Foraminifera. The aragonitic Involutinina was placed under the otherwise calcitic Spirillinida, whereas the aragonitic Robertinina of the 1987 classification was given the status of a separate order, Robertinida, and thus separated from the calcitic Buliminida and Rotaliida. The present adaptation

reverts to the hierarchy in Loeblich and Tappan (1987), with a rank elevation, thus retaining both the Involutinida and Spirillinida as orders. The family Planispirillinidae (aragonitic wall) is retained within the Involutinida as the only extant family within this order, and not transferred to Spirillinida (calcitic wall).

There are many ambiguities in the superfamily and family designations in Loeblich and Tappan (1987). The problems are mainly of two kinds: (1) the defining characters of a larger taxon being inadequate for the inclusion of all subordinate taxa listed under it, and (2) the defining characters of two taxa of the same rank being inadequate for their separation. An example of the first problem is the inclusion of the Notodendrodidae (bulbous central region and tubular arms) within the Hippocrepinacea (proloculus followed by tubular or flaring second chamber); that of the second problem is the distinction between the Cornuspiridae and Hemigordiopsidae, a streptospiral to planispiral coiling being the characteristic of both (Haynes, 1990). Conflicts of these kinds are not resolved in Loeblich and Tappan (1992), because although a complete outline classification (down

to the subfamily level) is given there, the infraordinal taxa are not defined. Other than the assignment of the Planispirillinidae to the Involutinina, the classification summarized later in this chapter retains the placement of superfamilies and families as in Loeblich and Tappan (1992), notwithstanding unreconciled contradictions.

2.5.2   Supraordinal taxa

Kingdom PROTOCTISTA. Foraminifers, as eukaryotic unicellular organisms, belong to the Kingdom Protoctista, which includes all such organisms and some multicellular ones, i.e. 'the entire motley and unruly group of non-plant, non-animal, non-fungal organisms representative of lineages of the early descendants of eukaryotes' (Margulis, 1990). To avoid confusion, the recommended practice is to restrict an informal designation of Protista to only microscopic protoctists (Margulis, 1990). Following this usage, all foraminifers are protoctists, but not all are protists.

A contrary practice, the recognition of a subkingdom or phylum of single-celled animals, Protozoa (under Kingdom Animalia), is still in vogue. Margulis (1990) takes strong exception to this taxonomy: 'Even today, many scientists (e.g. especially cell biologists, plankton ecologists and geologists) routinely write about Protozoa and Algae as if they were phyla in the Animal and Plant kingdoms, respectively. These organisms are no more "one-celled animals and one-celled plants" than people are shell-less multicellular amoebas.' To most foraminiferal systematists, however, Protoctista/Protista vs. Protozoa is not a major controversy. Ever since the publication of Loeblich and Tappan (1964a), most of them have placed the foraminifers in the Protista (in the traditional sense, i.e. same as the current Protoctista) rather than in the Protozoa (see Hart and Williams, 1993, for a recent exception).

Phylum GRANULORETICULOSA. The phylum includes heterotrophic protoctists characterized by granular reticulopods (pseudopodial networks) with two-way streaming.

Complex sexual cycles are present in this group (Lee, 1990a).

Class FORAMINIFERA. The taxonomic rank of foraminifers was raised from order to class by Loeblich and Tappan (1992) because of the following characteristics of the organisms: (1) granuloreticulose pseudopodia, (2) outer cover (usually a test), (3) alternation of haploid and diploid generations, and (4) 'a test wall in some that is constructed of non-oriented calacareous or siliceous crystals (Textulariida, Fusulinida, Miliolida, Carterinida), such crystalline disorder being unknown elsewhere in the animal kingdom.' Accompanying this rank change was a change in nomenclature, from Foraminiferida to Foraminiferea, although the International Code of Zoological Nomenclature (International Commission of Zoological Nomenclature, 1985) does not require or suggest such a change, being silent on the nomenclature of orders or classes. Loeblich and Tappan (1992) chose 'Foraminiferea' because d'Orbigny's 'Foraminifères' (1826) was not a latinized name, and the 'earliest formal Latinized citation as a class' they found was the Foraminiferea of Lee (1990a). In fact, however, the usage of the latinized class name Foraminifera goes back to 1903 (Lister, p. 47), but more importantly, the rightful author of the class name Foraminifera is d'Orbigny, because the change from Foraminifères to Foraminifera is simply an emendation that calls for the retention of the original author and date. This is fitting. Regardless of later harsh opinions on d'Orbigny's approach to foraminiferal systematics, a consensus exists that in the world of foraminiferologists 'one name must always be held in an esteem which may be described as affectionate, and that is the name of Alcide d'Orbigny' (Heron-Allen, 1917).

2.5.3   Morphologic basis of present classification

The overwhelming importance of the chemistry, mineralogy, and structure of the foraminiferal test wall in the ordinal classification is obvious in Loeblich and Tappan (1992). In the present adaptation, the sole use of these features leads

to the following separations: (a) organic wall, Order Allogromiida; (b) agglutinated, with proteinaceous or mineralized matrix, Orders Astrorhizida, Lituolida, Trochamminida; (c) agglutinated, with low-Mg calcitic cement, Order Textulariida, (d) microgranular calcite, Order Fusulinida (extinct); (e) elongate, high-Mg calcite, Order Miliolida; (f) elongate, low-Mg calcite forming large spicules, Order Carterinida; (g) one or a few crystals of elongate, low-Mg calcite, Order Spirillinida; (h) numerous crystals of elongate, low-Mg calcite, forming monolamellar wall, Order Lagenida; (i) numerous crystals of elongate, low-Mg calcite, forming bilamellar wall, Orders Buliminida, Rotaliida, and Globigerinida (all extant and most extinct genera); (j) aragonite, Orders Involutinida, Robertinida, and Globigerinida (a few extinct genera); (k) silica, Order Silicoloculinida. A significant difference between the present classification and those of Loeblich and Tappan is the placement of the sole planktonic order, Globigerinida, under a calcitic group, as well as under the aragonitic group. This is because of the recognition by Simmons *et al.* (1997) that in the most primitive planktonic superfamily, the Favusellacea (Jurassic and early Cretaceous), the test wall is aragonitic, in contrast to the calcitic wall in all other planktonic groups, including the three modern superfamilies (Heterohelicacea, Globorotaliacea, and Globigerinacea).

Further distinctions of orders within groups b, i, and j are based on the number (one, two, or many) and arrangement of chambers, presence of toothplates, and benthic vs planktonic adaptations. Subordinal distinctions within most orders are based on numerous combinations of diverse morphological features, including wall pores, wall passages, and principal apertural features for superfamilies, and free or fixed nature of the test, mode of chamber addition, simple or divided nature of chamber interior, and apertural modifications for families (Loeblich and Tappan, 1987; Haman 1988). In one remarkable exception, a non-test character, biflagellate vs amoeboid gametes, has been used to separate two families of Allogromiida – Lagynidae and Allogromiidae (Loeblich and Tappan, 1987).

2.5.4 Identification key to orders

The present classification of 16 orders does not lend itself to the construction of a simple ordinal key, based on just two or three morphological features. The system designed by Loeblich and Tappan is complex, and takes into account not just the morphology but the long geological history and an interpreted phylogeny of the Foraminifera. In this context, it is hard to dispute that 'the fundamental purpose of classification ... is to provide an orderly hierarchical array of taxa reflecting the genetic lines of descent, not simply to provide a convenient pigeon-holing' and that a natural classification must not be confused with 'an artificial identification key or retrieval system' (Haynes, 1990). On the other hand, even a perfectly natural classification (a hypothetical construct for the Foraminifera, given the guesswork involved in determining lines of descent) is useless if we are unable to place major taxa into clearly marked compartments in that classification. With this practical aspect of taxonomy in mind, a key to the identification of foraminiferal orders (Loeblich and Tappan, 1992, modified) is given below. A simplified graphic version of this morphological key is given in Fig. 2.8. Representative genera (one per order) are illustrated in Fig. 2.9.

Class FORAMINIFERA

Group 1 Test or outer membrane made of organic material, in some cases with a few particles picked up from the environment: Order 1, ALLOGROMIIDA.

Group 2 Test agglutinated, i.e. made of particles picked up from the environment ('foreign particles'), 4 orders.

2.1 Test particles attached to a proteinaceous or mineralized matrix: 3 orders.
2.1.1 Test shape irregular; typically single-chambered or branching tubular; septa incomplete in multichambered forms: Order 2, ASTRORHIZIDA.
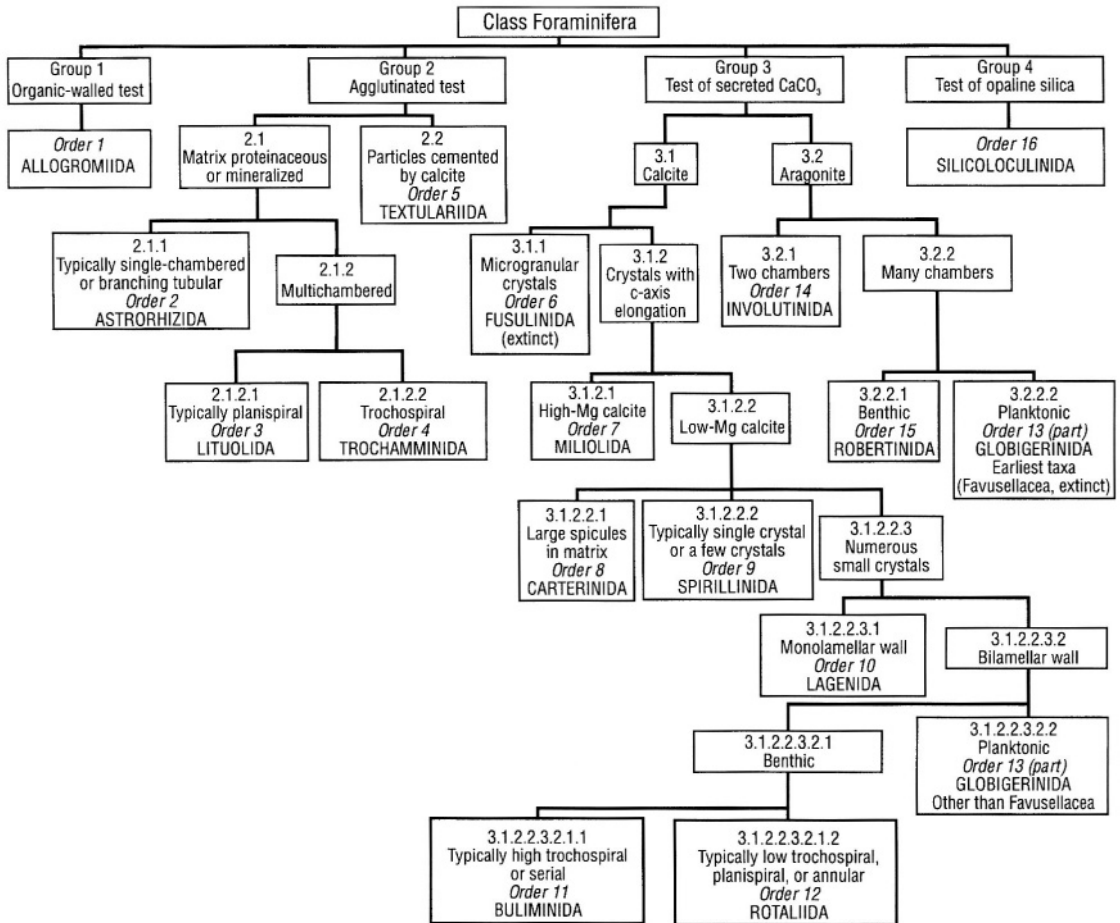
Figure 2.8 Simplified morphological key to foraminiferal orders. See text for further explanations.

Figure 2.9 Representative genera, foraminiferal orders; 1, photomicrograph; 2–21, scanning electron micrographs. Scale bars: 500 µm in 2, 7, and 13; 10 µm in 11; 100 µm in others. 1, *Allogromia* (Allogromiida); 2, *Saccammina* (Astrorhizida); 3, *Ammodiscus* (Lituolida); 4, 5, *Trochammina* (Trochamminida), dorsal and ventral views; 6, *Siphotextularia* (Textulariida); 7, *Triticites* (Fusulinida); 8, *Miliolinella* (Miliolida); 9–11, *Carterina* (Carterinida), dorsal view, ventral view, and arrangement of large and small spicules; 12, *Spirillina* (Spririllinida); 13, *Dentalina* (Lagenida); 14, *Bolivina* (Buliminida); 15, 16, *Ammonia* (Rotaliida), dorsal and ventral views; 17, 18, *Globigerinoides* (Globigerinida), dorsal and ventral views; 19, *Planispirillina* (Involutinida); 20, *Robertinoides* (Robertinida); 21, *Miliammellus* (Silicoloculinida). Species illustrated: 1, *A. laticollaris* (Arnold); 2, *S. comprima* (Parker); 3, *A.* sp.; 4, 5, *T. nana* (Brady); 6, *S. affinis* (Fornasini); 7, *T. secalicus* (Say); 8, *M. warreni* (Andersen); 9–11, *C. spiculotesta* (Carter); 12, *S.* sp.; 13, *D. albatrossi* (Cushman); 14, *B. lowmani* (Parker); 15, 16, *A. beccarii* (Linné); 17, 18, *G. ruber* (d'Orbigny); 19, *P. papillosa* (Cushman); 20, *R. charlottensis* (Cushman); 21, *M. legis* (Saidova and Burmistrova). All species are extant, except *Triticites secalicus* (Late Carboniferous). [Sources: 1, S.T. Goldstein (reprinted with permission); 2, 8, 14, E. Platon (reprinted with permission); 6, M.H. Jones (1997, reprinted with permission); 9–11, S. Deutsch and J.H. Lipps (1976, reprinted with publisher's permission); 19, W.E. Piller (1983, reprinted with publisher's permission); 21, J.M. Resig *et al.* (1980, reprinted with publisher's permission); 3–5, 7, 12, 13, 15–18, 20, specimens collected by author, micrographs by E. Platon.]
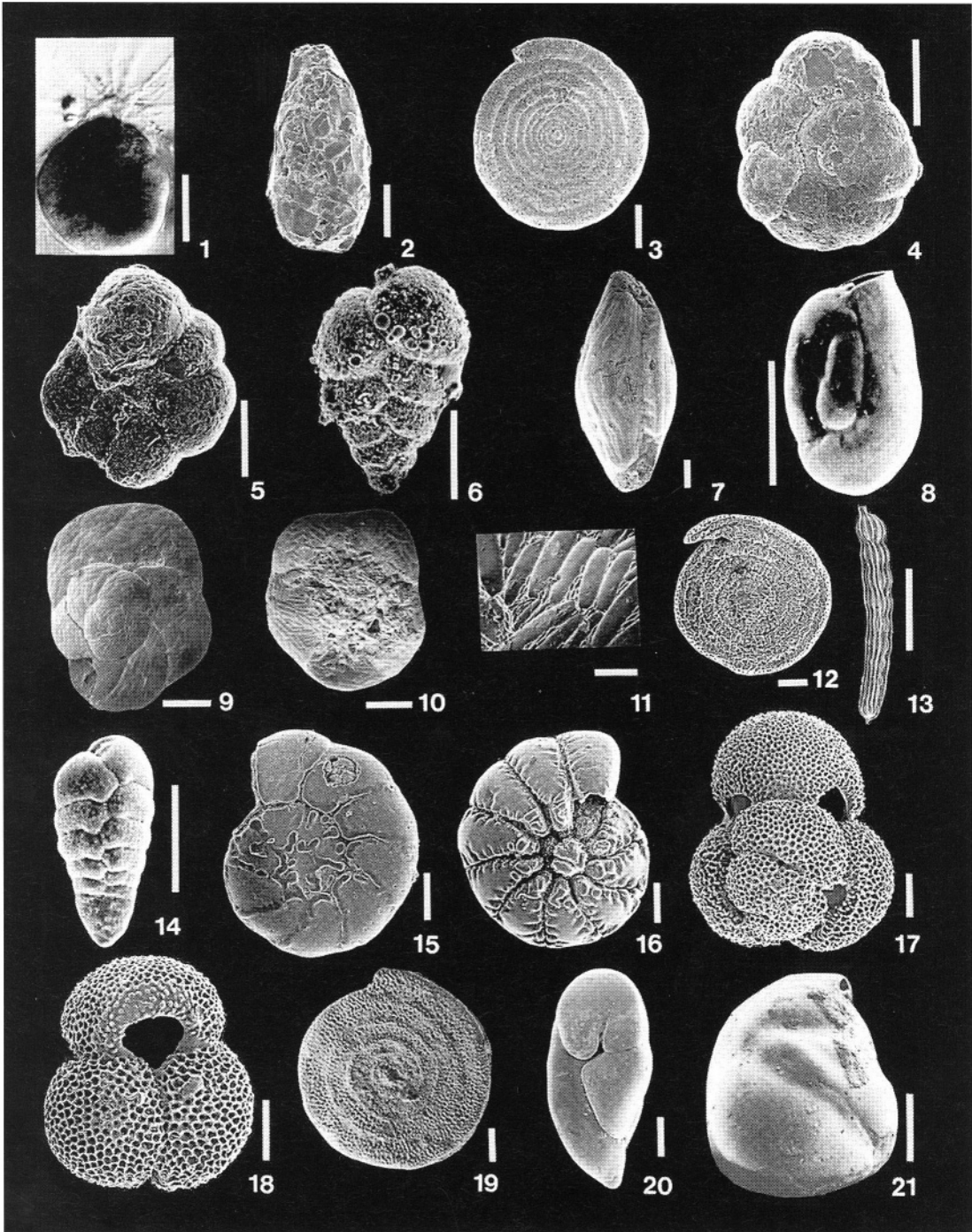
2.1.2 Multichambered, i.e. septa present: 2 orders.

2.1.2.1 Coiling usually planispiral, but in some cases streptospiral or trochospiral: Order 3, LITUOLIDA.

2.1.2.2 Coiling trochospiral: Order 4, TROCHAMMINIDA.

2.2 Test particles cemented by low-Mg calcite: Order 5, TEXTULARIIDA.

Group 3 Test wall made of secreted calcium carbonate: 9 orders.

3.1 Calcite: 8 orders.

3.1.1 Crystals microgranular, i.e. very small and nearly equidimensional; no preferred crystal orientation: Order 6, FUSULINIDA (Extinct).

3.1.2 Crystals elongate along the c-axis: 7 orders.

3.1.2.1 High-Mg calcite: Order 7, MILIOLIDA.

3.1.2.2 Low-Mg calcite: 6 orders.

3.1.2.2.1 Large spicules (unusually large crystals) in a matrix of fine spicules: Order 8, CARTERINIDA.

3.1.2.2.2 Optically, a single crystal or a few crystals (or, rarely, a mosaic of crystals): Order 9, SPIRILLINIDA.

3.1.2.2.3 Numerous small crystals; lamellar wall: 4 orders.

3.1.2.2.3.1 Monolamellar. Single-chambered or multichambered, but no complexly coiled forms beyond planispiral: Order 10, LAGENIDA.

3.1.2.2.3.2 Bilamellar. Multichambered: 3 orders.

3.1.2.2.3.2.1 Environmental adaptation benthic: 2 orders.

3.1.2.2.3.2.1.1 Chamber arrangement trochospiral (typically, high-trochospiral), triserial, biserial, or uniserial; aperture typically comma-shaped ot loop-shaped, typically with toothplate: Order 11, BULIMINIDA.

3.1.2.2.3.2.1.2 Chamber arrangement trochospiral (typically, low trochospiral), planispiral, annular, or irregular: Order 12, ROTALIIDA.

3.1.2.2.3.2.2 Environmental adaptation planktonic: Order 13, GLOBIGERINIDA, part (all modern and most fossil taxa).

3.2 Aragonite: 3 orders.

3.2.1 Two chambers: Order 14, INVOLUTINIDA.

3.2.2 Many chambers: 2 orders.

3.2.1.1 Environmental adaptation benthic: Order 15, ROBERTINIDA.

3.2.1.2 Environmental adaptation planktonic: Order 13, GLOBIGERINIDA, part (only Favusellacea, extinct).

Group 4 Test wall made of silica: Order 16, SILICOLOCULINIDA.

2.5.5 Superfamilies and families

The characteristic features of Holocene superfamilies and representative families are briefly summarized below, with examples of extant genera. The listing does not include subfamilies and some minor families. Only essential descriptions are given here, summarized from Loeblich and Tappan (1987) and corrected for contradictions or ambiguities, especially in cases (e.g. Spiroplectamminacea) where superfamily characters, as reported by Loeblich and Tappan, do not accommodate those of all constituent families. Unfortunately, some uncertainties still remain in the distinction between closely related superfamilies or families, because the present modification of Loeblich and Tappan (1992) leaves the subordinal hierarchy untouched. For full descriptions of the taxa, and for generic descriptions, see Loeblich and Tappan (1987). Only 283 genera are mentioned below as examples, out of a total of 878 extant genera described in Loeblich and Tappan (1987). For a complete listing of genera and suprageneric taxa under the Loeblich and Tappan (1987) hierarchy, see Decrouez (1989), but the status and placement of some subfamilies, families, and superfamilies are different in Loeblich and Tappan (1992), and thus in the present adaptation.

Most morphological terms used in the following brief descriptions are simple, and require no further explanation. A few are defined

when they first appear. One frequently used apertural term, 'interiomarginal,' refers to an opening at the basal margin of the final chamber (Loeblich and Tappan, 1964a). The principal types of chamber arrangement and aperture are sketched in Figs. 2.10 and 2.11.

Order 1, ALLOGROMIIDA. Organic wall. Includes freshwater forms. No superfamily named. Examples of extant families and genera:

Family Lagynidae. Single-chambered or colonial; agglutinated matter rare; biflagellate gametes. *Myxotheca, Ophiotuba.*

Family Allogromiidae. Single-chambered; agglutinated matter common; amoeboid gametes. *Allogromia* (Fig. 2.9), *Dendrotuba, Hospitella.*

Order 2, ASTRORHIZIDA. Agglutinated wall with particles attached to a proteinaceous or mineralized matrix; single-chambered, branching tubular, or irregularly multichambered with incomplete septa.

(1) Superfamily Astrorhizacea. Test of various shapes, including branching; no septa, although the single chamber may be partially divided. Examples of extant families and genera:

Family Astrorhizidae. Branching test, branches diverging from the central part of the test. *Astrorhiza, Pelosina.*

Family Bathysiphonidae. Test a straight or slightly curved tube. *Bathysiphon.*

Family Rhabdamminidae. Test a branching or twisted tube. *Psammatodendron, Rhabdammina, Rhizammina.*

Family Psammosphaeridae. Test globular or irregular; several may be joined together. With large pores, but no distinct apertures. *Psammosphaera.*

Family Saccamminidae. Test globular or elongate. Single or multiple apertures. *Lagenammina, Saccammina* (Fig. 2.9), *Technitella.*

Family Hemisphaeramminidae. Test with subglobular or discoidal chambers. *Crithionina, Iridia.*

(2) Superfamily Komokiacea. Test formed of multiple branching tubules. With pores, but no

distinct aperture. Examples of extant families and genera:

Family Komokiidae. Bushlike or tree-like arrangement of tubules. *Komokia, Normanina.*

(3) Superfamily Hippocrepinacea. Test tubular with one closed end, or two-chambered, with rounded or irregular first chamber and tubular or flaring second chamber. Examples of extant families and genera:

Family Hippocrepinidae. Test typically tubular; terminal aperture slightly constricted. *Hippocrepina, Hyperammina, Jaculella, Saccorhiza.*

Family Notodendrodidae. Test with a bulbous center, an arborescent upper part, and a branching lower part serving as anchor. With small pores but no distinct aperture. *Notodendrodes.*

Order 3, LITUOLIDA. Agglutinated wall with particles attached to a proteinaceous or mineralized matrix; planispirally (or in some cases, streptospirally or trochospirally) coiled throughout, or uncoiled in the later stage; also, arranged in series throughout.

(1) Superfamily Ammodiscacea. Two-chambered test, with a globular initial chamber and a tubular (coiled or uncoiled) second chamber with terminal aperture.

Family Ammodiscidae. The only family under Ammodiscacea; defining characters same as those of the superfamily. Examples: *Ammodiscus* (Fig. 2.9), *Ammolagena, Glomospira.*

(2) Superfamily Rzehakinacea. Test planispiral or with milioline coiling (chambers arranged in various planes); imperforate.

Family Rzehakinidae. The only family under Rzehakinacea; defining characters same as those of the superfamily. Examples: *Ammoflintina, Miliammina.*

(3) Superfamily Hormosinacea. Test with uniserial chambers. Examples of extant families and genera:

Family Reophacidae. Test wth asymetrical chambers (made of a single layer of agglutinated material) arranged in a slightly arcuate series; terminal aperture on a neck. *Nodulina, Reophax.*

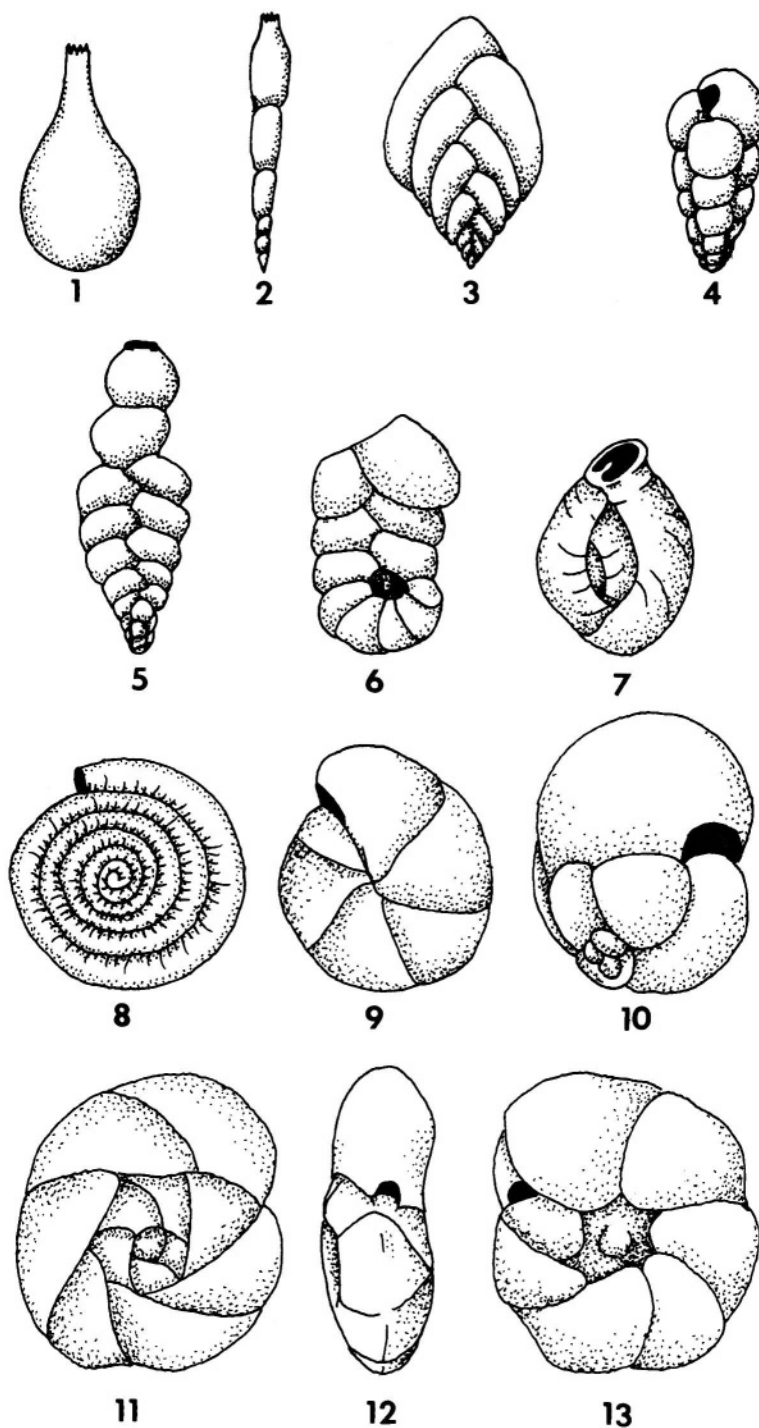Family Hormosinidae. Thick-walled test with symmetrical chambers arranged in a rectilinear

Figure 2.10 Principal types of chamber arrangement. 1, single-chambered; 2, uniserial; 3, biserial; 4, triserial; 5, triserial to biserial to uniserial; 6, planispiral to biserial; 7, milioline; 8, planispiral evolute; 9, planispiral involute; 10, streptospiral; 11–13, trochospiral (11, dorsal view; 12, edge view; 13, ventral view). 2–13 redrawn from Loeblich and Tappan, 1964a.
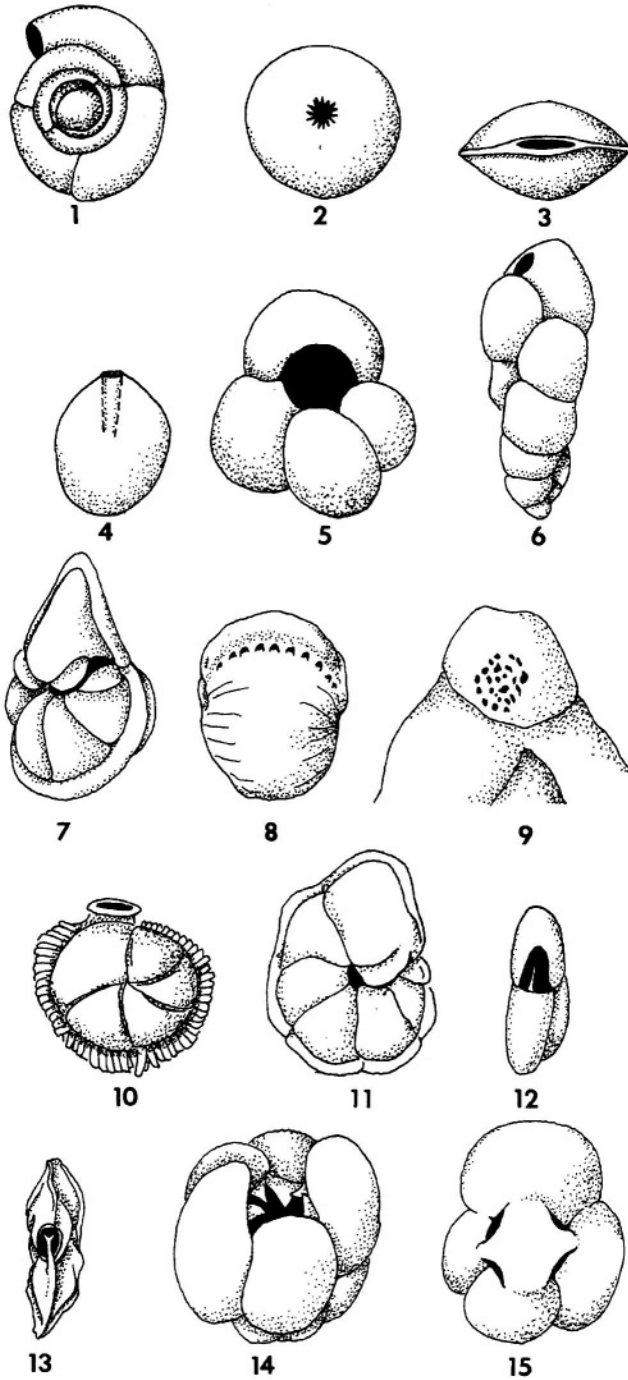
Figure 2.11 Principal types of aperture. 1, open end of tube; 2, terminal radiate; 3, terminal slit; 4, terminal with entosolenian tube; 5, umbilical; 6, loop-shaped; 7, interiomarginal; 8, interiomarginal multiple; 9, areal, cribrate; 10, with phialine lip; 11, with simple apertural lip; 12, with simple tooth; 13, with bifid tooth; 14, with umbilical teeth; 15, with umbilical bulla. 1–3, 5–11, 13–15 redrawn from Loeblich and Tappan, 1964a.

series; terminal aperture on a neck. *Hormosina, Pseudonodosinella.*

(4) Superfamily Lituolacea. Imperforate test with multiple chambers; planispirally coiled throughout or in early stage. Examples of extant families and genera:

Family Haplophragmoididae. Chambers in a fully or partially involute coil. Aperture single or multiple, interiomarginal or areal. *Cribrostomoides, Haplophragmoides.*

Family Lituotubidae. Initial chamber followed by a coiled, tubular second chamber, and then by a series of coiled or uncoiled adult chambers with interiomarginal or terminal aperture. *Lituotuba, Trochamminoides.*

Family Lituolidae. Coiled throughout, or later chambers in a linear series, with terminal aperture. *Ammoastuta, Ammobaculites, Ammomarginulina, Ammotium, Lituola.*

Family Placopsilinidae. Attached test, with coiled, curved, or biserial early portion, and uncoiled later portion with terminal aperture. *Ammocibicides, Placopsilina.*

(5) Superfamily Haplophragmiacea. Test streptospirally coiled throughout or in the initial part, with interiomarginal or areal aperture. Examples of extant families and genera:

Family Ammosphaeroidinidae. Streptospiral, with a small number of chambers. *Adercotryma, Recurvoides.*

(6) Superfamily Coscinophragmatacea. Test attached, uniserial or branching, but initial part may be coiled; coarsely perforate. Examples of extant families and genera:

Family Coscinophragmatidae. Test with alveolar wall, aperture terminal. *Bdelloidina.*

(7) Superfamily Loftusiacea. Test with planispiral, Streptospiral, or trochospiral coil; wall with an imperforate outer layer and an alveolar inner layer. Examples of extant families and genera:

Family Cyclamminidae. Test planispiral involute, with interiomarginal or areal aperture. *Alveophragmium, Cyclammina.*

(8) Superfamily Spiroplectamminacea. Chamber arrangement variable: (a) planispiral or Streptospiral in early part, and biserial or uniserial in later part, (b) biserial to uniserial,

(c) high spiral. Examples of extant families and genera:

Family Spiroplectamminidae. Planispiral or Streptospiral in early part, and biserial or uniserial in later part. *Spiroplectammina, Vulvulina.*

Family Nouriidae. Chambers arranged biserially or in a high spiral, with terminal aperture. *Nouria.*

(9) Superfamily Verneuilinacea. Test trochospiral, triserial, or biserial; last part may be uniserial. Examples of extant families and genera:

Family Verneuilinidae. Triserial throughout or in the early part, with biserial or uniserial later part. *Gaudryina.*

(10) Superfamily Ataxophragmiacea. Trochospiral throughout or in the early part, with triserial, biserial, or uniserial later part. Examples of extant families and genera:

Family Globotextulariidae. Test high trochospiral throughout or with triserial or biserial later part; aperture interiomarginal or areal. *Globotextularia, Liebusella.*

Family Textulariellidae. Test trochospiral in early part, later triserial, biserial, or uniserial; wall alveolar. *Guppyella, Textulariella.*

Order 4, TROCHAMMINIDA. Agglutinated wall with particles attached to a proteinaceous or mineralized matrix; trochospirally coiled throughout or uncoiled in later part.

(1) Superfamily Trochamminacea. Trochospirally coiled throughout or uncoiled in later part. Examples of extant families and genera:

Family Trochamminidae. Test with low trochospiral coil; with interiomarginally or areally located single or multiple apertures. *Ammoglobigerina, Arenoparrella, Jadammina, Tipotrocha, Tritaxis, Trochammina* (Fig. 2.9).

(2) Superfamily Remaneicacea. Test with low trochospiral coil; chambers subdivided by secondary partitions.

Family Remaneicidae. The only family under Remaneicacea; defining characters same as those of the superfamily. Example: *Remaneica.*

Order 5, TEXTULARIIDA. Agglutinated wall, with particles cemented by low-Mg calcite.

Superfamily Textulariacea. Test trochospiral,

triserial, or biserial throughout, or with biserial or uniserial later part; wall with canals. Examples of extant families and genera:

Family Eggerellidae. Test trochospiral or triserial throughout, or with biserial or uniserial later part, with interiomarginally or areally located single or multiple apertures. *Eggerella, Karreriella, Martinottiella.*

Family Textulariidae. Test biserial throughout or uniserial in later part, with interiomarginally or areally located single or multiple apertures. *Bigenerina, Cribrobigenerina, Siphotextularia* (Fig. 2.9), *Tawitawia, Textularia.*

Family Pseudogaudryinidae. Test triserial in early part, later biserial or uniserial, with interiomarginal aperture. *Pseudogaudryina.*

Family Valvulinidae. Test trochospiral, triserial, or biserial throughout, or with uniserial later part; aperture single (with tooth) or multiple. *Clavulina, Goesella.*

Order 6, FUSULINIDA. Extinct. Microgranular, calcitic test wall. Example: *Triticites* (Fig. 2.9).

Order 7, MILIOLIDA. Test of high-Mg calcite; surface texture porcelaneous; adult chambers imperforate, except in a few fossil genera; surface pitted in some genera.

(1) Superfamily Squamulinacea. Test imperforate, single-chambered.

Family Squamulinidae. The only family under Squamulinacea; defining characters same as those of the superfamily. Example: *Squamulina.*

(2) Superfamily Cornuspiracea. Test imperforate, two-chambered. Initial chamber rounded; second chamber tubular, and planispirally, streptospirally, or irregularly coiled, or uncoiled in later part.

Family Cornuspiridae. The only family under Cornuspiracea; defining characters same as those of the superfamily. Examples: *Cornuspira, Meandrospira.*

(3) Superfamily Hemigordiopsacea. Test imperforate, two-chambered. Initial chamber rounded; second chamber streptospiral throughout or planispiral in later part.

Family Hemigordiopsidae. The only family under Hemigordiopsacea; defining characters same as those of the superfamily. Example: *Gordiospira.*

(4) Superfamily Nubeculariacea. Test imperforate, multichambered, coiled planispirally, streptospirally, trochospirally, or irregularly. Examples of extant families and genera:

Family Fischerinidae. Test coiled planispirally; initial chamber rounded, second chamber coiled tubular, succeeding chambers arranged in a spiral. *Fischerina, Nodobaculariella. Planispirina, Vertebralina. Wiesnerella.*

Family Nubeculariidae. Test planispiral, trochospiral, or irregularly coiled throughout, or uncoiled in later part. *Calcituba, Nodophthalmidium, Nubecularia.*

Family Ophthalmidiidae. Chambers arranged planispirally or in various planes. Initial chamber and coiled tubular second chamber succeeded by chambers one-half to one coil in length. *Cornuloculina, Edentostomina.*

(5) Superfamily Discospirinacea. Test imperforate, multichambered, planispiral, discoid; first chamber rounded, second chamber coiled tubular, later chambers one-half coil in extent or annular.

Family Discospirinidae. The only family under Discospirinacea; defining characters same as those of the superfamily. Example: *Discospirina.*

(6) Superfamily Miliolacea. Test imperforate, multichambered; chambers arranged in various planes. Examples of extant families and genera:

Family Spiroloculinidae. Initial chamber rounded, second chamber coiled tubular, adult chambers one-half coil in extent; aperture terminal, toothed or partly covered. *Spiroloculina, Cribrospiroloculina.*

Family Hauerinidae. Initial chamber rounded, succeeding chambers arranged in one or several planes, each chamber covering one-half coil or less; later part of test may be uncoiled; aperture terminal, toothed or partly covered. The test may have an outer agglutinated layer. *Ammomassilina, Biloculinella, Cruciloculina, Hauerina, Massilina, Miliolinella* (Fig. 2.9), *Pyrgo, Quinqueloculina. Siphonaperta, Sigmoilina, Sigmoilopsis, Triloculina.*

Family Tubinellidae. Test coiled in early part, with chambers arranged in one or several planes, but uncoiled in later part. *Articulina, Tubinella.*

Family Miliolidae. Test with pitted surface, coiled in one or several planes; aperture terminal, open or partly blocked. *Rupertianella.*

(7) Superfamily Alveolinacea. Test imperforate, wall thickened, with passages and pillars; chambers (with chamberlets in some genera) arranged planispirally, streptospirally, or in various planes; aperture multiple. Examples of extant families and genera:

Family Alveolinidae. Test coiled around the long axis; initial chamber rounded, second chamber coiled tubular, adult chambers in a planispiral coil and divided into chamberlets. *Borelis, Alveolinella.*

Family Keramosphaeridae. Globular test with concentric chambers and chamberlets. *Keramosphaera.*

(8) Superfamily Soritacea. Adult chambers imperforate, except in a few fossil genera. Early chambers pitted or perforate; chamber arrangement planispiral, multispiral, annular, or serial. Examples of extant families and genera:

Family Peneroplidae. Chamber arrangement planispiral in early part, multispiral, serial, or annular in later part; chambers undivided. *Dendritina, Monalysidium, Peneroplis.*

Family Soritidae. Chamber arrangement planispiral throughout, or multispiral, annular, or serial in later part; chambers subdivided into chamberlets. *Amphisorus, Archaias, Cyclorbiculina, Marginopora, Parasorites, Sorites.*

Order 8, CARTERINIDA. Wall of secreted low-Mg calcite, with large spicules in a matrix of small spicules; imperforate. No Superfamily designated.

Family Carterinidae. Test trochospiral, attached; later chambers may be subdivided by septula. *Carterina* (Fig. 2.9).

Order 9, SPIRILLINIDA. Test with wall of low-Mg calcite, optically a single crystal, a few crystals, or a mosaic of crystals; imperforate or perforate; coiling planispiral or trochospiral. No superfamily designated. Examples of extant families and genera:

Family Spirillinidae. Test coiled, with two chambers; first chamber globular, second chamber tubular. *Spirillina* (Fig. 2.9).

Family Patellinidae. Test conical, multichambered; first chamber globular, second chamber spiral tubular, two chambers in each later whorl. *Patellina.*

Order 10. LAGENIDA. Test of low-Mg calcite; wall monolamellar; perforate; single-chambered or multichambered with serial or planispiral chamber arrangement.

(1) Superfamily Nodosariacea. Test single-chambered or multichambered, with serial or spiral chamber arrangement; aperture terminal. Examples of extant families and genera:

Family Nodosariidae. Test (a) multichambered with uniserial or biserial chamber arrangement, or (b) single-chambered, with a long slitlike aperture. *Dentalina* (Fig. 2.9), *Frondicularia, Lingulina, Nodosaria, Rimulina.*

Family Vaginulinidae. Test coiled throughout or in early stage. *Amphicoryna, Astacolus, Lenticulina, Marginulina, Saracenaria, Vaginulina.*

Family Lagenidae. Test single-chambered; aperture round or radiate. *Lagena.*

(2) Superfamily Polymorphinacea. Test single-chambered or multichambered with serial or elongate spiral chamber arrangement; apertural modifications include the presence of an internal tube (entosolenian tube). Examples of extant families and genera:

Family Polymorphinidae. Test multichambered; chamber arrangement serial or elongate spiral, with round, radiate, or slitlike terminal aperture. *Globulina, Guttulina, Polymorphina, Ramulina, Sigmomorphina, Webbinella.*

Family Ellipsolagenidae. Test single-chambered, aperture with an internal tubular extension. *Oolina, Fissurina.*

Family Glandulinidae. Test multichambered, uniserial, biserial, or elongate spiral; aperture terminal, with an internal tubular extension. *Glandulina, Laryngosigma, Seabrookia, Tappanella.*

Order 11, BULIMINIDA. Test of low-Mg calcite; wall bilamellar, perforate, multichambered, with high trochospiral, triserial, biserial.

or uniserial chamber arangement; aperture in many advanced forms with internal toothplate.

(1) Superfamily Bolivinacea. Test biserial throughout, or uniserial in later part; aperture elongate, with a toothplate. Wall optically radial. Examples of extant families and genera:

Family Bolivinidae. Aperture loop-shaped, interiomarginal or areal. *Bolivina* (Fig. 2.9).

(2) Superfamily Loxostomatacea. Aperture interiomarginal or terminal, without toothplate. Wall optically radial or granular. Examples of extant families and genera:

Family Bolivinellidae. Test biserial, palmate; aperture cribrate. *Bolivinella.*

(3) Superfamily Bolivinitacea. Test biserial: aperture interiomarginal. rounded, with toothplate. Wall optically radial.

Family Bolivinitidae. The only family under Bolivinitacea; defining characters same as those of the Superfamily. Example: *Bolivinita.*

(4) Superfamily Cassidulinacea. Test biserial, coiled planispirally or trochospirally throughout or in early part; aperture interiomarginal or terminal, with or without toothplate: wall optically radial or granular. Examples of extant families and genera:

Family Cassidulinidae. Coiling planispiral. *Cassidulina, Cassidulinoides, Ehrenbergina, Globocassidulina, Islandiella.*

(5) Superfamily Turrilinacea. Test high trochospiral, triserial, or biserial throughout, or changing to biserial or uniserial in later part; aperture with or without toothplate; wall optically radial or granular. Examples of extant families and genera:

Family Stainforthiidae. Test (a) triserial in early part and twisted biserial in later part, or (b) twisted biserial throughout; aperture large, elongate; rimmed or lipped apertural margin, partly infolded and linked with internal toothplate. *Hopkinsina, Stainforthia.*

(6) Superfamily Buliminacea. Test high trochospiral throughout, or modified to biserial or uniserial in later part. Aperture interiomarginal, loop-shaped, with internal toothplate; wall optically radial. Examples of extant families and genera:

Family Siphogenerinoididae. Test triserial or biserial in early part, biserial or uniserial in later part. *Rectobolivina, Rectuvigerina, Sagrina. Siphogenerina.*

Family Buliminidae. Test triserial. *Bulimina, Globobulimina.*

Family Buliminellidae. Test high trochospiral. with numerous chambers in a whorl. *Buliminella.*

Family Uvigerinidae. Test triserial throughout or in early stages; aperture terminal, extended into a neck, with internal toothplate. *Angulogerina, Trifarina, Uvigerina.*

Family Reussellidae. Test triserial throughout, or changing to biserial or uniserial in later part: periphery angular; aperture interiomarginal or terminal, slitlike or cribrate. *Reussella.*

Family Pavoninidae. Test biserial in early part, uniserial later: fan-shaped. *Pavonina.*

(7) Superfamily Fursenkoinacea. Test twisted or flat biserial. or triserial. Aperture loop-shaped, with internal toothplate. wall optically granular. Examples of extant families and genera:

Family Fursenkoinidae. Test twisted biserial throughout, or uniserial in later part. *Fursenkoina. Sigmavirgulina.*

Family Virgulinellidae. Test triserial or biserial, with partly covered sutural apertures. *Virgulinella.*

(8) Superfamily Delosinacea. Test trochospiral or triserial throughout, or biserial in later part. Aperture areal, elongate, or in the form of sutural pores. Wall optically granular. Examples of extant families and genera:

Family Delosinidae. Test high triserial; with sutural pores, but no primary aperture. *Delosina.*

(9) Superfamily Pleurostomellacea. Test triserial or biserial, changing to uniserial, or uniserial throughout; aperture areal, slitlike (and partly covered) or cribrate; aperture and foramina connected by internal siphon; wall optically granular.

Family Pleurostomellidae. The only family under Pleurostomellacea; defining characters same as those of the superfamily. Examples: *Ellipsoglandulina, Pleurostomella.*

(10) Superfamily Stilostomellacea. Test uniserial; aperture terminal, with phialine lip and small tooth.

Family Stilostomellidae. The only family under Stilostomellacea; defining characters same as those of the superfamily. Examples: *Nodogenerina, Siphonodosaria, Stilostomella.*

(11) Superfamily Annulopatellinacea. Test low conical; round initial chamber enclosed by second chamber; succeeding uniserial chambers arranged in annuli on the convex side, but overlapping on concave or flat side, and subdivided by small tubules (internal extensions of surface pores); no aperture, but conspicuous pores.

Family Annulopatellinidae. The only family under Annulopatellinacea; defining characters same as those of the superfamily. Example: *Annulopatellina.*

Order 12, ROTALIIDA. Test of low-Mg calcite; wall bilamellar, perforate; chamber arrangement low or (rarely) high trochospiral, planispiral, annular, or irregular.

(1) Superfamily Discorbacea. Chamber arrangement low trochospiral; aperture umbilical, interiomarginal, with or without supplementary apertures; wall structure optically radial. Examples of extant families and genera:

Family Bagginidae. Test wall finely perforate overall, but imperforate in a part of ventral side. *Baggina, Cancris.*

Family Eponididae. Aperture interiomarginal and slitlike (or a narrow arch) or areal and cribrate. *Eponides, Ioanella, Paumotua, Poroeponides.*

Family Heleninidae. Primary aperture interiomarginal; secondary apertures sutural. *Helenina.*

Family Mississippinidae. With distinct, translucent or opaque bands near periphery on one or both sides. *Mississippina, Stomatorbina.*

Family Pegidiidae. Coiling modified trochospiral, with resorbed early chambers; apertures open ends of tubes on ventral side. *Pegidia.*

Family Discorbidae. Umbilical area partly covered by chamber extensions; each chamber partly divided by an imperforate wall. *Discorbis, Neoeponides.*

Family Rosalinidae. Aperture a low interiomarginal arch; chamber interiors simple; umbilicus partly covered by chamber extensions or closed. *Gavelinopsis, Neoconorbina, Rosalina.*

Family Sphaeroidinidae. Chambers strongly overlapping, arranged trochospirally or in different planes; aperture areal and slitlike or sutural and multiple. *Sphaeroidina.*

(2) Superfamily Glabratellacea. Aperture umbilical, interiomarginal. Umbilicus depressed, surrounded by radial sutures or ornamentation; wall structure optically radial. Examples of extant families and genera:

Family Glabratellidae. Test low trochospiral; radially aligned striations or granules around umbilicus. *Glabratella.*

Family Heronallenidae. Test low trochospiral, planoconvex; aperture closed by a plate; radial striations around umbilicus. *Heronallenia.*

(3) Superfamily Siphoninacea. Test low trochospiral throughout or in early part; aperture interiomarginal or areal. with a lip (usually on a short neck); wall structure optically radial or granular.

Family Siphoninidae. The only family under Siphoninacea; defining characters same as those of the superfamily. Example: *Siphonina.*

(4) Superfamily Discorbinellacea. Test low trochospiral or nearly planispiral; aperture wholly or partly interiomarginal, arch-like or slitlike; wall structure optically radial. Examples of extant families and genera:

Family Pseudoparrellidae. Test low trochospiral; aperture partly interiomarginal and partly an almost vertical slit on the terminal chamber face. *Eilohedra, Epistominella, Stetsonia.*

Family Discorbinellidae. Test flat trochospiral or nearly planispiral; primary aperture interiomarginal, with or without secondary apertures under umbilical flaps. *Laticarinina, Discorbinella.*

(5) Superfamily Planorbulinacea. Test low trochospiral throughout or in the early part, with planispiral, uniserial, biserial, or irregular arrangement in the later part; coarsely perforate; primary aperture interiomarginal in coiled forms, with or without secondary apertures; wall structure optically radial or intermediate. Examples of extant families and genera:

Family Planulinidae. Test evolute or partly evolute on both sides; chamber arrangement

trochospiral throughout or planispiral in the later part. *Hyalinea, Planulina.*

Family Cibicididae. Test attached; chamber arrangement (a) low trochospiral throughout, or uniserial or biserial in the later part, or (b) planispiral or annular. Aperture interiomarginal in trochospiral forms, usually extending from ventral to dorsal side. *Cibicides, Cibicidoides, Cyclocibicides, Dyocibicides.*

Family Planorbulinidae. Chamber arrangement trochospiral throughout, or planispiral. annular, or irregularly multispiral in the later part. Aperture in adult forms peripheral and multiple. *Caribeanella, Planorbulina.*

Family Cymbaloporidae. Chamber arrangement trochospiral in early part, annular in later part; numerous apertures, usually as large pores. *Cymbaloparetta.*

(6) Superfamily Acervulinacea. Earliest chambers may be coiled; adult chambers numerous and irregularly arranged, producing diverse test forms; aperture present only as mural pores; test coarsely perforate; wall structure optically radial. Examples of extant families and genera:

Family Acervulinidae. Chambers spirally arranged in early part, and spreading irregularly in layers in later part. Test attached or free. *Acervulina, Gypsina.*

Family Homotrematidae. Chambers arranged spirally in early part, and forming a massive or branching structure in the later part. Test attached. *Homotrema, Miniacina.*

(7) Superfamily Asterigerinacea. Chamber arrangement trochospiral to nearly planispiral; chambers fully or partly subdivided by internal partitions; primary aperture interiomarginal or areal; secondary apertures sutural or areal; wall structure optically radial. Examples of extant families and genera:

Family Epistomariidae. Test trochospiral; chambers with complete or incomplete chamberlets. *Nuttallides, Palmerinella.*

Family Asterigerinidae. Test trochospiral; alternating larger and smaller chamberlets in a stellate arrangement on the ventral side. *Asterigerina.*

Family Amphisteginidae. Test trochospiral; numerous chambers and chamberlets with sinuous sutures. *Amphistegina.*

(8) Superfamily Nonionacea. Test fully or nearly planispiral; aperture distinct or pore-like, with interiomarginal, areal, sutural, or peripheral location; wall structure optically granular or radial. Examples of extant families and genera:

Family Nonionidae. Test fully planispiral throughout or in early part; aperture slitlike or a series of pores. *Astrononion, Haynesina. Melonis, Nonion, Nonionella, Nonionellina, Pullenia.*

(9) Superfamily Chilostomellacea. Test trochospiral to planispiral throughout, or in the early part, with uncoiled later part; aperture interiomarginal in coiled forms, terminal in uncoiled forms; wall structure optically granular. Examples of extant families and genera:

Family Chilostomellidae. Test low trochospiral to planispiral; later chambers enveloping earlier ones; chambers without internal partitions. *Allomorphina, Chilostomella.*

Family Quadrimorphinidae. Test low trochospiral; chambers not enveloping, with internal partitions. *Quadrimorphina.*

Family Osangulariidae. Test low trochospiral; aperture (a) partly interiomarginal, partly areal oblique, or (b) wholly areal. *Osangularia.*

Family Oridorsalidae. Test low trochospiral; primary aperture interiomarginal; secondary apertures sutural, on both sides of test. *Oridorsalis.*

Family Gavelinellidae. Test low to high trochospiral; aperture interiomarginal, usually bordered by a narrow or wide extension of chamber wall. *Gyroidina, Gyroidinoides, Hansenisca, Hanzawaia.*

Family Karreriidae. Test attached. Chamber arrangement low trochospiral in early part, serial later. *Karreria.*

(10) Superfamily Rotaliacea. Test typically low trochospiral or planispiral, with numerous chambers; intercameral septa doubled by the addition of a lamina during new chamber formation, usually with various internal passages; aperture interiomarginal or areal, single or multiple; wall structure optically radial, with a few granular exceptions. Examples of extant families and genera:

Family Rotaliidae. Test low trochospiral

throughout, usually with radial, intraseptal, or sutural canals or fissures. *Ammonia* (Fig. 2.9), *Asterorotalia, Pararotalia.*

Family Calcarinidae. Test low trochospiral to planispiral; symmetrical or nearly so; usually spinose. *Baculogypsina, Calcarina.*

Family Elphidiidae. Test planispiral to low trochospiral; with sutural canal system and pores. *Cribroelphidium, Elphidium, Elphidiella, Ozawaia, Parrellina.*

(11) Superfamily Nummulitacea. Chamber arrangement planispiral or annular; numerous chambers, with or without chamberlets; spiral or interseptal canals present. Examples of extant families and genera:

Family Nummulitidae. Test form lenticular, discoidal, or stellate; numerous chambers on the equatorial plane; with or without lateral chambers; with a complex canal system. *Cycloclypeus, Operculina, Heterostegina.*

Order 13, GLOBIGERINIDA. The only planktonic order of the Foraminifera. Test of low-Mg calcite in all extant and most extinct taxa, but aragonitic in the Favusellacea (Jurassic to early Cretaceous); wall bilamellar, perforate; chamber arrangement trochospiral, planispiral, or serial; wall structure optically radial.

(1) Superfamily Heterohelicacea. Chamber arrangement biserial or triserial throughout, or in the early part (with fewer or more series in the later part). Examples of extant families and genera:

Family Guembelitriidae. Test triserial throughout or in the early part. *Gallitellia.*

Family Chiloguembelinidae. Test biserial; aperture with a rim. *Laterostomella.*

(2) Superfamily Globorotaliacea. Chamber arrangement trochospiral or streptospiral; surface nonspinose; primary aperture interiomarginal. Examples of extant families and genera:

Family Globorotaliidae. Chamber arrangement low trochospiral; wall smooth or pustulose; aperture with rim. *Berggrenia, Clavatorella, Globorotalia, Neogloboquadrina, Turborotalia.*

Family Pulleniatinidae. Chamber arrangement streptospiral in the adult stage; chambers inflated. *Pulleniatina.*

Family Candeinidae. Chamber arrangement trochospiral; primary aperture interiomarginal and single, or sutural and multiple, in some forms covered by bullae. *Candeina. Tenuitella. Tinophodella.*

(3) Superfamily Globigerinacea. Chamber arrangement trochospiral to planispiral: test surface characteristically spinose; primary aperture usually interiomarginal, secondary apertures sutural; aperture may be replaced by surface pores. Examples of extant families and genera:

Family Globigerinidae. Chamber arrangement trochospiral throughout or changing to planispiral in later part; test partially or completely enclosed by the final chamber in some genera. Spines loosely attached. *Beella, Bolliella, Globigerina Globigerinella, Globigerinoides* (Fig. 2.9), *Orbulina, Sphaeroidinella.*

Family Hastigerinidae. Chamber arrangement trochospiral in early part, planispiral or streptospiral in later part. Spines growing from collar-like projections. *Hastigerina, Hastigerinopsis, Orcadia.*

Order 14, INVOLUTINIDA. Test made of aragonite. Two chambered test; initial chamber enclosed by coiled, tubular second chamber. No designated superfamily.

Family Planispirillinidae. The only extant family in this suborder. Asymmetrical test, coiling planispiral or trochospiral; umbilical area, at least on one side, filled by lamellar growth; aperture terminal. Examples: *Alanwoodia, Conicospirillinoides, Planispirillina* (Fig. 2.9). *Trocholinopsis.*

Order 15, ROBERTINIDA. Test made of aragonite, perforate, multichambered.

(1) Superfamily Ceratobuliminacea. Chambers with internal partitions and arranged in a trochospiral coil; aperture areal or interiomarginal. Examples of extant families and genera:

Family Ceratobuliminidae. Primary aperture entirely interiomarginal or with areal extension. *Ceratobulimina.*

Family Epistominidae. Primary aperture a slit on the test margin. *Hoeglundina.*

(2) Superfamily Robertinacea. Chambers

with double internal partitions; secondary chambers clearly distinguishable from primary chambers.

Family Robertinidae. The only family under Robertinacea; defining characters same as those of the superfamily. Examples: *Alliatina*. *Cushmanella, Robertina, Robertinoides* (Fig. 2.9). *Sidebottomina*.

Order 16, SILICOLOCULINIDA. Test made of opaline silica; imperforate. No superfamily designated.

Family Silicoloculinidae. Multichambered coiled test; chambers arranged in various planes: aperture terminal, partly blocked. Example: *Miliammellus* (Fig. 2.9).

2.6 GEOLOGICAL RECORD OF EXTANT FORAMINIFERAL TAXA

Many foraminiferal species and genera were first reported as fossils rather than as living organisms. Any massive compilation of geological ranges of such taxa is likely to miss a few later reports of their occurrence in modern sediments. Thus, some genera continuing into the Holocene (e.g. *Loxostomum, Suggrunda*) are listed as extinct in Loeblich and Tappan (1987). On the other hand, about half of the nearly 900 extant foraminiferal genera mentioned in Loeblich and Tappan (1987) have no pre-Holocene record (Tappan and Loeblich, 1988). This does not necessarily mean that the earliest species of all these genera actually evolved in the last 10,000 years; the earlier history may be lost, because of taphonomic processes (see chapter 16) and diagenesis, and by the destruction of the sedimentary record by diverse geological processes. Organic-walled tests (Allogromiida) are preserved only under exceptionally favorable conditions; they have a very poor and erratic fossil record. Agglutinated tests with loosely attached grains or with organic cement frequently disintegrate in many sedimentary environments, and during diagenesis. Aragonitic tests (Robertinida and Involutinida) are destroyed in diagenesis more readily than calcitic tests. Compared to low-Mg calcitic tests, both aragonitic and high-Mg calcitic tests (Miliolida) are preferentially dissolved in the deep sea. Apparently, tests made of calcite spicules (Carterinida) are also poorly preserved: they are known from the Eocene and Holocene. but not from the intervening epochs.

The geological record of extant families is given in Table 2.3. About three-fourths of these 164 families have a pre-Holocene record. Eleven can be traced as far back as early Paleozoic (Cambrian and Ordovician); all of these taxa are organic-walled or agglutinated (orders Allogromiida. Astrorhizida, and Lituolida). The most specialized calcareous order of the Paleozoic (Fusulinida) is extinct. Among modern families with secreted calcareous tests, only two can be traced to the Paleozoic (early Carboniferous); both of these are characterized by imperforate walls (Miliolida). A few extant hyaline families (calcareous perforate tests) extend back to the Triassic. but for the two most diverse groups of Holocene calcareous Foraminifera, the record of modern families begins in the Cretaceous; 27% of extant families of the Buliminida and 37% of extant families of the Rotaliida started in this 78-my-long period. The effect of the mass extinction at the Cretaceous-Paleogene boundary was much more severe on planktonic Foraminifera. All seven extant families of the Globigerinida were present in the Miocene, but only one family, Guembelitriidae (with a single Holocene genus, *Gallitellia*), can be traced back to the Cretaceous. Overall, the stratigraphic record shows that 62 benthic families originated in the Cretaceous, of which 22 are extinct. For planktonic families, the numbers are 10 and 9, respectively.

2.7 CONCLUDING REMARKS

The Loeblich and Tappan classification of 1987. emended by them in 1992. and further modified for ordinal taxa in this chapter, is the most

Table 2.3 Origination record of extant families. The number of extant families beginning in a given period or epoch is shown under each order. The total number of extant families within each order is in parentheses after the order number. Data on geological ranges from Loeblich and Tappan (1987). Order numbers (as in fig. 2.8): 1, Allogromiida; 2, Astrorhizida; 3, Lituolida; 4, Trochamminida; 5, Textulariida; 6, Fusulinida (extinct, not in table); 7, Miliolida; 8, Carterinida; 9, Spirillinida; 10, Lagenida; 11, Buliminida; 12, Rotaliida; 13, Globigerinida; 14, Involutinida; 15, Robertinida; 16, Silicoloculinida.

Period/Epoch	Order 1 (4)	Order 2 (15)	Order 3 (28)	Order 4 (2)	Order 5 (5)	Order 7 (15)	Order 8 (1)	Order 9 (2)	Order 10 (6)	Order 11 (22)	Order 12 (52)	Order 13 (7)	Order 14 (1)	Order 15 (3)	Order 16 (1)	All orders (164)
Holocene	2	5	6	1	1	1				4	5		1			26
Pleistocene																
Pliocene											1					1
Miocene			1			1				3	2	2			1	10
Oligocene											6					6
Eocene	1		2			2	1			5	14	2				27
Paleocene					2	1				4	5	2				14
Cretaceous		1	6		1	3		1		6	19	1		2		40
Jurassic			4		1	5			2							12
Triassic			3					1	4					1		9
Permian																
Carboniferous		2	3	1		2										8
Devonian																
Silurian																
Ordovician	1	6	2													9
Cambrian		1	1													2

elaborate hierarchical classification of the Foraminifera ever produced. Although the 1987 classification was not as well-received as their simpler 1964 classification (Haman, 1988), it is the current standard, at least for the placement of genera into families and superfamilies. Hierarchical biological classifications are inherently subjective, especially where a large part of the data is derived from the fossil record. There is disagreement between Loeblich and Tappan (1987, 1992) and other taxonomists even on some well-known foraminiferal taxa, e.g. (a) about the recognition of superfamilies, families, subfamilies, and their constituent genera within the Buliminida (Revets, 1996), (b) about the inclusion of *Discorbis, Rosalina, Eponides,* and *Gavelinopsis* in the Discorbacea, rather than in the Rotaliacea or Eponidacea, a superfamily not recognized by Loeblich and Tappan (Hansen and Revets, 1992), and (c) about the placement of the Elphidiidae in the Rotaliacea, rather than in the Nonionacea (Haynes, 1990). In the context of the entire classification, however, these problems are not overwhelming.

On the positive side, the major improvement over the 1964 version is the de-emphasizing of the optical property of hyaline walls in the 1987 expansion. The use of the radial and granular wall structures (as seen in polarized light) for superfamily distinctions has been considered an 'unnecessarily rigid constraint' for a long time (e.g. Cifelli, 1976). This constraint was removed by Loeblich and Tappan in 1987. For example, *Cassidulina* and *Islandiella,* two similar genera, were placed in two different superfamilies (Cassidulinacea and Buliminacea) in Loeblich and Tappan (1964a); they are now in the same family (Cassidulinidae). The problem is not fully resolved, however. In view of the fact that both radial and granular structures have been observed within a single genus (*Elphidium*), the usefulness of this optical property at any level of taxonomic hierarchy needs reexamination. At the ordinal level, the status of the Silicoloculinida and the placement of the extant members of the Involutinida are uncertain; the decisions in Loeblich and Tappan (1992) are different from those in Loeblich and Tappan (1987).

Foraminiferal classifications are largely the outcome of paleontological research. Those reported in relatively recent protozoological literature (e.g. Levine *et al.,* 1980; Lee, 1990a) generally agree in concept and overall structure, if not in the ranks of taxa, with one of the Loeblich and Tappan schemes. However, a startling regression to chamber count as the chosen primary criterion is observed in one classification (Cavalier-Smith, 1993). In this, the Foraminifera (as a subphylum within the Kingdom Protozoa) is split into two classes, one with single-chambered forms (Monothalamea), the other with multichambered forms (Polythalamea). The Monothalamea, reminiscent of d'Orbigny's Monostègues, is not split further into lower suprageneric categories. The included genera are not named, but by defintion, this group would include *Myxotheca* (organic-walled), *Saccammina* (agglutinated), *Squamulina* (calcareous imperforate), and *Lagena* (calcareous perforate), i.e. genera representing four separate orders (three of them with numerous multichambered genera) in the schemes of Haynes (1981), Lee (1990a), and Loeblich and Tappan (1992). Such taxonomy is a denial of the enormous body of extant information on foraminiferal wall compositions, stratigraphic distributions, and probable phylogenies.

On the other hand, it is almost axiomatic that scientific classification of the Foraminifera must not be based on skeletal morphology alone. The geological record of fossils and the DNA signatures of living species, both providing significant clues to phylogenetic connections, must support any logical scheme of classification. The geological history of the Foraminifera has been taken into consideration by most systematists, starting with Cushman, but the genetic study is still in its infancy (see, e.g. Pawlowski *et al.,* 1994a, b, 1996; Wray *et al.,* 1995; Holzmann and Pawlowski, 1997), and has not yet become a cause for restructuring the suprageneric classification. In any case, the half-century old statement of Alan Wood is still true: 'If classifications of the future are to be "natural," reflecting the evolutionary history of the group, they will be not less but more complicated than those at present in favour' (Wood, 1949).

2.8   ACKNOWLEDGMENTS

3

Foraminifera:
A biological overview

Susan T. Goldstein

3.1 INTRODUCTION: FORAMINIFERA AS LIVING ORGANISMS

The Foraminifera are an enormously successful group of amoeboid protists. Branching very deeply within the eukaryotic evolutionary tree (Pawlowski *et al.*, 1998b), they first appeared in the Cambrian, and, over the course of the Phanerozoic, invaded most marginal to fully marine environments and diversified to exploit a wide variety of modes of life. Foraminifera are abundant and diverse in modern oceans where they occur from coastal settings to both planktonic and benthic habitats of the deep sea. They occupy tiered epibenthic to deep infaunal microhabitats and utilize a diversity of trophic mechanisms.

Some representatives have attained gigantic proportions. The extinct *Lepidocyclina elephantina,* for example, at over 14cm is among the largest reported (Grell. 1973). The Foraminifera, although exclusively unicellular, accomplish nearly all of the fundamental functions of life performed by the myriad of multicellular animals. Foraminifera eat, defecate, move, grow, reproduce, and respond to a variety of environmental stimuli. Whereas metazoans evolved

organs and other specialized features through multicellularity, Foraminifera and other protists specialized by diversifying subcellular components or organelles to perform these various functions.

Two broad morphological features distinguish the Foraminifera from other protists. First, all Foraminifera possess granuloreticulopodia (Figs. 3.1, 3.2), which are fine, thread-like, pseudopodia that anastomose (split and rejoin) and have a granular texture when viewed with the light microscope. Second, nearly all Foraminifera possess a test or shell that encompasses the organism and separates it from the surrounding milieu. The test may be organic (not mineralized), agglutinated (constructed of foreign particles cemented together by the foraminifer), composed of calcium carbonate or, in rare cases, silica (see chapter 2). In addition, the Foraminifera are united by a life cycle characterized by a fundamental alternation of sexual and asexual generations that has become secondarily modified in some groups. Having made these generalizations, it is interesting to note that the freshwater rhizopod *Reticulomyxa* has pseudopodia that are strikingly similar to those of the Foraminifera (Orokos *et al.,* 1997). though it

lacks a shell. Genetically, this protist is a foraminiferan (Pawlowski *et al.*. 1998a).

Our understanding of the Foraminifera as living, amoeboid protists dates to Dujardin's (1835a,b,d) observations on several living shallow-water Foraminifera (*Triloculina, Elphidium, Ammonia, Peneroplis*) which he obtained by washing fucoid and coralline algae collected from the Mediterranean into glass vessels. He also observed *Gromia oviformis,* a protistan relative of the Foraminifera that superficially resembles the foraminifer *Allogromia* (*Gromia's* pseudopodia and life cycle differ from those characteristic of the Foraminifera; see Arnold, 1972). Watching live milioline Foraminifera climb the walls of his vessels, Dujardin (1835b) described granule-filled, anastomosing 'filaments' (pseudopodia) which slowly extended and retracted as the Foraminifera adhered to the vessel walls and slowly moved. Dujardin coined the term 'sarcode' to describe amoeboidal cytoplasm, and established the 'Rhizopodes', suggesting a relationship between the Foraminifera and other amoebae.

3.2 PSEUDOPODIA

The key to Dujardin's (1835a,b,d) correct identification of the Foraminifera as amoeboid organisms, thus removing them from the cephalopods where d'Orbigny (1826) had previously placed them (see Cole, 1926; Lipps, 1981), were his observations on the undifferentiated body ('sarcode') of the Foraminifera and on the anastomosing, granular pseudopodia which all Foraminifera possess (see Fig. 2.2). We now know that pseudopodia accomplish many essential life functions for the Foraminifera and are. therefore, of fundamental importance (Travis and Bowser, 1991). Pseudopodia are essential not only for motility and attachment, as recognized by Dujardin (1835a,b,d), but also for feeding, building and structuring tests, protection, and some aspects of respiration and reproduction. Pseudopodia provide the mechanism by which Foraminifera interact with their surroundings.

Foraminifera extrude pseudopodia through one or more apertural openings in the test. The first pseudopodia extruded commonly are fine filaments or 'filopodia' that are often straight. As this process continues, the pseudopodial trunk or 'peduncle' thickens and virtually fills the apertural opening(s), branching into numerous finer pseudopodia that often anastomose. The result, if the foraminifer is provided a hard smooth surface, is an intricate, sticky pseudopodial network of 'reticulopodia' that rivals the complexity of a spider's web (Carpenter *et al.,* 1862; Leidy, 1879). Unlike a spider's web, however, reticulopodia are continuously remodeled and transport a variety of materials. Particle movement, as many early observers remarked, is bidirectional, even within a single pseudopodial strand (Allen, 1964).

The intricacy and function of reticulopodia captivated many of the early foraminiferal biologists who provided detailed and sometimes poetic accounts of their observations (Dujardin, 1835a,b,d; Carpenter *et al.,* 1862; Leidy, 1879 [though his descriptions were based largely on freshwater protists included in *'Gromia'*]: Lister, 1903; Winter, 1907; Sandon, 1934; Jepps. 1942). Contemporary cell biologists have found foraminiferal pseudopodia excellent experimental systems for a number of processes including cell motility and the assembly and disassembly of microtubules (e.g. Jahn and Rinaldi, 1959; Allen, 1964; Travis and Allen, 1981; Bowser and Reider, 1985; Bowser *et al.,* 1986; Travis and Bowser, 1986a,b; Bowser *et al.,* 1988; Travis and Bowser, 1988; Welnhofer and Travis. 1996).

Though some benthic Foraminifera do indeed live attached to hard or firm surfaces such as seagrasses, macroscopic algae, shells, sponges, or rocks (Lutze and Altenbach, 1988; Lutze and Thiel, 1989; Langer, 1993), and probably extend reticulopodial nets in the field much as they do on glass slides, most live associated with fine-grained sediments through which they actively migrate (Severin and Erskian, 1981; Severin. 1987b; Wetmore, 1988; Weinburg. 1991; Hemleben and Kitazato, 1995; Bornmalm *et al.,* 1997). When offered abundant fine-grained sediment, most Foraminifera use their pseudopodia to col-

lect a variety of materials, including sediment, algal cells, bacteria, and organic detritus (see Goldstein and Corliss, 1994). Such collections are formed into mounds that may be large enough to completely encompass the test and are riddled with a three-dimensional reticulopodial array. Though commonly associated with feeding, many benthic Foraminifera construct somewhat similar mounds or cysts during the formation of a new chamber or prior to reproduction.

Structurally, foraminiferal pseudopodia are encased by a cell membrane and contain a cytoskeletal core of microtubules which may occur singly, but more typically as loosely organized bundles (Fig. 3.3) (reviewed in Travis and Bowser, 1991). These loosely arranged microtubules in the Foraminifera lack the intricate microtubular patterns found in cross sections of the 'axopodia' of such amoeboid protists as the heliozoans (Kitching, 1964; Smith and Patterson, 1986) and radiolarians (Cachon and Cachon, 1971, 1972; Anderson, 1983). However, perhaps not unlike the heliozoans, the Foraminifera have developed specialized mechanisms for rapid assembly and disassembly of microtubules, which allow rapid retraction of reticulopodia and their redeployment when needed (Welnhofer and Travis, 1996, and references therein).

Ultrastructural studies show that the characteristic granular appearance of foraminiferal pseudopodia is due to the presence of several organelles or structures that include mitochondria, 'dense bodies', phagosomes, defecation vacuoles, and a variety of other smaller structures (Fig. 3.3) (reviewed in Travis and Bowser, 1991). Mitochondria are the most prominent pseudopodial granules. They move bidirectionally, are essential for aerobic respiration, and are probably responsible for transporting metabolic energy (ATP) within the reticulopodial network. 'Dense bodies' are membrane-bound vesicles that appear refractile under the light microscope and opaque with TEM (transmission electron microscopy). Their function has not yet been determined, though Travis and Bowser (1991) suggest that they may serve as storage vesicles for phospholipids (building blocks of membranes). Phagosomes

are vacuoles that contain materials captured for ingestion, and their content varies widely, depending on the diet of the foraminifer. Xanthosomes, packets of undigested materials along with metabolic wastes, are transported out and away from the foraminifer along pseudopodia in defecation vacuoles (illustrated in Bowser *et al.,* 1985). For more information on pseudopodial structure and function, see Travis and Bowser (1991).

3.3 TROPHIC MECHANISMS

As a group, the Foraminifera utilize a broad range of feeding mechanisms and nutritional resources, including grazing, suspension feeding, deposit feeding, carnivory, parasitism, the direct uptake of DOC, and symbiosis. Many smaller Foraminifera that live within the photic zone commonly feed on selected species of algae (Fig. 3.4) (see reviews by Arnold, 1974, and Anderson *et al.,* 1991). but are also known to ingest bacteria, yeasts, fungi, and in some cases, small animals (Lee *et al.*, 1966; Lipps. 1983; Lee. 1980; Bernhard and Bowser, 1992). Bacteria appear to play an indispensable role in the nutrition of many Foraminifera (Lee, 1980). Though the diet of most Foraminifera may be quite varied, feeding experiments have shown that many species feed selectively (Lee *et al.,* 1966; Lee, 1980). Pseudopodia play an indispensable role in feeding in that they function to gather food (e.g. Jepps, 1942), subdue prey (Bowser *et al.,* 1992), and, in at least some species, may also function in extrathalamous digestion (Jepps, 1942; Meyer-Reil and Köster, 1991; Lee *et al.*, 1991b; Faber and Lee, 1991b).

Foraminifera that live below the photic zone cannot rely on living algal cells as a food source. However, the influx of phytodetritus to the seafloor from the plankton provides important primary and secondary food resources for Foraminifera and other members of the benthos. Gooday (1988) documented the selective exploitation of phytodetritus by several small species that appear to reproduce very rapidly, thus colonizing fresh phytodetritus as it arrives on the

seafloor. A number of subsequent investigations support these findings (Thiel *et al.,* 1989; Gooday and Lambshead, 1989; Lambshead and Gooday, 1990; Gooday and Turley, 1990; Gooday, 1993). More degraded forms of organic detritus, and, especially, the microbiotas (largely bacteria) associated with this material provide important food resources for shallow (Heeger, 1990) to deeper infaunal taxa (Goldstein and Corliss, 1994).

Grazing, found in some shallow-water Foraminifera, is accomplished by feeding largely on algal cells while moving over a surface such as a seagrass blade, kelp, or coralline algae. This process can be observed easily in culture. Jepps (1942), for example, described individuals of *'Polystomella' (= Elphidium) crispum* feeding on lawns of cultured diatoms. The foraminifers would use their pseudopodia to collect mounds of diatoms so extensive that they completely covered the test. After feeding within one mound for some time (usually hours), the foraminifer would discard it, move on, then construct a fresh mound. Discarded mounds, or 'feeding cysts' contained small orange xanthosomes (waste particles) that were shed by the foraminifer.

Suspension feeding Foraminifera make use of the small organisms and detritus that are suspended in the water column. This mode of feeding occurs in Foraminifera that occupy elevated epibenthic substrates as well as some of those that live in association with soft sediments.

Lipps (1983) suggested that suspension feeding is widespread in Foraminifera that elevate their aperture(s) above the sediment–water interface and extrude their pseudopodia directly into the water column. Because Foraminifera lack a mechanism for creating water currents as do many suspension-feeding invertebrates and ciliated protists, the suspension-feeding Foraminifera are most likely 'passive' suspension feeders (Lipps, 1983).

Suspension feeding occurs in both agglutinated and calcareous taxa. *Astrorhiza limicola,* for example, is a biconvex, agglutinated, monothalamous foraminifer with multiple apertures, each positioned at the end of a tube. In life position, this foraminifer rises up on its edge, positioning some apertures into the sediment and others into the overlying water column. Pseudopodia extend from all apertures. Those protruding into the sediment serve to anchor the foraminifer while those protruding from elevated apertures extend into the water column, and trap food particles (Cedhagen, 1988). *Pelosina arborescens,* another monothalamous agglutinated foraminifer that lives in soft sediments, similarly utilizes suspension feeding as a trophic mechanism (Fig. 3.5, 3.6) (Cedhagen, 1993). Suspension feeding also occurs in several calcareous species that occupy elevated habitats: *Rupertina stabilis, Cibicides wuellerstorfi,* and *Planulina ariminensis* (Lutze and Altenbach, 1988; Lutze and Thiel, 1989) as well as the agglu-

Figure 3.1 Juvenile *Cribrothalammina alba* with reticulopodia extended. Scale bar approximately 50 μm.

Figure 3.2 Higher magnification of apertural region of *Cribrothalammina alba* in Fig. 3.1. Note large pennate diatom near aperture. Scale bar approximately 10 μm.

Figure 3.3 TEM micrograph of a single pseudopodial strand from *Spiroloculina hyalina,* illustrating some of the various 'granules' found in foraminiferal pseudopodia: mitochondria (m), microtubules (mt), dense bodies (arrow). Scale bar = 1 μm. Micrograph provided by Samuel S. Bowser.

Figure 3.4 TEM micrograph of a partially digested diatom in a large food vacuole in *Cribrothalammina alba.* Chloroplasts and lipid vesicles appear to be the most persistent components within the diatom. Scale bar = 2 μm.

Figure 3.5 The large agglutinated species *Pelosina arborescens.* This foraminifer utilizes suspension feeding as a trophic mechanism. Micrograph provided by Tomas Cedhegan.

Figure 3.6 A reticulopodial net extended by *Pelosina arborescens* (see Fig. 3.5) that functions in suspension feeding. Micrograph provided by Tomas Cedhagen.

Figure 3.7 TEM micrograph of a food vacuole which contains sediment and a bacterium in the deposit-feeding foraminifer *Globobulimina pacifica.* Scale bar = 0.5 μm.

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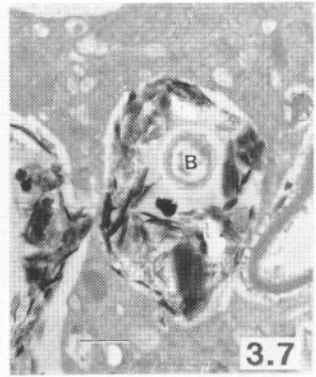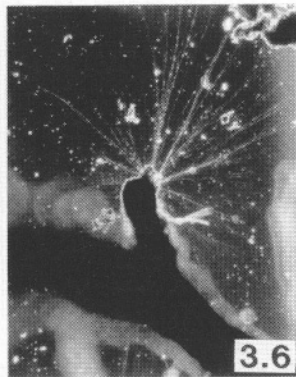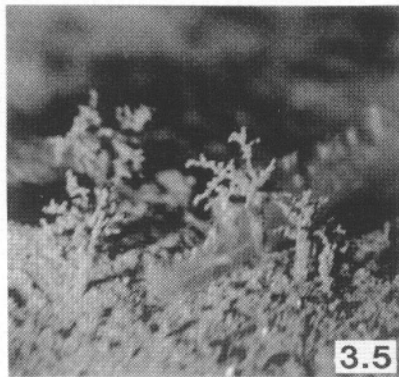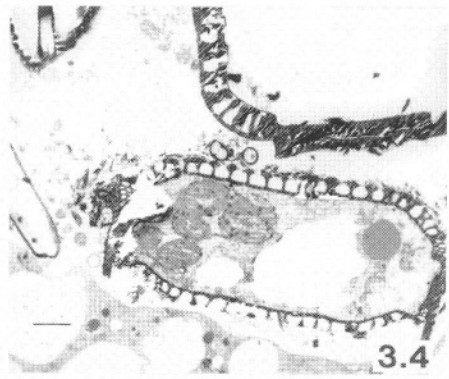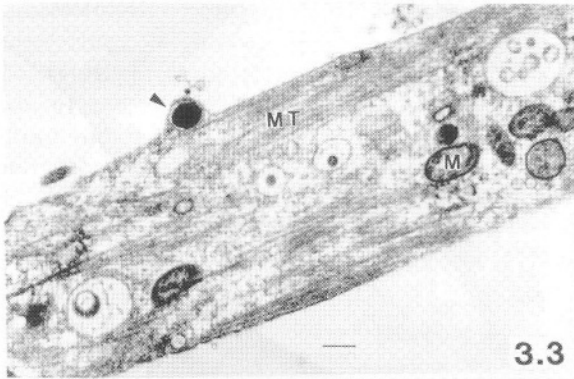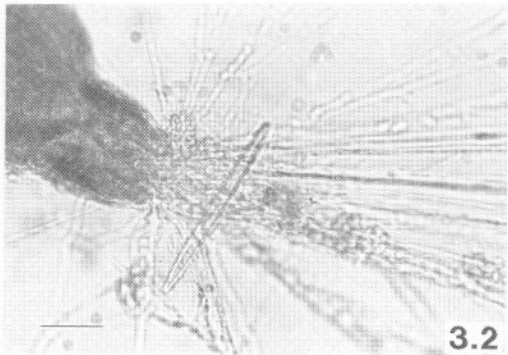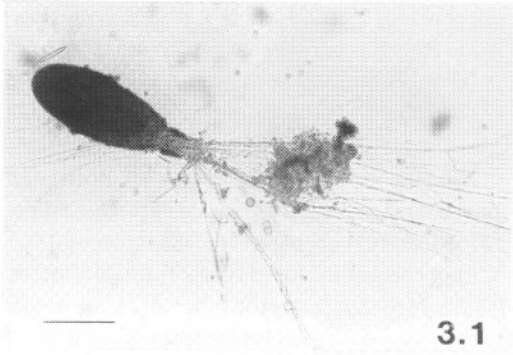
tinated *Saccorhiza ramosa* (Altenbach *et al.,* 1988). Epizoic Foraminifera that reside on the shells of living brachiopods may also utilize suspension feeding and benefit from brachiopod feeding currents (Zumwalt and DeLaca, 1980).

The construction of feeding cysts, as in *Elphidium crispum,* is not limited to grazing, but is also an integral part of *deposit feeding.* Many benthic Foraminifera that live in muddy sediments, both within and below the photic zone, use their pseudopodia to construct feeding cysts (Hofker, 1927; Nyholm, 1957; Goldstein and Corliss. 1994) with sediment, algal cells (or their remains in the form of phytodetritus), bacteria, and organic detritus (Goldstein and Corliss, 1994). Some of the material gathered by the pseudopodia is partitioned into small parcels which the foraminifer ingests by phagotrophy within the terminal chamber (Fig 3.7). Deposit feeding Foraminifera, such as the deep-sea dwellers *Globobulimina pacifica* and *Uvigerina peregrina* and the shallow-water *Ammonia beccarii,* ingest a surprisingly large amount of sediment as well as algal cells, bacteria, and organic detritus. Bacteria appear to constitute an important element in the diet of deposit-feeding Foraminifera (Goldstein and Corliss, 1994).

Carnivory is utilized by some Foraminifera, including both benthic and planktonic species and both symbiont-bearing and non-symbiont-bearing forms. The large symbiont-bearing foraminifer *Peneroplis pertusus,* for example, feeds on copepods, but ingests only portions of the prey, leaving the empty carapace behind (Winter, 1907). The large non-symbiont-bearing agglutinated foraminifer *Astrorhiza limicola* is at least partly carnivorous, and captures prey as large as 2–3 cm, including several types of small crustaceans (cumaceans, caprellids), and echinoid larvae (Buchanan and Hedley, 1960). Some carnivorous Foraminifera are quite small. Hallock and Talge (1994) described a small predatory foraminifer (*Floresina amphiphaga*) that attacks the larger foraminifer, *Amphistegina gibbosa. F. amphiphaga* attaches to the test of its prey and drills up to 10 holes per attachment site, often killing its prey. Carnivory has been reported in several additional benthic species (see Boltovskoy and Wright, 1976).

Carnivory also occurs in some planktonic Foraminifera. Anderson and Bé (1976) and Bé *et al.* (1977a) found the remains of copepods and other small crustaceans within the bubble capsule of *Hastigerina pelagica* and among the spines and pseudopodia of *Globigerinella aequilateralis.* These and several other planktonic taxa (*Orbulina universa, Globigerinoides ruber. Globorotalia menardii,* and *Pulleniatina obliquiloculata*) would prey on copepods and nauplii of the brine shrimp, *Artemia,* in laboratory cultures.

The pseudopodia of carnivorous Foraminifera may be specially adapted for capturing prey. In the large agglutinated foraminifer *Astrammina rara*, pseudopodia secrete an extracellular matrix material that functions to strengthen pseudopodia and maintain their integrity as prey resist capture. Non-carnivorous Foraminifera lack this material and have pseudopodia that are many times weaker than those from carnivorous Foraminifera (Bowser *et al.,* 1992). In addition, some carnivorous Foraminifera may have the ability to secrete an adhesive material in the area where prey contact pseudopodia (Anderson and Bé. 1976; Bowser *et al.,* 1992).

Many carnivorous Foraminifera, however, are not strictly carnivorous, but utilize carnivory in addition to at least one other trophic mechanism. Cedhagen (1988), for example, reported suspension feeding in *Astrorhiza limicola,* a foraminifer better known for its carnivory (Buchanan and Hedley, 1960). *Astrammina rara* ingests bacteria and diatoms in addition to metazoan prey (Bowser *et al.,* 1992), and some carnivorous planktonic Foraminifera also ingest diatoms (Bé *et al.,* 1977a). Some species, both benthic and planktonic, utilize carnivory in conjunction with algal endosymbiosis.

Though the vast majority of Foraminifera are free-living, a few species show *parasitism,* primarily infesting other foraminifers, bivalve molluscs, sponges, or stone corals. Le Calvez (1947) first documented parasitism in the Foraminifera by reporting the ectoparasitic existence of the unilocular *‘Entosolenia’* (= *Fissurina) marginata* on the foraminifer *Discorbis vilardeboanus. F. marginata* attaches to the spiral side of the

host and uses its pseudopodia to capture granules from the host's extrathalamous cytoplasm. This species could be cultured only in association with *D. vilardeboanus* and not when offered alternative foods such as algae or other species of Foraminifera. The small foraminifer *Metarotaliella tuvaluensis* may potentially parasitize several miliolid species (Collen, 1998). *M. tuvaluensis* attaches to the surface of juvenile miliolids, and causes deformations of the host test as the host overgrows this small foraminifer; living material, however, was not observed. The foraminifer *Cibicides refulgens* parasitizes the Antarctic scallop *Adamussium colbecki* by eroding through the scallop's shell and feeding on the nutrient-rich fluids in the extrapallial cavity; this species also feeds by grazing and suspension feeding (Alexander and DeLaca, 1987). Unlike other parasitic Foraminifera, *Hyrrokkin sarcophaga* infests multiple hosts (selected bivalves, sponges, and stone corals). This foraminifer penetrates the body wall of the hosts and feeds on soft tissues (Cedhagen, 1994).

Pawlowski (1989) and Pawlowski and Lee (1992) described an unusual association between the small foraminifer *Rotaliella elatiana* and the macrophytic alga *Enteromorpha*. The foraminifer lives inside the filaments of the alga and will not grow in culture unless the alga is present. Pawlowski (1989), therefore, suggests that this foraminifer is nutritionally dependent on the alga.

The large arborescent foraminifer *Notodendrodes antarctikos* is capable of utilizing *dissolved organic carbon* (DOC) (DeLaca *et al.,* 1981; DeLaca, 1982). Labeled amino acids and glucose introduced into sterile seawater were taken up by the foraminifer and rapidly metabolized. Given the opportunity, however, this foraminifer also ingests bacteria and paniculate organic matter, and thus, does not rely exclusively on the uptake of DOC. Reservoirs of DOC present in sediments may provide an important nutritional resource during particularly oligotrophic seasons in the Antarctic (DeLaca, 1982). This potentially widespread trophic mechanism, however, has received little attention.

Symbiotic relationships, discussed in detail in chapter 8, are quite varied in the Foraminifera, and include algal endosymbiosis (Lee and Anderson, 1991a), chloroplast husbandry (Lopez, 1979; Lee *et al.,* 1988; Bernhard, 1996), and bacterial endosymbiosis (Bernhard, 1996). Of these, algal endosymbiosis, which occurs in larger calcareous benthic Foraminifera (Fig. 3.8) and many planktonic species, is the best known. Chloroplast husbandry, the process by which Foraminifera sequester and house chloroplasts but not the entire algal cell, occurs in some benthic Foraminifera from both shallow-water habitats (Lopez, 1979; Leutenegger, 1984; Lee *et al.,* 1988; Lee and Anderson, 1991a) and low-oxygen microhabitats located well below the photic zone (Bernhard, 1996). In addition, bacterial endosymbionts have been identified in some benthic Foraminifera that live in anoxic or very low-oxygen microhabitats, though the actual mechanisms involved in this relationship have not yet been determined (Bernhard, 1996).

Algal endosymbiosis occurs in some representatives from three Foraminiferal orders: Miliolida, Rotaliida, and Globigerinida. Symbiont-bearing Foraminifera include most, though not all, large shallow-water dwellers from oligotrophic tropical and subtropical environments. Symbionts in the Miliolida are the most diverse, and include chlorophytes (Soritidae), rhodophytes (Perneoplidae), dinoflagellates (Soritidae), and diatoms (Alveolinidae). Only diatoms, however, are found in the algal symbiont-bearing members of the Rotaliida (Amphisteginidae, Calcarinidae, Nummulitidae). Planktonic Foraminifera (Globigerinida) may host either dinoflagellate or chrysophyte symbionts (see chapter 8, and reviews by Leutenegger, 1984, and Lee and Anderson. 1991a).

This broad array of potential algal endosymbionts allows different foraminiferal hosts to thrive at different depths within the photic zone (Leutenegger, 1984; Hallock. 1988a, 1988b; see chapter 8). The shallowest-water habitats are home to benthic Foraminifera with all types of symbionts. Those bearing chlorophytes, however, are limited to the shallowest depths (~30 m), whereas those with rhodophytes or
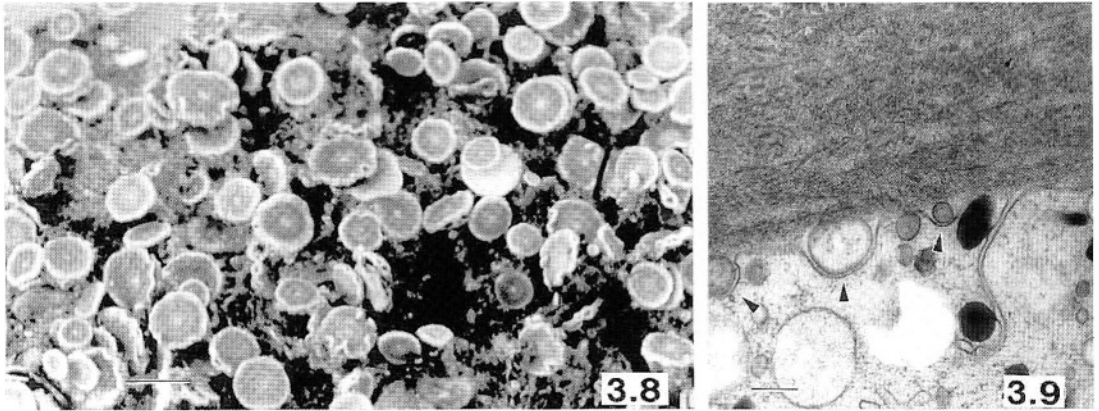
Figure 3.8 Live individuals of *Marginopora vertebralis* collected at the Lizard Island Research Station, northern Great Barrier Reef (ICOP Foram Biology Workshop; July, 1997). Scale bar approximately 1 cm.

Figure 3.9 TEM micrograph of a section across the contact between the test and cytoplasm in *Myxotheca* sp. The test is characterized by a fine meshlike structure (see also Angell, 1971). This foraminifer adds material to its test (vesicles at arrows) at regions distant from the aperture. Specimen prepared by high pressure freezing and freeze substitution. Scale bar = 0.25 μm. Micrograph by E.A. Richardson and S.T. Goldstein.

dinoflagellates extend to deeper habitats (60–70 m). Those with diatoms are found as deep as ∼130 m. The photosynthetic pigments of different algal groups are activated by light of different wavelengths. Diatoms utilize light in the blue to green range, allowing them to exploit the deepest habitats (Leutenegger, 1984). Though diatom-bearing Foraminifera occur at all depths, those in shallow-water habitats may protect themselves behaviorally by avoiding direct sunlight (*Heterostegina depressa*) or possessing a test that morphologically prevents overexposure (calcarinids) (Leutenegger, 1984; Hallock *et al.*, 1991b; Lee and Anderson, 1991a).

Relationships between Foraminifera and their algal endosymbionts are often not specific. A single foraminiferal species may host different species of symbionts, particularly if they are diatoms (Lee *et al.*, 1989, 1992; Lee and Anderson, 1991a). In addition, the same species of symbiont may occur in more than one species of Foraminifera. The dinoflagellate *Gymnodinium béii,* for example, has been reported from four different species of planktonic Foraminifera (see review by Lee and Anderson, 1991a). Relationships between the foraminiferal host and symbiont are varied and complex. In general, however, symbionts release exudates to the host, and

can in some cases supply the foraminifer with all the organic carbon it requires (Jørgensen *et al.,* 1985). Algal symbionts also promote calcification in some planktonic and benthic hosts (Bé *et al.*, 1982; Duguay, 1983). The foraminifer, in return, provides the symbiont with a fairly stable microenvironment in addition to dissolved nitrogen, phosphorus, and potentially other nutritional requirements (see Lee and Anderson, 1991a). Carnivory plays an important dietary role in some symbiont-bearing Foraminifera by providing a source for nitrogen and phosphorus for the host-algal system (Jørgensen *et al.,* 1985).

Foraminifera that host algal symbionts are quite dependent on their presence and well being. Hosts do not grow well in the dark or where the symbionts have been experimentally removed. Most symbionts, however, can be grown in culture quite readily without their foraminiferal host, and this is perhaps an essential feature of the relationship. Though symbionts are transmitted to offspring during asexual reproduction (multiple fission), gametes and (presumably) zygotes are symbiont-free. How and when the developing zygotes acquire symbionts in not known.

Some benthic Foraminifera belonging to the families Nonionidae, Elphidiidae, and Rotalielli-

dae sequester and house chloroplasts obtained from algal food sources (Lopez, 1979; Lee and Anderson, 1991a). Such chloroplasts retain their ability to photosynthesize in some hosts that reside within the photic zone. Over time, however, the foraminiferal host digests its chloroplasts, suggesting that the foraminifer must constantly replenish its supply (Lee and Anderson, 1991a). Interestingly, Bernhard (1996) identified a similar relationship in a nonionid that lives well below the photic zone in low-oxygen, benthic microenvironments of the Santa Barbara Basin.

3.4 GROWTH AND TEST MORPHOGENESIS

Growth in the Foraminifera is accomplished by either increasing the size of a single chamber (unilocular forms) or, more commonly, by intermittently adding a new chamber. Details of the former process are sketchy for agglutinated taxa and unknown in unilocular calcareous ones; the latter is better known in both calcareous and agglutinated representatives.

In allogromiid Foraminifera, new shell material appears to be added near the aperture (Angell, 1980), and this may also be the case for many members of the Astrorhizida. In addition, however, single-chambered agglutinated Foraminifera, such as *Cribrothalammina alba,* add material to the inner organic lining of the test at sites distant from the aperture (Goldstein and Barker, 1988). Figure 3.9. for example, illustrates the addition of vesicles (probably containing glycosaminoglycans; see Langer, 1992) to the base of the inner organic lining of *Myxotheca* sp.

Astrammina rara is a large single-chambered, coarsely agglutinated foraminifer that occurs abundantly in shallow-water habitats of the Antarctic. This astrorhizid is perhaps unusual in that it frequently sheds its test, and after a brief shell-less existence, stops and builds a new one (Bowser *et al.*, 1995). The interior of the test is characterized by a fibrous inner organic lining that is continuous with cables of bioadhesive (organic cement of other authors) that anchor sediment grains in place. Finer sediment grains fill the spaces between larger grains along the distal surface of the test and are also bound with bioadhesive (Bowser and Bernhard, 1993). As the foraminifer rebuilds its test, it initially gathers sediment of a variety of sizes, then appears to separate it by size by extending and retracting its pseudopodia. This concentrates the larger sediment grains to the interior of the forming test (Kinoshita *et al.*, 1996).

Many pioneers of foraminiferal biology observed and described the process of chamber formation in calcareous Foraminifera at the level of the light microscope (see comments in: Bé *et al.,* 1979; Hemleben *et al.*, 1986; 1989). Angell (1967b), however, provided the first ultra-structural account of chamber formation in a calcareous perforate foraminifer, *Rosalina floridana* (Order Rotaliida). This benthic species begins the process by forming a translucent algal cyst that is cemented to the substrate and extends over the entire spiral surface of the test. Next, pseudopodia coalesce within the cyst to form a template or anlage in the shape of the new chamber. This anlage is highly vesicular, and contains mitochondria, fibrillar material, electron-dense vesicles, and vesicles that appear to be empty. The inner organic lining (IOL) of the new chamber forms by the activities of pseudopodia over the surface of the anlage. Once the IOL is complete, cytoplasm from within the test floods the interior of the forming chamber and forces the vesicular material of the anlage out through the new aperture, thus forming a sheath over the entire test surface. A layer of calcite is then deposited over both the new chamber and the entire test. The sheath breaks up as the foraminifer frees itself from its cyst and resumes feeding. This process produces a 'monolamellar' test (terminal chamber is one layer thick) which, overall, is multilayered (see chapter 4). Figure 3.10 illustrates a very similar sequence of events during chamber formation in the calcareous perforate foraminifer *Ammonia tepida* (Order Rotaliida). Older chambers of the test consist of layers of calcite separated by organic linings that are continuous with the organic materials that fill the pores (Fig. 3.11 and 3.12) (Angell, 1967a).
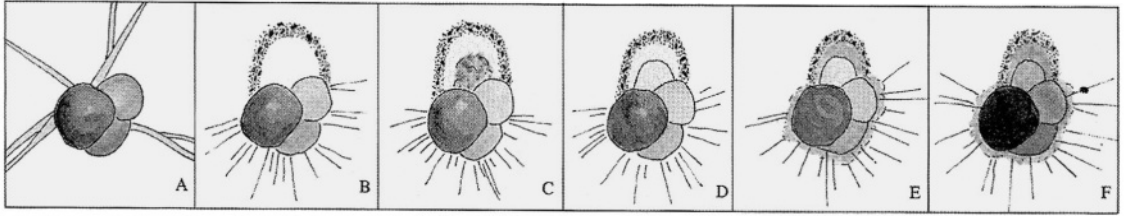
Figure 3.10 The sequence of chamber formation in the calcareous perforate species *Ammonia tepida*. A. Juvenile with three chambers. B. Construction of a cyst that includes foreign materials over the region where the fourth chamber will form (cyst does not cover the entire test). Pseudopodia appear finer and more numerous. C. Anlage constructed of cytoplasm in the shape of the new chamber. D. Organic lining constructed on the outside of the anlage cytoplasm. E. Sheath of 'frothy' cytoplasm extruded to cover the entire test. F. Calcification occurring over the surface of the new chamber and the entire test. Illustration by Elizabeth Gardiner.

In subsequent tracer studies using Ca^{45} and C^{14}, Angell (1979) showed that *R. floridana* (calcareous perforate species) does not pool either calcium or carbonate ions in the cytoplasm, but rather extracts them from the surrounding seawater during calcification. This, however, is not universal among calcareous perforate Foraminifera. The symbiont-bearing, calcareous perforate foraminifer *Amphistegina lobifera* indeed pools fairly large reserves of carbonate in the cytoplasm for use during calcification. The symbiont-bearing, calcareous imperforate *Amphisorus hemprichii,* however, does not pool carbonate, but obtains it directly from seawater during calcification (ter Kuile and Erez, 1987; ter Kuile, 1991).

Chamber formation in planktonic Foraminifera, also calcareous and perforate, shows broad similarities to the process in *R. floridana,* as well as significant differences. In the non-spinose *Globorotalia truncatulinoides, G. hirsuta,* and *G. menardii,* a protective organic envelope is formed (Hemleben *et al.,* 1977, 1986), comparable to the translucent cyst described by Angell (1967b). A cytoplasmic bulge ultimately fills the envelope and forms a 'primary organic lining' (POM) between the envelope and the cytoplasmic bulge. The POM and the envelope collectively comprise the anlage for the new chamber (a slightly different usage than that of Angell, 1967b), and calcification occurs as patches of calcite are deposited on both sides of the POM, thus forming a bilamellar shell (Hemleben *et al.,* 1977; Bé *et al.,* 1979; Hemleben *et al.,*

1989). Chamber formation is generally similar in spinose and non-spinose taxa with spines being added once the chamber is otherwise complete (Hemleben *et al..* 1986).

In the planktonic, non-spinose taxa, the newly formed chamber undergoes subsequent modification. Pores form secondarily by pseudopodia that pass through the wall and form rudimentary pores. Further, additional calcite is added to the surface of the chamber, thus thickening the test (Hemleben *et al.,* 1977, 1986). This differs significantly from the formation of a monolamellar, multilayered shell in *Rosalina floridana.*

Among the Miliolida (calcareous imperforate Foraminifera), chamber formation at the ultrastructural level has been described in *Calcituba polymorpha* (Berthold, 1976a; Hemleben *et al.,* 1986) and in *Spiroloculina hyalina* (Angell, 1980). *C. polymorpha* is an unusual miliolid in that its shell is cemented to a substrate and consists of somewhat randomly arranged, bifurcating calcareous tubes that are partially subdivided by constrictions. Occasionally, these individuals reproduce by what appears to be multiple fission, forming numerous young with milioline coiling that grow by forming long branching tubes (Arnold, 1967). *C. polymorpha* adds a new tube or chamber by forming an 'outer organic lining,' then transporting vesicles of preformed calcite needles to the site of calcification where they are released to form the shell. An inner organic lining is the last element added

to the shell (Berthold, 1976a; Hemleben *et al.,* 1986).

Chamber formation in *Spiroloculina hyalina,* reported by Angell (1980), begins with the construction of a cyst that surrounds the entire test and is composed of algal cells and detritus bound by a transparent membrane, similar to the process in *Rosalina floridana.* Fine pseudopodia anchor the foraminifer within the cyst and remain active throughout the process. Cytoplasm begins to flow from the test, and starting near the aperture, forms the shape of the new chamber which is being simultaneously secreted and calcified. Calcification occurs beneath a cytoplasmic sheath (probably comparable to the outer organic lining in *C. polymorpha*), beginning near the aperture of the last chamber and progressing from the base to the new aperture of the forming chamber. The interior of the chamber is formed and calcified by pseudopodia. The aperture and apertural tooth are the last to form. The resulting new chamber wall in miliolids consists of calcite needles randomly oriented in an organic matrix (Fig. 3.13), both of which are preformed within the cytoplasm and transported in vesicles to the developing wall where they are released. Older chambers are thicker than younger ones, but are 'nonlamellar.' Angell (1980) suggests that additional calcite is added to older portions of the test during chamber formation.

Chamber formation in the miliolid *Spiroloculina hyalina* differs from that in the rotaliid *Rosalina floridana* and globigerinids in two important regards. First, *S. hyalina* does not form an anlage of membranes or organic linings as does *R. floridana* and the planktonic Foraminifera, and calcification does not occur on the template of an organic lining. Rather, calcite needles and their associated organic matrix are preformed within the cytoplasm and transported to the forming chamber where they are released into the wall. Second, calcification occurs as cytoplasm is being extruded from the last complete chamber, proceeding from the base of the new chamber to the aperture and tooth. That is, extruded cytoplasm does not first form the shape of the new chamber and then the wall.

The agglutinated foraminifer *Textularia candeina* utilizes both organic and calcitic cements in the construction of its test (Bender, 1992). Chamber formation begins with the foraminifer
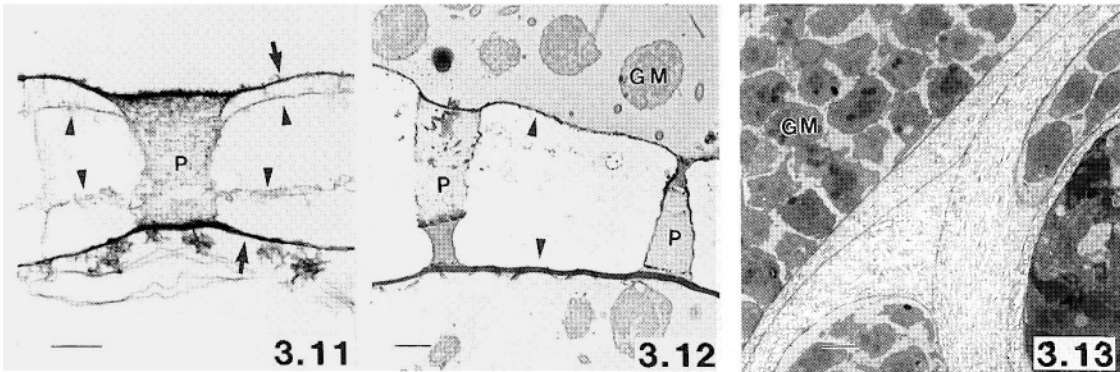
Figure 3.11 TEM micrograph of a decalcified test of the foraminifer *Chilostomella* sp. showing the continuity of the organic linings (large arrow), organic layers (small arrow), and pore material (p). Scale bar = 0.5 μm.

Figure 3.12 TEM micrograph of a an internal chamber from a decalcified test of *Ammonia tepida,* illustrating the organic linings and pore material. Organic layers between the organic linings, however, are absent, probably because the chamber was internal. The foraminifer was in the process of releasing gametes (GM). Scale bar = 1 μm.

Figure 3.13 TEM micrograph of the juncture of several internal chambers in the miliolid *Triloculina oblonga.* The test wall is composed of calcite needles (white linear structures) embedded in organic material (gray component of shell). The shell was decalcified during sample preparation using EDTA (see Goldstein, 1997). The foraminifer was in the process of releasing gametes (GM). Scale bar = 2 μm.

gathering sediment grains into a mound near the aperture. Once a cavity is formed within this mound of sediment, the foraminifer begins constructing a chamber by first coating grains with a thin organic envelope, and then cementing them together with a small amount of organic cement, beginning on the surface of the penultimate chamber and working outward toward the aperture. Calcite is then added primarily to the external surface of the chamber in the form of calcite bundles that fill in the open spaces in the test and further cement the agglutinated materials together. Pores, characteristic of the test of *T. candeiana,* appear during calcification, with their position depending on the orientation of the agglutinated grains and the position of the calcite bundles (Bender, 1992).

It should also be noted that many Foraminifera are capable of repairing their shells. Angell (1967c) showed that *Rosalina floridana,* decalcified with HCl, recalcified their shells, though the laminated wall structure was not restored. The planktonic foraminifer *Globigerinoides sacculifer* can reconstruct its shell after major injury, though extensive shell repair often results in very aberrant morphologies (Bé and Spero, 1981). The large nummulitid *Cycloclypeus carpenteri* can also repair a damaged shell (Song *et al.,* 1994) within about four months (Krüger *et al.,* 1996). Shell repair has also been reported in *Heterostegina depressa* (Röttger, 1978; Röttger and Hallock, 1982), the miliolid *Triloculina barnardi* (Collen, 1998), and a number of fusulinids (e.g. Kahler, 1942; Wilde, 1965). The ability to repair damaged shells appears to have evolved in the Paleozoic and is widespread among Foraminifera. It imparts obvious advantages to individuals subjected to attacks by predators or to mechanical damage.

3.5   REPRODUCTION AND THE FORAMINIFERAL LIFE CYCLE

3.5.1

The typical foraminiferal life cycle is characterized by a heterophasic alternation of sexual and asexual generations (Fig. 3.14). Though 'species pairs' (now recognized as dimorphic tests) had been identified as early as the mid-1800s (Lister, 1895), the fundamental outline of the life cycle was first presented by Lister (1895), with additional comments supplied by Schaudinn (1895). The foraminifer *Polystomella (= Elphidium) crispum,* a fairly large, regionally abundant, shallow-water dweller, was the subject of both studies.

The life cycle of *Elphidium crispum* includes a number of features that are shared by numerous other taxa, and it is perhaps fortuitous that Lister and Schaudinn selected this foraminifer as the subject of their observations. Had they studied any of a number of other species (e.g. *Allogromia laticollaris. Spirillum vivipara, Patellina corrugata,* or any of the 'microforaminifera' studied by Grell; see Grell, 1979), these early accounts of the life cycle might have taken a very different form.

Elphidium crispum is a dimorphic foraminifer (Lister, 1895, 1903; Schaudinn, 1895; Jepps, 1942). The adult gamont, which produces gametes, has a single nucleus and a megalospheric test characterized by a relatively large proloculus but a relatively small overall diameter. The adult agamont, which produces numerous young by multiple fission, is multinucleate and has a microspheric test characterized by a tiny proloculus but a relatively large overall test diameter. The terms megalospheric and microspheric, therefore, refer to the size of the proloculus, not the size of the entire test.

E. crispum produces biflagellated gametes and is gametogamous (gametes liberated directly into the surrounding seawater; see below), which is the case for most species of Foraminifera (see Goldstein, 1997). Fertilization then takes place by the fusion of two gametes, generally from different parents. Flagellated foraminiferal gametes typically are quite small (~1–4 μm), and the resulting zygote is also small. In gametogamous species, the zygote may spend a brief phase as a naked (shell-less) amoeba during which it feeds and grows before it calcifies, forming the microspheric proloculus.

In higher animals, meiosis typically occurs as
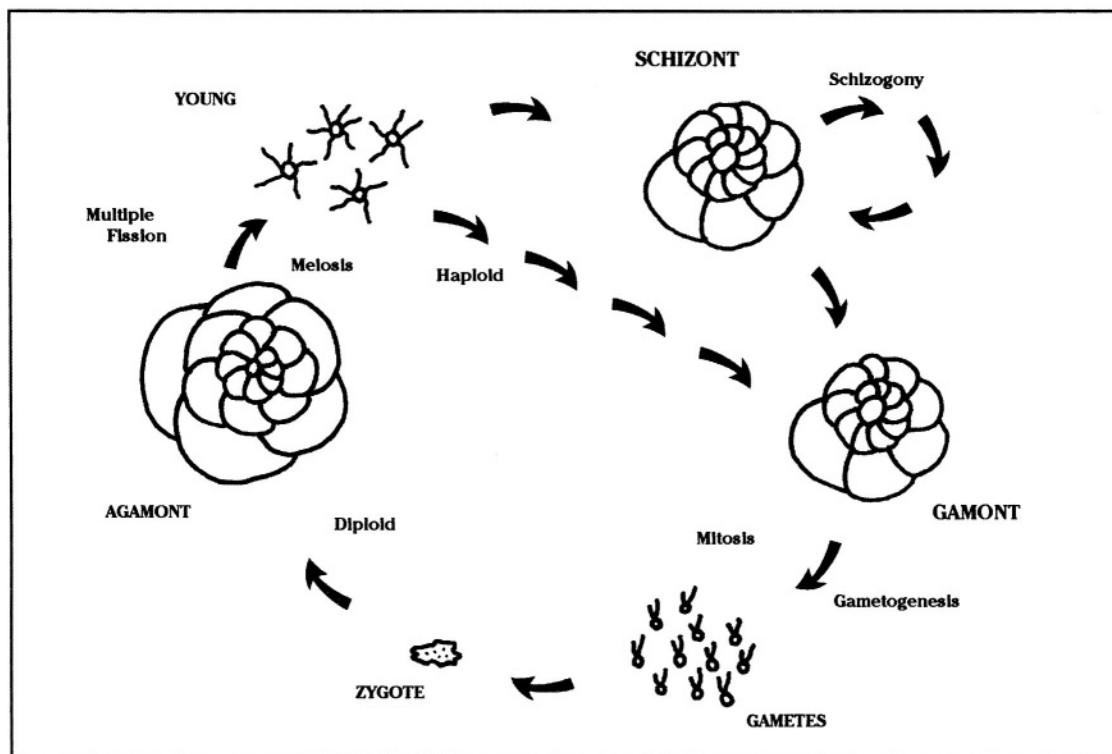
Figure 3.14 Outline of the foraminiferal life cycle which classically includes a regular alternation between a haploid, uninucleate, megalospheric gamont, and a diploid, multinucleate, microspheric agamont. Meiosis occurs in the agamont as part of multiple fission, and gametes are produced by mitosis. In some species, the life cycle also includes a schizont which is produced from the agamont and reproduces asexually. It can interject numerous successive asexual cycles. Meiosis typically occurs in the agamont. However, the type of nuclear divisions in the schizont have not been documented for any species. See text for discussion.

an integral part of gametogenesis. Meiosis is a reduction division in that it halves the diploid number of chromosomes and produces haploid daughter cells. In the Foraminifera, however, meiosis occupies an intermediate position in the life cycle, occurring in the agamont as an integral part of multiple fission. The resulting young are haploid individuals that typically grow to become adult, uninucleate gamonts. Gametogenesis then occurs in haploid individuals and involves only mitotic nuclear divisions.

Perhaps limited by technology or the small size of nuclei in *E. crispum*, none of these pioneers in foraminiferal biology (J.J. Lister, F. Schaudinn, M.W. Jepps) were able to document the correct position of meiosis. This element of the life cycle was first documented by Le Calvez (1946, 1950) who reexamined the life cycles of *Patellina corrugata* and *Discorbis vilardeboanus* and recognized meiotic division figures that preceded multiple fission in the agamont. Grell (1954) and Arnold (1955) soon verified Le Calvez's findings by documenting the intermediate position of meiosis in *Rotaliella heterocaryotica* and *Allogromia laticollaris*, respectively.

3.5.2 Variations on the general theme

Today, reasonably complete life cycles are known for fewer than 30 of the > 10,000 extant species of Foraminifera. In spite of this limitation, these relatively few well-documented life cycles illustrate a significant range of variation in the life cycle and in the corresponding morphological variation imparted to the test (Table 3.1). These variations relate to the

Table 3.1 List of selected features of Foraminifera for which reasonably complete life cycles are known. Partial life cycles are known for a number of other taxa (see Lee *et al.*, 1991a; Goldstein, 1997).

Species	Alteration of generations	Morphology	Gametes	Fertilization	Nuclear dimorphism	References
Allogromia laticollaris	facultative; budding, plasmotomy	variable	amoeboid	autogamous	no	Arnold, 1954; McEnery and Lee, 1976
Heterotheca lobata	obligatory	gamonts generally larger than agamonts	biflagellated	gametogamous	no	Grell, 1988
Myxotheca arenilega	? obligatory	agamont larger than gamont	biflagellated	gametogamous	no	Grell, 1958c
Iridia lucida	? obligatory	no morphological differeence between gamont and agamont	biflagellated	gametogamous	unknown	LeCalvez, 1936a, 1938
Nemogullmia longevariabilis	unknown	no morphological difference between gamont and agamont	biflagellated	gametogamous	unknown	Nyholm, 1956
Saccammina alba	facultative; budding, plasmotomy	gamont larger than agamont	biflagellated	gametogamous	possibly	Goldstein, 1988a
Ovammina opaca	facultative; budding	secondary pores form in circumapertural ring in test of gamont prior to release of gametes	biflagellated	gametogamous	unknown	Dahlgren, 1962, 1964; Goldstein, unpublished observations
Cribrothalammina alba	facultative; budding	secondary pores form in test of gamont prior to release of gametes	biflagellated	gametogamous	unknown	Goldstein and Barker, 1988, 1990; Goldstein, unpublished observations
Patellina corrugata	obligatory	reversed test dimorphism	amoeboid	gamontogamous	no	Myers, 1935; Grell, 1958c
Spirillina vivipara	obligatory	reversed test dimorphism	amoeboid	gamontogamous	no	Myers, 1936
Spiroloculina hyalina	apogamic	not applicable	not applicable	not applicable	only uninucleate individuals known	Arnold, 1964
Fissurina marginata	apogamic	not applicable	not applicable	not applicable	unknown	Le Calvez, 1947
Elphidium crispum	obligatory	classically dimorphic	biflagellated	gametogamous	unknown	Lister, 1895; Schaudinn, 1895; Jepps, 1942
Ammonia tepida	facultative	variable	biflagellated	gametogamous	unknown	Bradshaw, 1957; Schnitker, 1974a; Goldstein and Moodley, 1993
'Tretomphalus' bulloides (= Rosalina globularis)	obligatory	classically dimorphic, but a terminal float chamber occurs in mature gamonts	biflagellated	gametogamous	unknown	Le Calvez, 1936b; Myers, 1943a
Discorbis patelliformis	obligatory	classically dimorphic	triflagellated	gamontogamous	unknown	Myers, 1940
Discorbis mediterranensis	obligatory	classically dimorphic	triflagellated	gamontogamous	unknown	Le Calvez, 1950
Discorbis vilardeboanus	?obligatory	classically dimorphic	biflagellated	gametogamous	unknown	Føyn, 1936; Le Calvez, 1950
Glabratella sulcata	obligatory	gamont larger than agamont	triflagellated	gamontogamous	yes; number variable	Grell, 1958b, 1979

Table 1 (Continued.)

Species	Alteration of generations	Morphology	Gametes	Fertilization	Nuclear dimorphism	References
Rubratella intermedia	obligatory	not dimorphic	amoeboid	gamontogamous	yes; 1 somatic, 5 generative	Grell, 1958a, 1979
Metarotaliella simplex	obligatory	not dimorphic	amoeboid	gamontogamous	yes; 1 somatic, 3 generative	Grell, 1973, 1979
Metarotaliella parva	obligatory	not dimorphic	amoeboid	gamontogamous	yes; 1 somatic, 3 generative	Grell, 1973, 1979
Rotaliella roscoffensis	obligatory	not dimorphic	amoeboid	autogamous	yes; 1 somatic, 3 generative	Grell, 1957, 1979
Rotaliella heterocaryotica	obligatory	not dimorphic	amoeboid	autogamous	yes; 1 somatic, 3 generative	Grell, 1954, 1979
Rotaliella elatiana	?facultative	gamont generally smaller	amoeboid	mostly autogamous	yes; number variable from 1–4	Pawlowski and Lee, 1992
Heterostegina depressa	biologically trimorphic	?trimorphic	biflagellated	gametogamous	no	Röttger et al., 1990
Amplistegina gibbosa	biologically tripmorphic	trimorphic	biflagellated	gametogamous	unknown	Harney et al., 1998; Dettmering et al., 1998
Planktonic taxa	?gamic	unknown	biflagellated	gametogamous	unknown	see review in Hemleben et al., 1989

sequence of 'alternating' generations, trimorphism, apogamic and possibly gamic life cycles, binary fission and various forms of budding, type of gametes, mode of fertilization, occurrence of nuclear dimorphism, and test dimorphism. Overall, the life cycle is more varied in the Foraminifera than in virtually any other group of protists.

The *alternation of generations* in the Foraminifera may be *obligatory* in some species, and *facultative* in others. In the obligatory alternation of generations, reproduction in the agamont always includes meiosis as a precedent to multiple fission. The resulting young are always haploid and uninucleate, and they grow to form mature gamonts. With the possible exception of *Iridia lucida* in which both gamonts and agamonts are uninucleate (Le Calvez, 1936a, 1938), the uninucleate forms are gamonts that produce gametes which ultimately form zygotes and mature into agamonts. This type of life cycle does not deviate from this regular alternation of generations. Examples include *Elphidium crispum* (Lister, 1895, 1903; Jepps, 1942), *Glabratella sulcata* (Grell, 1958b), *Rotaliella heterocaryotica* (Grell, 1954), and *Patellina corrugata* (Myers, 1935; Grell, 1958c).

Alternatively, the life cycle may be characterized by a facultative alternation of generations. In some species, the life cycle includes successive asexual cycles that include reproduction by multiple fission (e.g. *Ammonia tepida* – Bradshaw, 1957; Schnitker, 1974a; Goldstein and Moodley, 1993). In this case, the agamont (B) begins as a zygote, and is diploid. The agamont may undergo meiosis and multiple fission to produce haploid young that mature into uninucleate gamonts (A_2). Alternatively, the agamont (B) may produce, by multiple fission, a second asexual generation, the schizont (A_1), which in turn may produce a number of successive asexual generations. The type of nuclear divisions that occurs in schizonts, however, has not been documented.

This facultative alternation of generations is referred to as biological trimorphism, and has been documented in the living nummulitid *Heterostegina depressa* by Röttger et al. (1990) and in the amphisteginid *Amphistegina gibbosa* by Harney et al. (1998) and Dettmering et al. (1998). This type of life cycle includes one microspheric generation (B) and two megalospheric generations, the gamont (A_2) and the schizont (A_1). A number of foraminiferologists have

reported biological trimorphism, particularly in regard to the larger, algal symbiont-bearing Foraminifera (see Röttger *et al.,* 1986, 1990; Harney *et al.,* 1998; Dettmering *et al.,* 1998).

Does biological trimorphism extend to trimorphism of the test? The validity of this hypothesis requires two observations: (a) the presence of three morphologically distinct types of tests based on the diameter of the proloculus, and (b) the correlation of each of these distinct morphologies to a specific phase of the life cycle (gamont, agamont, schizont) (Röttger *et al.,* 1986, 1990). Most studies on test trimorphism, however, have relied almost exclusively on morphological observations.

Rather than adding alternative cycles to the life cycle as in biological trimorphism, some taxa are apogamic and appear to have reduced the complexity of the life cycle by omitting one of the generations. At least two species, *Fissurina marginata* and *Spiroloculina hyalina,* have apparently lost the sexual phase of the life cycle (the gamont and gametogenesis) (Le Calvez, 1947; Arnold, 1964). Only successive asexual generations were observed in these species, and in *S. hyalina,* asexual reproduction occurs in uninucleate individuals (Arnold, 1964).

Only sexual reproduction has been observed in planktonic Foraminifera, in spite of numerous investigations. As a result, Hemleben *et al.* (1989) proposed a possible 'gamic' life cycle for planktonic Foraminifera in which the agamont and multiple fission have been lost. Gamonts, which are uninucleate, undergo gametogenesis, producing thousands of free-swimming, biflagellated gametes that are released directly into the surrounding seawater. Zygotes presumably form as gametes from separate parents fuse. It is possible then that zygotes mature to adult gamonts and that meiosis occurs in the zygote, immature gamont, or adult gamont, though this has yet to be demonstrated.

The life cycle of some allogromiids and astrorhizids appears to be more plastic or variable than in other Foraminifera. In addition to multiple fission, several other forms of asexual reproduction have been observed, including: binary fission in *Allogromia laticollaris* (McEn-

ery and Lee, 1976); budding in *Saccammina sphaerica* (Rhumbler, 1894), *S. alba* (Goldstein, 1988a), *Allogromia laticollaris* (Arnold, 1954, 1955), *Halyphysema tumanowiczii* (Hedley, 1958), *Technitella legumen* (Haman, 1971), *Astrammina ram* (DeLaca, 1986a), *Ovammina opaca* (Goldstein, unpublished observations), and *Psammophaga simplora* (Goldstein, unpublished observations); serial budding in *Nemogullmia longevariabilis* (Nyholm, 1956) and *Cylindrogullmia alba* (Nyholm, 1974); and plasmotomy or multiple budding in *Allogromia laticollaris* (Arnold, 1955) and *Saccammina alba* (Goldstein, 1988a). In addition, fragmentation occurs in the miliolid *Calcituba polymorpha* (Arnold, 1967), and *Spiroloculina hyalina* and *Floresina amphiphaga* are capable of producing multiple broods (Arnold, 1964; Hallock and Talge, 1994).

Gametes in the Foraminifera may be biflagellated, triflagellated, or amoeboid. Of these, biflagellated gametes (Fig. 3.15) are by far the most common, and occur in many extant groups, including planktonic taxa and the most diverse benthic suborders. The sequence of events by which biflagellated gametes are produced is remarkably similar, even in distantly related taxa, suggesting that this mode of gametogenesis is probably primitive within the Foraminifera (Goldstein, 1997). The other types of gametes and the processes that produce them, therefore, are most likely derived from the more primitive biflagellated type (Grell, 1967; Goldstein, 1997).

Triflagellated and amoeboid gametes have evolved on more than one occasion and independently in different groups of Foraminifera. Triflagellated gametes are best known in a few plastogamic (forms in which the gamonts fuse before gamete release, see below) discorbids and glabratellids (e.g. *Discorbis patelliformis. D. mediterranensis, Glabratella sulcata* – Myers, 1940; Le Calvez, 1950; Grell, 1958b). However, they also occur in at least one (*Nummulites venosus* – Röttger *et al.,* 1998), but not all of the few extant nummulitids. It is noteworthy that *N. venosus* is gametogamous (see below) and not plastogamic. Amoeboid gametes occur in the
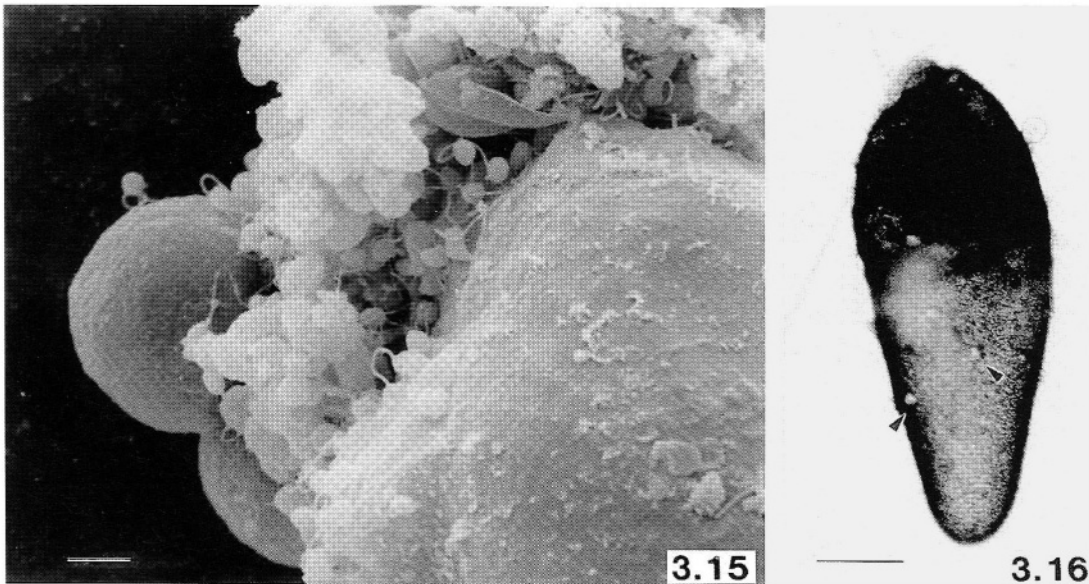
Figure 3.15 SEM micrograph of gamete release in the miliolid *Triloculina oblonga*. Gametes in this and most (but not all) gametogamous Foraminifera are biflagellated. Scale bar = 5 μm.

Figure 3.16 Light micrograph of gamete release in *Cribrothalammina alba*. Note the secondary pores scattered over the surface of the test. Pores form just prior to gamete release in the species and provide an example of 'heterothalamy.' Scale bar approximately 100 μm.

allogromiid *Allogromia laticollaris* (Arnold, 1955), but are also known in several of the small rotaliellids (e.g. *Rotaliella heterocaryotica, R. roscoffensis, Metarotaliella simplex, M. parva, Rubratella intermedia* – Grell, 1973, 1979) and in the spirillinids *Patellina corrugata* (Myers, 1935) and *Spirillina vivipara* (Myers, 1936). Amoeboid gametes may also occur in the saccamminid *Psammophaga simplora*. However, although Arnold (1984) reported the formation of amoeboid structures during gametogenesis, he also reported that they may become flagellated before their release from the shell. Triflagellated and amoeboid gametes generally are larger than biflagellated ones and are produced in fewer numbers.

Fertilization in the Foraminifera may be gametogamous, gamontogamous, or autogamous (Grell, 1973). Gametogamy is the most common mode found in the Foraminifera and involves the release of numerous gametes directly into the surrounding seawater where fertilization occurs. Gametogamy is generally associated with the production of numerous (often thousands), small (~1–4 μm), biflagellated gametes. However, although rare, gametogamy may also occur in Foraminifera with triflagellated gametes, as in the nummulitid *Nummulites venosus* (Röttger *et al.*, 1998).

Alternatively, rather than simply broadcasting gametes, gamonts can associate in pairs or groups (e.g. *Spirillina vivipara, Patellina corrugata, Metarotaliella parva, M. simplex*) prior to the release of gametes. This mode of fertilization is referred to as gamontogamy, and most gamontogamous Foraminifera produce either triflagellated or amoeboid gametes. Plastogamy is a specific type of gamontogamy in which two gamonts attach to each other along the umbilical margins of the tests. Gametes are then released within the shared space of the joined tests (internal septa are generally removed during gametogenesis). Examples of plastogamic Foraminifera include: *Discorbis patelliformis, D.*

pulvinata, D. ornatissima (Myers, 1940), *D. mediterranensis* (Le Calvez, 1950), and *Glabratella sulcata* (Grell, 1958b).

The gamonts of some gamontogamous species are differentiated into 'sexes' or mating types. No morphological features distinguish conspecific gametes or gamonts. However, gamonts of *Discorbis mediterranensis* from one mating type will pair only with those from another (Le Calvez, 1950). In species that associate in groups (e.g. *Patellina corrugata*), both mating types must be present for reproduction to occur (Grell, 1958c). It is not known whether or not mating types occur in gametogamous species as well.

Autogamy (self fertilization) is known in some taxa. Amoeboid gametes are produced, but are not released from the parental test. Rather, fertilization occurs within the parental test from which the resulting young then escape. Autogamy occurs in *Allogromia laticollaris* (Arnold, 1955), *Rotaliella heterocaryotica* (Grell, 1954), and *R. roscoffensis* (Grell, 1957). In culture, this mode of fertilization can be very difficult to distinguish from multiple fission (asexual reproduction), although the size of offspring may provide a clue for some species. Arnold (1955) reported that sexually produced young are generally smaller than those produced by multiple fission in *Allogromia laticollaris*.

Nuclear dimorphism is perhaps best known in ciliated protozoans, but also occurs in some small calcareous perforate Foraminifera, particularly *Glabratella sulcata* and members of the Family Rotaliellidae (see Grell, 1973, 1979). In Foraminifera with nuclear dimorphism, different types of nuclei occur simultaneously in the agamont. Generally, there is one somatic nucleus and one to live generative nuclei. The generative nuclei remain in the proloculus until the agamont reproduces, at which time all undergo meiosis. The somatic nucleus resides in an intermediate chamber, is generally larger, and contains more DNA than the generative nuclei; it is involved in the cell's metabolic functions. The somatic nucleus, however, degenerates at the onset of meiosis in the generative nuclei (Grell, 1973). Zech (1964) showed that nuclear dimor-

phism does not occur in the foraminifer *Patellina corrugata*. Whether this phenomenon occurs elsewhere in the Foraminifera, however, remains to be demonstrated.

The classical form of test dimorphism in which the gamont (and schizont if it occurs) is relatively small and megalospheric, and the agamont is relatively large and microspheric, has been identified in numerous modern and fossil taxa. However, not all Foraminifera that show an alternation of generations also display classical test dimorphism. *Patellina corrugata* and *Spirillina vivipara*, for example, have reversed test dimorphism (Myers, 1935, 1936). The agamonts are smaller and 'megalospheric,' whereas the gamonts are larger and 'microspheric.' This foraminifer produces fairly large amoeboid gametes, and the resulting zygotes are generally larger than the young produced by multiple fission.

Test dimorphism in *Glabratella sulcata* also deviates from the norm. In this species, the gamont typically is larger than the agamont, and no significant differences in size identify the proloculus as either megalo- or microspheric. In many of the tiny Foraminifera studied by Grell (see Grell, 1973, 1979), the gamonts and agamonts are morphologically indistinguishable.

Some Foraminifera are characterized by a wide range of morphological variability which may extend to the size of the proloculus. Gamonts of *Ammonia tepida*, for example, have a wide range of prolocular diameters (Goldstein and Moodley, 1993), making it difficult to distinguish gamonts from agamonts by the morphology of empty shells.

What causes test dimorphism? Early workers on the foraminiferal life cycle explained test dimorphism as the result of the small size of the proloculus formed by amoeba-form zygotes that had resulted from the fusion of two very small biflagellated gametes, and observations on *Elphidium crispum* seemed to support this view (Myers, 1935). Myers (1935), however, proposed that the controlling factor more likely was the size of the nucleus, and not the size of the zygote. This, he believed, better explained why in some species, the shape and form of the proloculus

were similar in tests of both generations (though not in *Patellina corrugata,* the subject of his 1935 paper). Similarly, Le Calvez (1938) proposed that the number of nuclei in the young agamont determined the size of the proloculus. This may also provide a reasonable explanation for the size of proloculi in the small heterocaryotic foraminifer *Rotaliella elatiana* (Lee *et al.,* 1991a).

Test dimorphism was defined with regard to multilocular taxa, and application of this term should therefore be restricted to these forms. However, morphological differences may also occur in unilocular taxa for which Grell (1988) coined the term heterothalamy. In some cases the distinction occurs only with regard to size. Gamonts of *Heterotheca lobata* (Grell, 1988) and *Saccammina alba* (Goldstein, 1988a) are significantly larger than the corresponding agamonts. In *S. sphaerica* (Føyn, 1954) and *Myxotheca arenilega* (Grell, 1958c), however, the agamonts are larger. Because all four of these species liberate numerous, small, biflagellated, free-swimming gametes, the size of gametes does not explain this form of heterothalamy.

Ovammina opaca and *Cribrothalammina alba* exhibit another variation. The gamonts of both species form secondary pores during gametogenesis that serve as the sole avenue for the release of numerous biflagellated gametes (Fig. 3.16). In *O. opaca,* pores form in a ring just behind the aperture (Dahlgren, 1962, 1964), whereas in the larger *C. alba,* pores are distributed over the entire test, with the exception of the abapertural tip (Goldstein and Barker, 1988, 1990).

3.6 ACKNOWLEDGMENTS

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4

Shell construction in modern calcareous Foraminifera

Hans Jørgen Hansen

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4.1 INTRODUCTION

The majority of foraminiferal species build their shells (or 'tests') with $CaCO_3$. Such calcareous species constitute 11 out the 15 extant orders of the class Foraminifera (see chapter 2). The present chapter is focused on the modes in which various types of walls are built by modern calcareous taxa.

4.2 WALL OF SECRETED CALCITE SPICULES (CARTERINIDA)

The order Carterinida is represented by a single genus, *Carterina,* which constructs its shell with concentrically laminated, ovoid spicules (Figs. 2.9, 4.1) that are held in place by organic material (Hansen and Grønlund, 1977). To test the possibility that the shell may be agglutinated, Deutsch and Lipps (1976) searched for loose spicules in the sediments of Eniwetok atoll, from where they had collected specimens of *C. spiculotesta,* but did not find any. In addition, adult specimens were found attached to hard substrate where sedi-
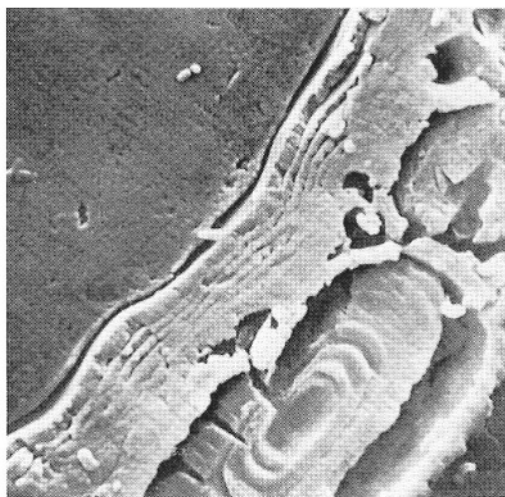
Figure 4.1 Concentric lamellae in sectioned and etched spicules of *Carterina.* Note the laminated inner organic lining. Reprinted from Hansen and Grønlund (1977), with the permission of the publisher.

mentary particles do not accumulate. Such evidence led to the suggestion that the spicules in the test of *Carterina* were secreted. The spicules are made of calcite (with c-axis parallel to elonga-

tion) which contains blebs of organic matter. They come in two size groups, with the smaller spicules packed tightly between the larger ones (Fig. 2.9), and reported as a 'ground mass' by earlier observers (e.g. Brady, 1884; Loeblich and Tappan, 1964a). The rounded shapes of the spicules and the lack of connections between adacent spicules show that they are not formed *in situ* in the shell (Hansen and Grønlund, 1977).

4.3   PORCELANEOUS, IMPERFORATE WALLS (MILIOLIDA)

The non-lamellar porcelaneous wall is constructed of rods/laths of high magnesium calcite (Blackmon and Todd, 1959). The calcite units of the wall are arranged in a disorderly manner in the embedding organic material. On the basis of ultrastructural studies, Berthold (1976a) reported that in *Calcituba polymorpha,* calcite rods are present in cytoplasmatic vesicles formed during chamber construction. Similar observations were made by Angell (1980) in a study of chamber formation in *Spiroloculina hyalina.* Some porcelaneous forms possess a smoothly finished outermost layer of well crystallized calcite, with rhombohedral crystal faces arranged parallel to the surface ('tile roof pattern'). It is difficult to imagine how these crystallites could have formed away from their position, since many show an interlocking pattern (see also Debenay *et al.,* 1996). Haake (1971) recorded a 'cobble pattern' on the surface of porcelaneous forms in which calcite crystals are more or less perpendicular to the shell surface in the outermost layer. It may be concluded that the porcelaneous wall in this case is mainly constructed of calcitic units that are secreted by the foraminifer away from their final locations in the shell; the smoothly finished surface layer, however, is most likely formed *in situ.*

4.4   MONOCRYSTALLINE WALLS (SPIRILLINIDA)

The optically monocrystalline wall of *Patellina* has an a-axis-preferred orientation (Towe *et al.,*

1977). As observed by Berthold (1976c), new chamber material is added by lateral apposition. Growth is initiated in the apertural region of the preceding chamber where nearby structures such as radial septa grow faster than distant structures. Berthold (1976b) also found that during growth of the septa in the spiral (dorsal) wall, small spaces are formed, and they are not closed in the course of shell development, thus becoming rounded pores. The reason for the suppression of calcification in the pore regions may be linked to the filling of pores by granular organic material. The pores and both sides of the shell wall are covered by a delicate organic layer. At the inner entrance to a pore, this covering organic layer is finely perforated by openings of about 0.01 μm diameter. In contrast, the exterior pore opening apparently remains uncovered.

4.5   LAMELLAR WALLS

4.5.1

The lamellar shells are constructed of either calcite or aragonite. As a new chamber is added, one new layer of shell material is secreted, covering the exposed earlier part of the shell (which does not happen in non-lamellar walls). This leads to an increase in wall thickness from later to earlier chambers (Fig. 4.2). In non-lamellar Foraminifera the addition of a new chamber does not lead to the deposition of a layer of shell material onto the earlier exposed part of the shell.

4.5.2   Optical orientation of the wall material

Following the pioneering work of Wood (1949) on the optical orientation of the carbonate material of foraminiferal shells, Loeblich and Tappan (1964a) introduced the radial-granular distinction in foraminiferal classification (see chapter 2 and Figs. 2.5, 2.6). This was a very attractive feature of this classification, because major taxonomic groups could be distinguished by a simple optical character. The crystallographic orienta-
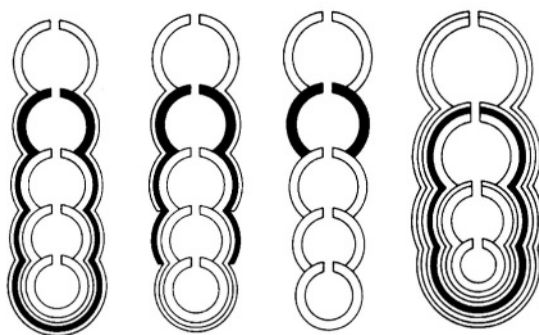
Figure 4.2 Monolamellar constructional designs: **a**, basic plan in which the one-layered wall material of the ultimate chamber continues uninterrupted to cover (as a secondary lamella) the exposed surfaces of earlier chambers; **b**, secondary lamella covering only two earlier chambers (*Dentalina pauperata* d'Orbigny); **c**, no addition of secondary lamella to earlier chambers (*Nodosaria subsoluta* Cushman); **d**, one to six secondary lamellae enveloping earlier chambers. From Grønlund and Hansen (1976), reproduced with permission.

tion of optically radial and granular walls has been studied by several authors (e.g. Towe and Cifelli, 1967; Hansen, 1968), and the terms 'radiate' and 'granulate' have also been used for the two optical properties. Their determination, however, is not necessarily easy under a polarizing microscope. For example, the presence of very narrow pores may give the impression of a radial optical structure in thin sections.

Both radial and granular optical properties have been observed within the same genus. Hansen (1972a) demonstrated a granular wall structure in an Eocene species of *Turrilina,* and a radial structure in an Oligocene species. Within the 26 species of elphidiids studied by Hansen and Lykke-Andersen (1976), 19 were radial and 7 were granular, thereby corroborating an earlier report of a granular elphidiid (Buzas, 1966). Thus, the optical orientation of shell material is not an infallible character for taxonomic distinctions above the species level. Ultrastructures of both radial and granular walls show considerable variability; several structural types have been identified (Bellemo, 1974a, b; 1976).

4.5.3 Monolamellar, hyaline, perforate walls (Lagenida)

In this group of hyaline Foraminifera, the latest added chamber is constructed of a single layer of shell material (Grønlund and Hansen, 1976).

When this new chamber is added, the layer that forms that chamber also covers the exposed exterior walls of earlier chambers. Thus, the ultimate chamber wall consists of one layer, the penultimate chamber of two layers, and so on (Fig. 4.2). Partial deviations from this mode of wall construction exist within the group. Secondary lamellae may cover only the two previous chambers or only part of the penultimate chamber, or as in *Lingulina,* the final chamber may be composed of one to six lamellae, all of which extend over the exposed earlier part of the shell (Fig. 4.2). Where one curved chamber meets another, the columnar morphology of calcite in the wall leads to a somewhat irregular structural arrangement. The pores in monolamellar walls (and those in aragonitic bilamellar walls) are all of small diameter. Present data show that monolamellar walls in modern species are constructed with only optically radial calcite.

4.5.4 Bilamellar, hyaline, perforate walls (Buliminida, Rotaliida, Globigerinida)

In the bilamellar group, the wall of the final chamber consists of two carbonate layers separated by an organic 'median layer.' Traditionally, the outside calcareous layer is termed the 'outer lamella,' while the inside calcareous layer is termed the 'inner lining' (Fig. 4.3); the latter is not to be confused with the inner organic lining of the calcareous wall. In some taxa, the
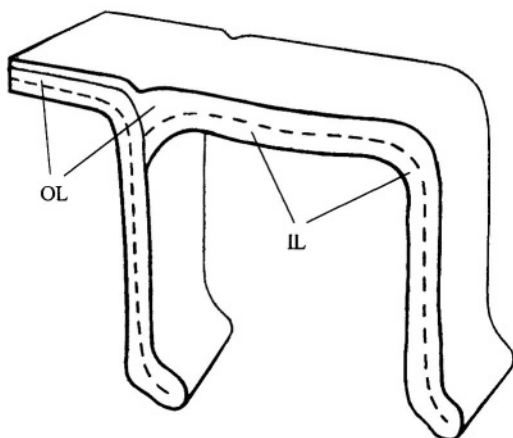
Figure 4.3 Bilamellar wall construction. IL, inner calcareous lining; OL, outer calcareous lamella; dashed line: median layer.

median layer is thin and well defined; in others, it may not be sharply delineated between the two carbonate lamellae. In *Cibicides* and *Stomatorbina,* the median layer contains particles (fine sedimentary grains, e.g. quartz) that are not secreted by the foraminifer. In *Stomatorbina,* these particles are absent in porous regions of the shell, but are clearly seen through the shell in non-porous areas. In *Cibicides,* they appear to be distributed randomly in the median layer. It is unclear if these particles in the median layer should be regarded as being truly agglutinated or as contaminations, but their distribution in *Stomatorbina* points to some degree of organization. The median layer apparently plays a significant role in the chamber forming process and calcification. In thin section under the light microscope, it may be seen as a dark line or a dark diffuse band that is usually most conspicuous in the septal part closest to the aperture and foramina. Sometimes the median layer and the boundaries between secondary lamellae are difficult to observe, but a parallel alignment of the two polarizers in the microscope improves the visibility of the lamellar boundaries, their planar orientation being at right angles to the plane of polarization. The thickness of each lamella may be only a few microns, or even less than a micron. In such cases, observations with a light microscope may not be adequate, and

scanning electron microscope (SEM) studies of embedded, sectioned, polished, and etched specimens may be necessary.

The basic bilamellar mode of wall construction was first explained by Reiss (1957) as a modification of the mode suggested by Smout (1954). The inner lining stops at the junction with the previous chamber, while the outer lamella continues over the exposed parts of the earlier chambers to form a secondary lamella. The septum of the previous chamber becomes isolated from the surface, and does not receive the secondary laminaton, thus becoming the shell interior (Fig. 4.3). The result is a shell where all septa (including the ultimate one) have two calcareous layers. In a variant of this constructional design, the inner lining does not stop at the junction with the previous apertural face but continues as a calcareous layer deposited onto the penultimate septum (former apertural face), leading to a three-layered septum (Fig. 4.4). In this model, the ultimate septum is two-layered while the penultimate and earlier septa are three-layered. The calcareous layer covering the penultimate septum is termed a 'septal flap.' Septal flaps have not been found in monolamellar forms and appear to be confined to the bilamellar group.
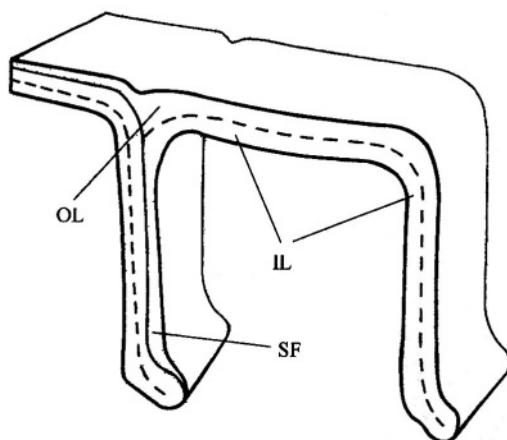
Figure 4.4 Bilamellar construction with septal flap. IL, inner calcareous lining; OL, outer calcareous lamella; SF, septal flap; dashed line, median layer.

4.5.5 Interlocular spaces and subsutural canals

The presence of a septal flap is often, but not always, connected with interlocular spaces, i.e. spaces between adjacent chambers. *Melonis pompilioides* has a septal flap, but no interlocular space (Fig. 4.5). It does, however, possess an umbilical spiral canal system (Fig. 4.6). *Nonion labradoricum* has septal flaps, but no interlocular spaces or umbilical canal system (Hansen and Lykke-Andersen, 1976). When an interlocular space is present, the attachment of one chamber to another is very fragile, and the weak shell architecture leads to breakage of the last chamber(s). In *Pseudorotalia*, interlocular spaces are present, but secondary lamellae build protrusions in both anterior and posterior directions from the sutures; after the addition of two or three chambers, pillars bridge the interlocular spaces, and thereby prevent breakage (Fig 4.7). The interlocular walls receive secondary lamination, showing that these walls are functional shell surfaces.

An alternative constructional design is seen in the presence of posterior extensions (retral processes) of the chamber lumen and surrounding walls (ponticuli); these are attached to the exterior-most part of the preceding apertural face when a new chamber is added (e.g. in *Elphidium,* Fig. 4.8). This leads to the formation of a well-anchored final chamber with little chance of mechanical damage, in spite of the presence of a deep interlocular space. Thus, both *Pseudorotalia* and *Elphidium* have deep interlocular spaces crossed by small bridges, but of different origin.

In *Asterigerina,* the addition of a new chamber produces a chamber lumen that is primarily divided into two sub-chambers. The peripheral part is termed the 'main chamber,' while the part with a rhombohedral outline found closest
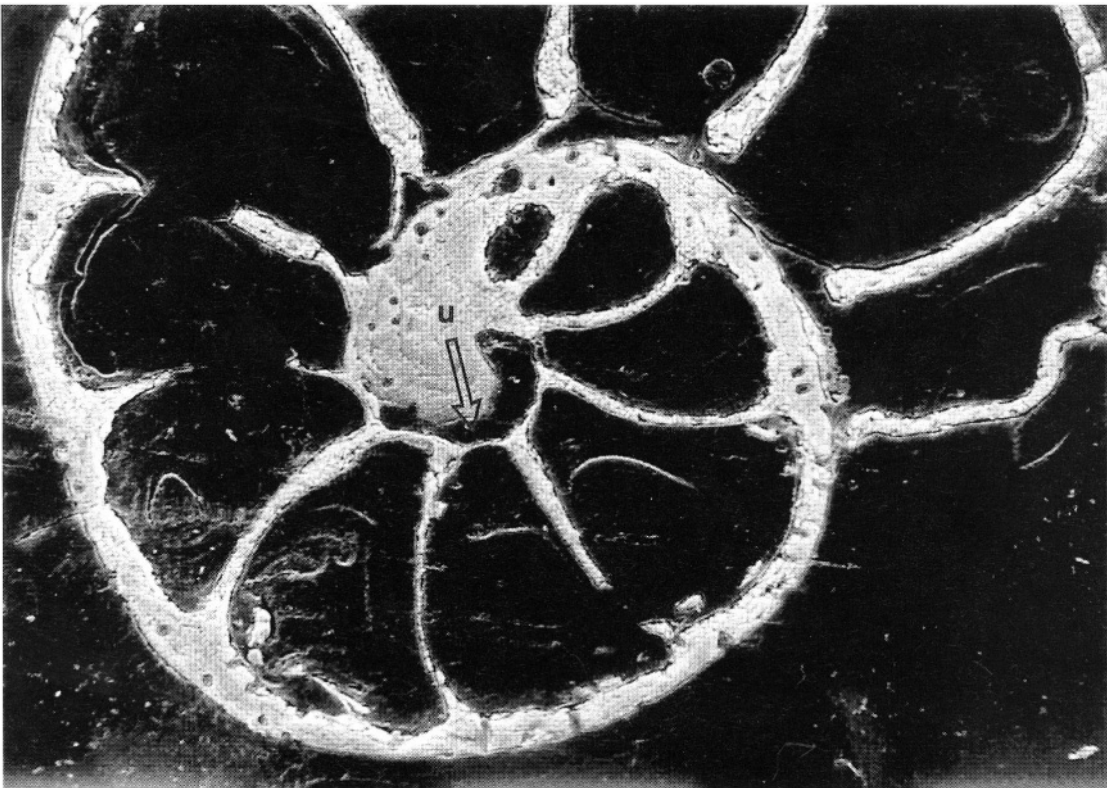
Figure 4.5 *Melonis pompilioides.* Section showing umbilical cover plates (u); scale bar ≈ 0.1 mm.

Figure 4.6 *Melonis pompilioides.* Internal mold showing position of umbilical cover plate (u); scale bar = 0.1 mm.
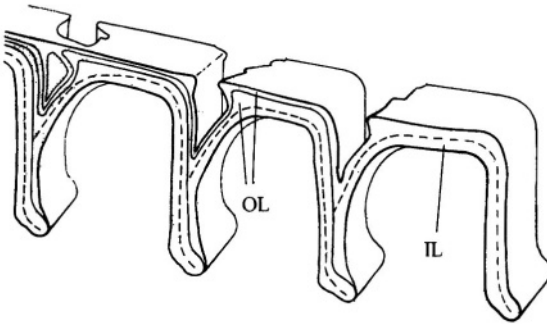
Figure 4.7 *Pseudorotalia.* Constructional design of secondary bridges spanning the interlocular spaces; IL, inner calcareous lining; OL, outer calcareous lamella; dashed line, median layer.
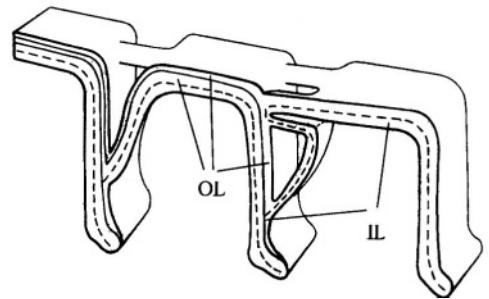
Figure 4.8 *Elphidium.* Bridging of interlocular spaces by ponticuli with retral processes; IL, inner calcareous lining; OL, outer calcareous lamella; dashed line, median layer.

to the umbilicus is the 'chamberlet.' These two units are separated from each other by a two-layered partition which bridges the previous aperture with an arch. Their development represents an 'instar,' i.e. a single episode in the formation of

the shell (see next section). When the two-layered partition is followed to the outer chamber wall, it is seen to be constructed by a doubled inner lining (Fig 4.9). In this case, the construction of the inner lining does not involve a simultaneous construc-
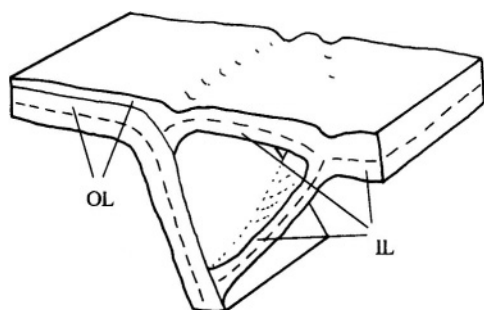
Figure 4.9 Constructional detail showing doubled inner lining separating chamber and chamberlet in *Asterigerina*; IL, inner calcareous lining; OL, outer calcareous lamella; dashed line, median layer.
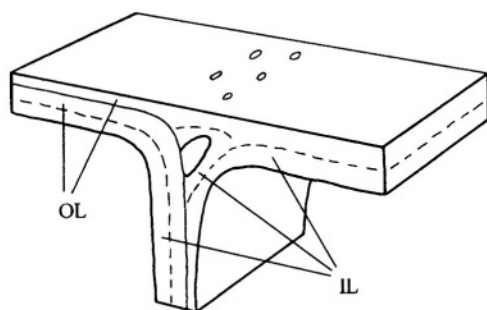
Figure 4.10 Constructional organization of subsutural canals in *Elphidiella*. The canals are delimited by double inner lining towards the chamber lumen, but by inner and outer lamella towards the shell surface; IL, inner calcareous lining; OL, outer calcareous lamella; dashed line, median layer.

tion of an outer lamella (Hansen and Reiss, 1972). Exactly the same plan of lamellar construction is found in *Elphidiella,* where the space between the ultimate and the penultimate chamber is delimited by the double inner lining of the ultimate chamber against the penultimate septum. (Fig. 4.10). Several openings in the roof (Fig. 4.11) connect the chamber interior with shell surface, thereby becoming true multiple apertures of the ultimate chamber (Hansen and Lykke-Andersen, 1976). Such openings in the sutures are sometimes misleadingly called 'sutural pores.'

4.5.6 Umbilical cover plates and foraminal plates

The concept of instars in shell formation was introduced by Smout (1954) who regarded the formation of a chamber and the associated deposition of a secondary lamella as one instar. This concept is useful in explaining the development of several shell structures. A chamber-forming instar in *Ammonia* also involves the deposition of structural elements in the penultimate chamber (Hansen and Reiss, 1971). The umbilical part of the final chamber in *Ammonia* is open to the umbilicus. However, the main umbilical opening in the penultimate chamber is closed by the deposition of a cover plate that is continuous with a folded, almost vertical, foraminal plate protruding in the proximal direction. In section, the folded plate is seen as a two-layered hook extending from the umbilical cover plate of the preceding chamber. These umbilical cover plates and the exposed parts of the hooks are secondarily laminated. The folded plate represents the site of attachment of the succeeding cover plate. These structures show up in a shell section as a continuous series of hooks and plates (Figs. 4.12. 4.13). This constructional pattern is characteristic of many trochospirally and planispirally coiled forms. Even in apparently simple forms such as *Astrononion* in which hooks (foraminal plates) are absent, the deposition of a cover plate in the penultimate chamber is easy to recognize in shell molds (Fig. 4.14).

The deposition of umbilical cover plates in the earlier chambers leads to the formation of the so-called umbilical spiral canal systems (shown by Carpenter *et al.,* 1862, in a natural mold of *Elphidium craticulatum*). The origin of this conspicuous canal system is in parts of the shell that are closest to the umbilicus. In *Elphidium,* the single umbilical chamber tip embraces the previous chamber tip and covers its proximal umbilical part, allowing the presence of a passage (aperture) into the final chamber. Along with this, a plate is deposited in such a way that it seals off the communication between the main part of the preceding chamber lumen and the part closest to the umbilicus (Figs. 4.15, 4.16). The plate, deposited through one of the multiple interiomarginal apertures (the one closest to the umbilicus) of the preceding chamber, is a two-layered structure consisting of an outer lamella
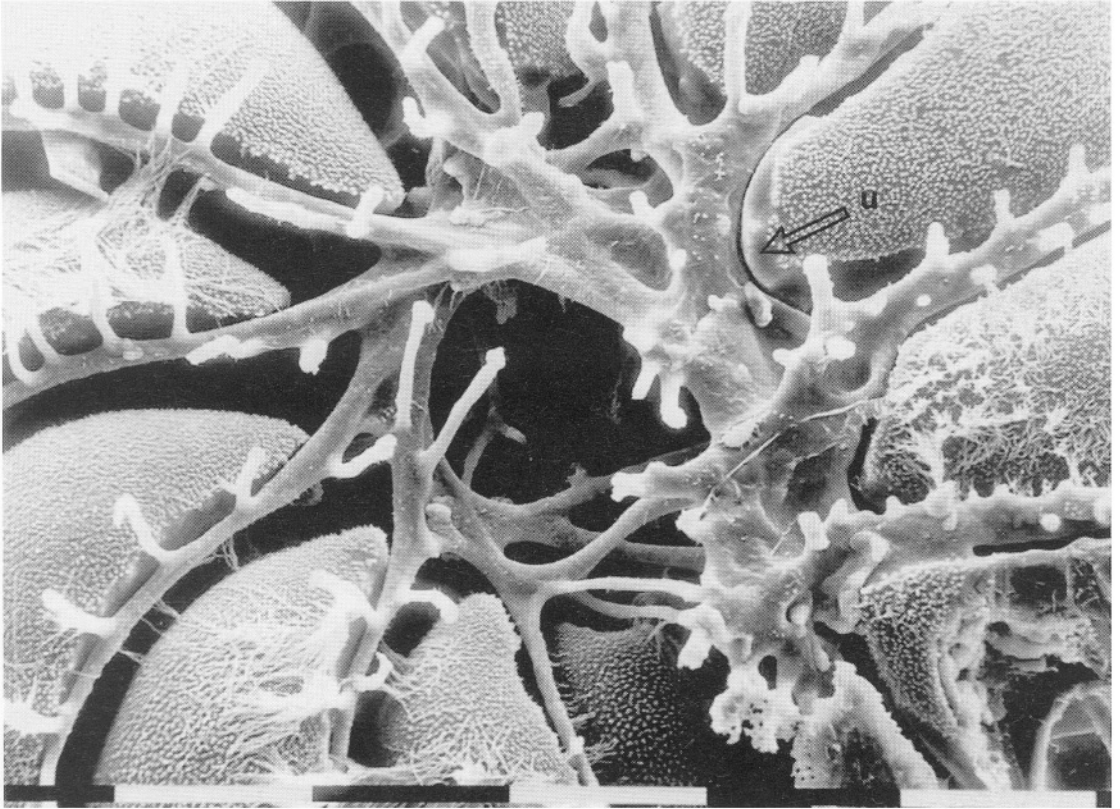
Figure 4.11 Detail of internal mold of *Elphidiella arctica*, showing connection of subsutural canals to shell surface and positions of umbilical cover plates (u); scale bar = 0.1 mm.
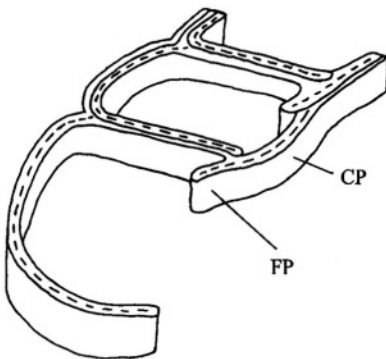
Figure 4.12 Constructional design of umbilical cover plates (CP) and associated foraminal plates (FP) in *Ammonia*; dashed line: median layer.

and an inner lining. The inner lining faces the chamber lumen and is covered by the outer lamella in the umbilical direction. In between chambers, the umbilical part of the interlocular

space retains an opening into the small space (closest to the umbilicus) now isolated by the umbilical cover plate. With the addition of new chambers, openings between adjacent chamber tips gradually form a spiral canal system in the umbilical region. When the umbilical chamber tip is not attached to the umbilicus (e.g. in *Ammonia*), the umbilical spiral canal remains open, demonstrating that the spiral canal is a functional surface, since it receives secondary lamination.

The cytoplasm leaves the chamber lumen in *Elphidium* through the interiomarginal multiple apertures or, posteriorly, through the opening constituted by a former aperture (closest to the umbilicus) of the penultimate chamber. Thus, it moves inside the umbilical spiral canal system, which is a functional surface, and then into interlocular spaces through openings in the spiral
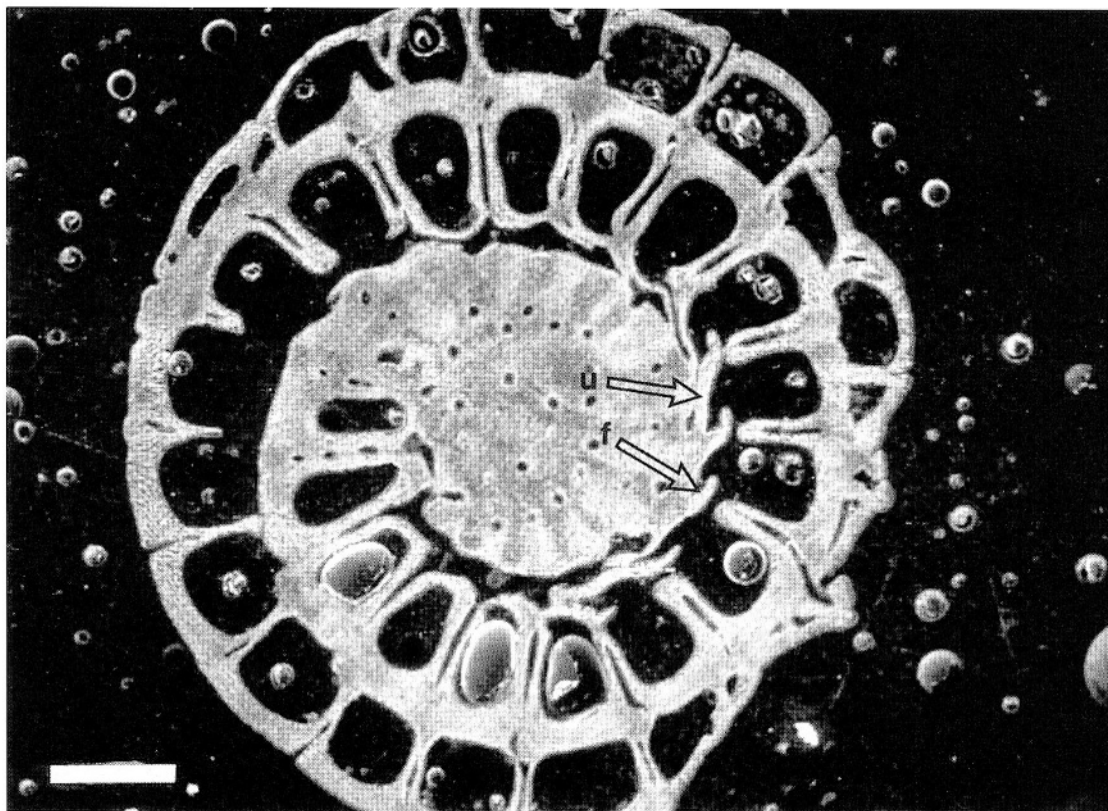
Figure 4.13 Detail of horizontal section through *Pseudorotalia* showing hooks (foraminal plates = f) and umbilical cover plates (u); scale bar = 0.2 mm.

canal. This allows the cytoplasm to emerge everywhere on the foraminiferal shell, between the ponticuli that bridge the interlocular spaces, as well as into interlocular spaces of previous whorls.

The nummulitids, in addition to possessing an umbilical spiral canal system, have developed a so-called marginal cord. This is a system of elongate 'islands' or ridges in the peripheral part of the final chamber, which, with the addition of secondary lamination, is gradually converted into a multi-pipe marginal channel. This channel communicates with all interlocular spaces, which are formed between the primary ridges of the septa and the septal flaps.

'Toothplates' are a special feature of some calcareous bilamellar Foraminifera. True tooth-plates are found within the Buliminida, and seem confined to that group. A buliminid tooth-

plate is constructed of a single inner lining (Revets, 1993). Following the construction principles outlined above, the toothplate, if it were a functional surface, would have received secondary lamination. That has never been observed.

All planktonic Foraminifera are known or assumed to construct bilamellar shells. Although a monolamellar structure was reported in *Hastigerina pelagica* (Hemleben *et al.*, 1989), the scanning electron micrograph of a wall section shows it to be bilamellar (Fig. 4.17). This wall is only about 2 μm thick, rendering observation of the lamellarity difficult.

4.5.7 Aragonitic walls (Robertinida)

The study of several taxa belonging to the aragonitic order Robertinida shows that the shell con-
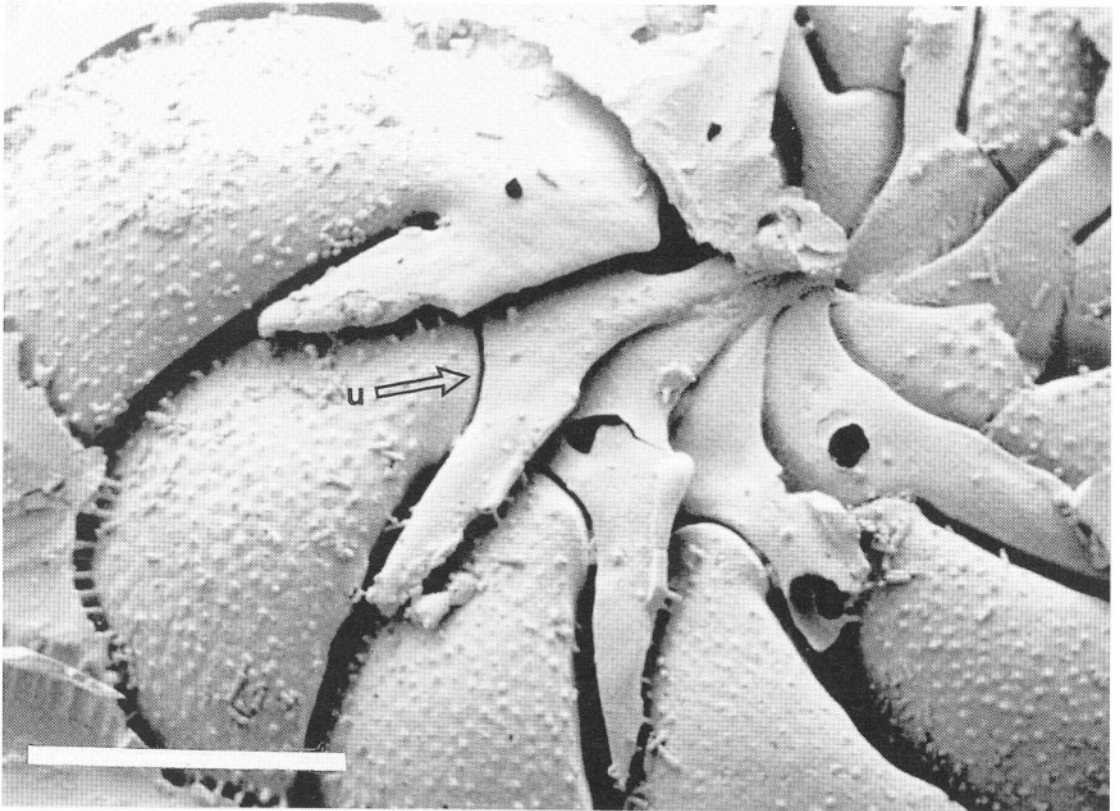
Figure 4.14 Detail of mold of *Astrononion* showing positions of umbilical cover plates (u); scale bar = 0.1 mm.

struction is bilamellar, although there is no obvious difference between the median layer and the boundary between the secondary lamellae. For example, the ultimate chamber wall in *Hoeglundina* is bilamellar, but in contrast to calcitic bilamellar walls, the aperture is not converted into a foramen with the addition of a new chamber. The aperture in *Hoeglundina* is positioned in the peripheral region of the final chamber; as a new chamber is added, this peripheral aperture is closed in the penultimate chamber by the deposition of a two-layered plate, while an opening is resorbed in the penultimate septal face, thereby creating a secondary foramen. Along with the formation of the outer chamber wall, *Hoeglundina* deposits a folded two-layered plate as a prolongation of the wall on the spiral side. This structure is often referred to as a toothplate, but it is not a true toothplate, which is a single-layered feature so

far found only in the buliminids (see earlier). The two-layered plate ends in a folded extension, and is attached to the previous septum where the inner lining continues as a septal flap. The plate extends in the anterior direction for about half the length of the chamber. The entry of the cytoplasm into a chamber interior and earlier chambers of *Hoeglundina* takes place over the free folded part and through a foramen on the spiral side of the plate, and then from one foramen into the next (see illustrations in Hansen, 1979). A Jurassic *Epistomina* has exactly the same construction pattern. Ceratobuliminid shells have identical two-layered plates with a folded edge, and show the resorption of a foramen in the penultimate chamber. *Cushmanella* and related genera are extremely delicate, and their inner structures are more complicated than those of *Hoeglundina* and *Ceratobulimina,* and some species have several apertures associated
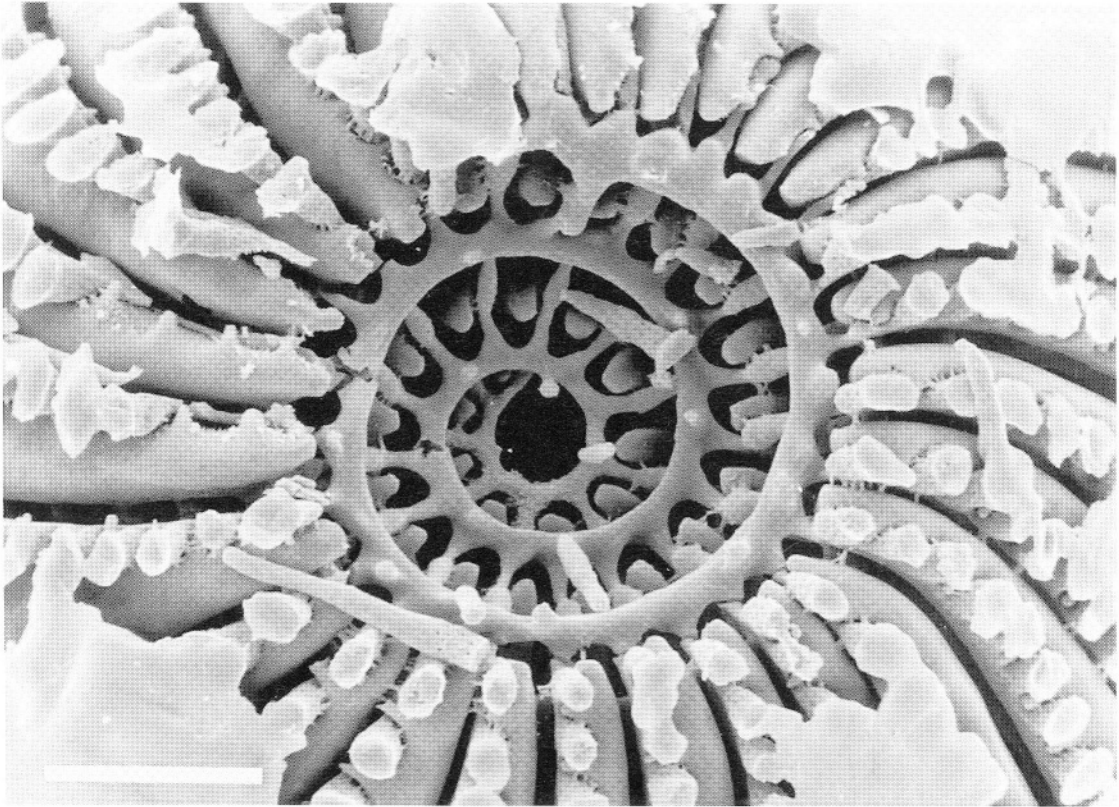
Figure 4.15 Mold of *Elphidium craticulatum* showing umbilical spiral canal; scale bar = 0.1 mm.

with partially closed inner pipes. The more complicated aragonitic shells appear to have evolved in the Jurassic, but the study of fossil aragonitic forms is hampered by the frequent recrystallization of their wall material. The record of simpler aragonitic forms goes back to the Permian (Loeblich and Tappan, 1987), but early involutinids may be unrelated to the structurally advanced forms of the Jurassic and later times (Piller, 1983).

4.5.8 The carbonate units of bilamellar forms

The shells of bilamellar forms are often described as being constructed of platelets of calcite. The platelets (0.1–0.2 μm thick) are arranged in stacks with identical orientation, but are apparently separated from each other by very thin organic layers. These organic layers are much thinner than those separating adjacent secondary lamellae, which, in turn, are thinner than the median layer.

There has been much speculation on the calcification process in bilamellar walls, but few direct observations have been made; such observations are hampered by the limited resolution of the light microscope. Angell (1979) made a study of shell formation in *Rosalina floridana,* but he had to clean various parts of the shell with chlorine; the effect of this procedure is uncertain, and some of the observed structures may be artifacts. Some speculative models of calcification are in poor agreement with the available ultrastructural evidence. In essence, explanations are needed for (a) the formation of stacks of platelets with the same orientation across spongy organic layers that separate adjacent secondary lamellae, and (b) the presence of pairs of euhedral calcite rhombohedrons that sandwich the median layer.
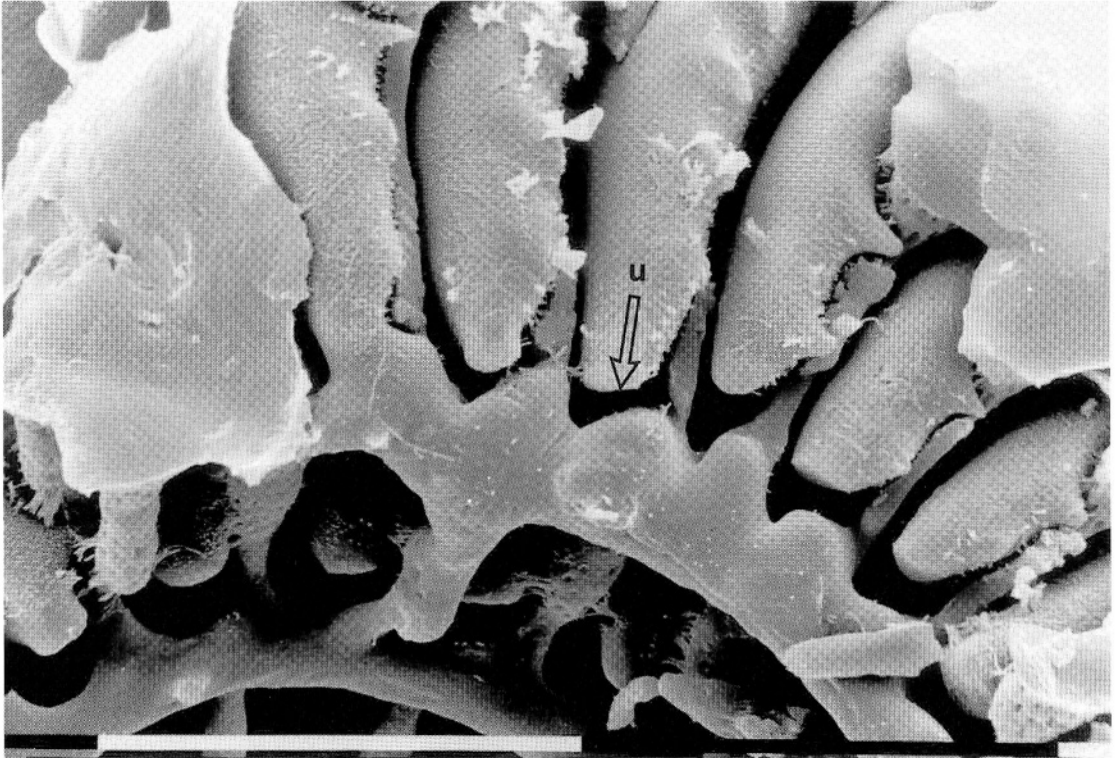
Figure 4.16 Detail of Fig. 4.15 showing positions of umbilical cover plates (u); scale bar = 0.1 mm. Note the absence of cover plate in the final chamber.

The difference between secondary lamellar boundaries and the median layer was noted by Hansen and Reiss (1971). In forms such as *Ammonia* and *Pseudorotalia,* the median layer was found to be composed of an organic sponge-like mat, sandwiched between calcite rhombohedrons whose obtuse angles protrude in the direction of the shell surface and the shell interior. Thus, from pure morphology, the optical axis is oriented perpendicular to the shell surface of this base pair of calcite crystallites. The rhombohedrons appear almost perfect, indicating that they formed without interference. The stacks of overlying platelets continue the orientation of the base-pair crystal faces. On etched shell sections, such stacks are separated by concentrations of organic material, which were regarded by Hansen (1970) as delimiters of 'crystal units.'

Debenay *et al.* (1996) illustrated two impor-

tant features from the surface of a naturally corroded specimen of *Helenina anderseni.* The first concerns the nature of crystal units. The platelets around a pore are steep, indicating that platelets in *H. anderseni* may be oriented according to a more acute crystallographic form than $\{10\bar{1}1\}$, with the pore oriented along the c-axis. The other observation is on the detail of the boundary between crystal units, which shows an almost whisker-like pattern, and points to uninhibited growth, with neighboring crystal units in identical crystallographical orientation.

Debenay *et al.* (1996) suggested a calcification model for calcareous Foraminifera in which the primary elements are globular crystallites. The existence of such globular units, however, has not been satisfactorily documented. The possibility exists that they are artifacts, because similar globules can be produced in the laboratory by etching a foraminiferal wall, from which they
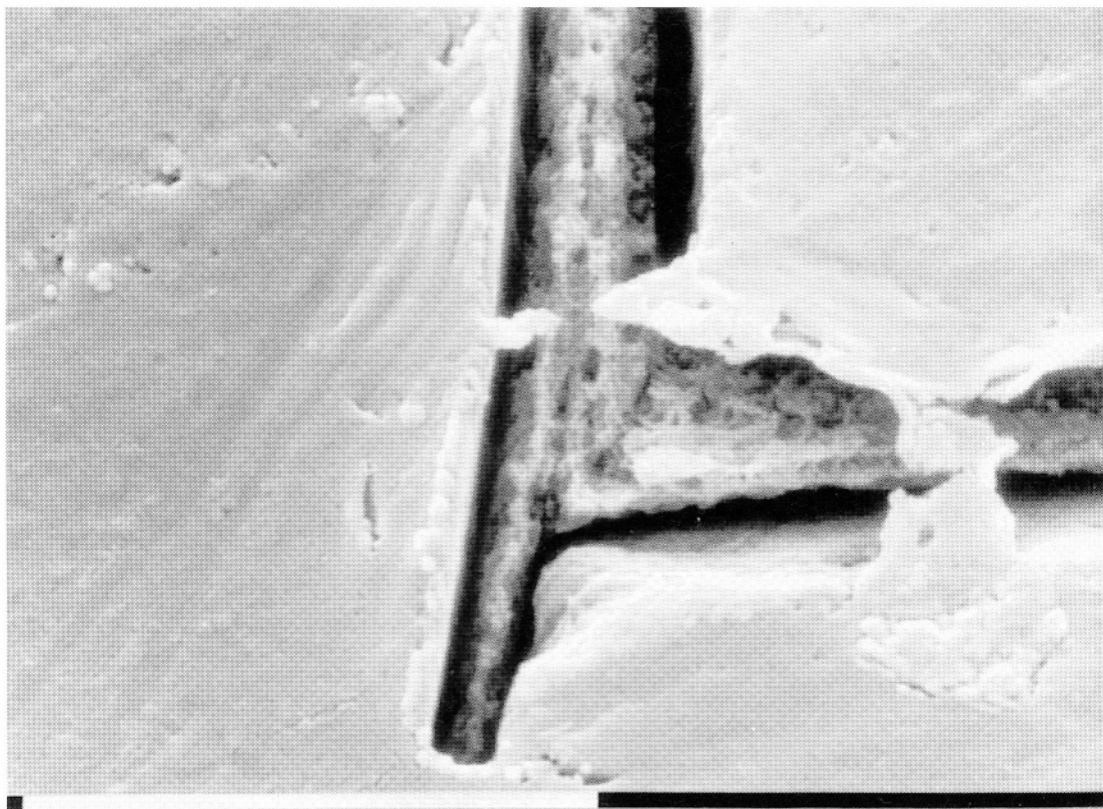
Figure 4.17 *Hastigerina pelagica*, junction between ultimate and penultimate chambers, detail of embedded, polished, and etched horizontal section; scale bar = 10 μm. Note the bilamellar construction.

can be completely or partially removed by extraction peels. Angell (1979) illustrated globular units of about 600 Å diameter on the surface of a *Rosalina floridana,* and there is a hint of a layered arrangement in these globules. However, Angell had removed organic material from the shell surface with sodium hypochlorite, and therefore there is a possibilty that these globules too may be etching artifacts.

4.6 THE PORES

Details of pore structures have been studied in just a few calcareous species. The pores in the monocrystalline *Patellina* were described by Berthold (1976b), who found an organic tubule and granular organic material filling the interior of the tubule, and demonstrated the uptake of

the neutral red dye through the pores. The construction of the pores in the bilamellar *Amphistegina* was described by Leutenegger (1977b). These pores have an organic tubule that is subdivided by organic plates; each plate corresponds to a boundary between secondary lamellae. The median layer also crosses the pore tubule, and carries calcite crystallites that may represent the crystal base pairs of the median layer, indicating a late time of formation of the pores. In contrast to the pores of *Amphistegina,* those in genera such as *Heterostegina, Cycloclypeus,* and *Operculina* are not lined with organic tubules (Leutenegger, 1977b). Leutenegger and Hansen (1979) demonstrated the uptake of radioactive CO_2 through the pores of symbiont-bearing *Amphistegina,* but neither ^{14}C-labeled glucose nor the neutral red dye passed in appreciable amounts. This is not surprising,

because it has been known for a long time that the Rose Bengal dye used for staining living Foraminifera generally produces coloration in only the youngest two or three chambers, while the remaining shell, in spite of the presence of cytoplasm, does not take up any dye, showing the impermeability of the pores for larger fluid molecules. Hemleben *et al.* (1989) found that the pores in some planktonic species originate through resorption in the late state of chamber formation. The pore tubules in planktonic Foraminifera apparently cross the median layer, but the boundary layers between secondary lamellae do not correspond to any structures crossing the pores.

So far, the presence of pore plates has been demonstrated only in lamellar forms. It appears that the so-called sieve plates of the pores in *Amphistegina* are nothing but a continuation of the organic material that separates adjacent lamellae (Hansen, 1972b). The extremely complicated pore-plate pattern illustrated by Jahn (1953) has not been found by other workers, and unfortunately, the species studied has never been identified.

A concentration of mitochondria in cytoplasmic material at the inner end of pores has been observed by Leutenegger and Hansen (1979) in some shells collected from low-oxygen environments. They interpreted this as an indication that pores serve as conduits for the passage of dissolved oxygen and carbon dioxide. This interpretation, however, is controversial, because of later observation that mitochondria are also concentrated in apertural cytoplasm (Bernhard and Alve, 1996) and that they move through pseudopodia (see chapter 12). Thin, thread-like structures emerging from pore plates in *Amphistegina* have been interpreted as extrusions of pseudopodial material (Hansen, 1972b). This has been challeged by Berthold (1976b) and Leutenegger (1977b), because the passage of cytoplasm could not be confirmed by TEM studies of pores. According to Berthold, the strands were most likely produced by fungi that invaded the pores in the laboratory culture.

Pore-like pits ('pseudopores' of authors) occur in some porcelaneous forms. They do not have an organic pore tubule, and a thin calcareous wall (about 10 μm thick) separates the bottom of the pits from the shell interior. In radio-tracer experiments, Hansen and Dalberg (1979) found uptake of labeled CO_2 directly through the thin lateral walls of living symbiont-bearing *Amphisorus*. They explained the uptake as being caused by CO_2 diffusion directly through the organic material of the shell wall, and considered the pits (pseudopores) as an adaptation to obligate algal symbiosis.

5

Quantitative methods of data analysis in foraminiferal ecology

William C. Parker and Anthony J. Arnold

5.1 INTRODUCTION

Undeniably, the Foraminifera offer a wealth of ecological information. Rarely, the data are sufficiently uncomplicated that knowledgeable observation is all that is required to reveal the critical ecological relationships. The desired information is most often camouflaged by aspects of the data involving undesired synecologic and autecologic factors, historical factors, sampling effects, etc. This is where quantitative analytical methods become necessary. The appropriate method can enhance the desired ecological signal in the data while suppressing the unwanted noise; it may simplify or condense the complicated structure of the data, making it easier to explore relationships; and it can facilitate testing an apparent relationship against the standard of chance occurrence. Additionally, the results of commonly used analytical techniques may be more convincing and more easily explained than an intuitive understanding of the data. Even when the relationship seems obvious, confirmatory analyses are a good idea.

With the proliferation in the 1980s and 1990s

of desktop microcomputers and packaged analytical software, most foraminiferal researchers now use some form of quantitative analysis, ranging from simple spreadsheet or database operations to complex multivariate statistical techniques. However, most workers have a limited background in statistics and, when faced with the prospect of choosing an analytical method, can make inappropriate choices. When using the techniques described here as exploratory devices to increase understanding of a complex and confusing array of data, there are no right or wrong techniques. Some are certainly more efficient or appropriate 'signal-enhancing' filters, depending on the nature of the data and the questions of the researcher. For most of these methods, evaluation of success or failure of the analysis depends on whether the results offer a meaningful view of the data in the context of the research focus. The purpose of this chapter is to explore the variety of available and commonly used techniques, and to comment on their characteristics and applicability, so as to (1) aid in understanding the choice, application, and interpretation of methods employed by other researchers, and (2) provide an introduction to

the selection of techniques for the reader's research. We will assume an understanding of simple statistical concepts (mean, standard deviation, etc.) and will focus on the more complicated multivariate techniques. The interested reader is referred to sources such as Shi (1993), Davis (1986), and Dillion and Goldstein (1984) for more general coverage of the methods discussed.

As an explanatory aid we will include analyses of a set of benthic foraminiferal assemblages collected from the Georgia–South Carolina continental slope. This data set includes counts of 183 species present in 38 samples of bottom sediment. The data and some analyses are discussed in Arnold (1977, 1983), Arnold and Sen Gupta (1981), and Sen Gupta and Hayes (1979). The data are available in Arnold (1977) or from the chapter authors at http://quartz.gly.fsu.edu/ ~ parker/data.html.

5.2   DATA

Stevens' classic paper (1946) on scales of measurement provides valuable insights into types of measurements and the operations that can be performed on them. Foraminiferal data can be (1) *nominal* (using numbers as labels, e.g. 0 = smooth, 1 = spined, etc.), (2) *ordinal* (numerical values record monotonically increasing states, but not necessarily with equivalent intervals, e.g. 0 = absent, 1 = rare, 2 = common, etc.), (3) *interval* (numbers indicating equal measurement intervals, but with no true zero, e.g. distance from a geographic point or depth/time from a stratigraphic marker), and (4) *ratio* (like interval, but with a fixed zero, e.g. counts of specimens in a sample). Note that calculation of means, standard deviations, and correlations are technically valid only with interval and ratio data. Calculations involving alteration of variance (e.g. log calculations or standardizations) are only appropriate for true ratio data.

Some foraminiferal studies may include types of data that require special coding. For example, angular data, such as angular morphometric or latitudinal/longitudinal measures can present problems due to the apparent numerical disconti-

nuity at the limits of the scale (e.g. 360°). This problem is best handled by orienting the measurement scale (in most senses an interval scale) such that the recorded observations fall only in the continuous portion. Quantitative chemical measurements, often used with environmental studies, present problems at the low end of the scale. A chemical constituent can rarely be said to be truly absent from a sample, even when the analytical technique fails to detect it. Such 'false zeroes' are more appropriately recorded as 'below detection limit,' reflecting a possible concentration somewhere between the analytical lower limit and true zero. Under these circumstances, a recorded value of some fraction of the detection limit (e.g. 1/2) is more appropriate. Finally, most data have a few samples for which all desired measurements are not possible. While in some cases it may be most desirable to simply discard the samples (or variables) concerned, this may also result in serious reduction in the study's coverage. Although the missing values can be estimated using a variety of techniques (e.g. regression, kriging. etc.), the resulting analysis utilizing the estimated values may be biased by the estimation process. A better approach is to code the missing values with some label or value designated as 'missing.' Most packaged analytical programs include the option of using missing value codes, and will provide options for dealing with such values that are most appropriate for the techniques available in the package.

Since many numerical techniques are sensitive to the relative sizes of the recorded values (e.g. variables recorded with 'big numbers' may dominate an analysis) or to the way in which the values are distributed (e.g. a normal distribution), it is often desirable to transform the data to make it numerically more suitable (see Davis. 1986, for a discussion, and Table 5.1 for the most common data transformation types). However, these recalculations can hide or distort some of the information originally present. For example, recalculation of species abundance as a percent of the sample is a common practice, but may disguise the presence of very depauperate samples, and hide major differences in variance. Some measurements, like species abundance in

Table 5.1 Types of data transformations.

Translations		*	Comments
Minimum → 0	$X_i' = X_i - [\min(X_1 \dots X_N)]$	V	sensitive to extremes
Mean → 0	$X_i' = X_i - [(\sum X)/N]$	V	
Scaling transforms			
Percent maximum	$X_i' = (X_i * 100/[\max(X_1 \dots X_N)]$	V	sensitive to extremes
Percent total	$X_i' = (X_i * 100/\sum X)$	S	most often used to transform samples to be of equal size, generates closure problem because one degree of freedom is lost
Percent range	$X_i' = \dfrac{[\max(X_1 \dots X_N) - X_i] * 100}{[\max(X_1 \dots X_N) - \min(X_1 \dots X_N)]}$	V	changes ratio data to interval
Standardization	$X_i' = X_i - [(\sum X)/N]/\text{STD}(X)$ where STD = standard deviation	V	each variable becomes a standard normal deviate
Algebraic transforms			
Log	$X_i' = \log_e(X_i)$ or $X_i' = \log_{10}(X_i)$	V	will 'pull in' a right-skewed tail, recall that log(0) is undefined
Root	$X_i' = (X_i)^a$	V	especially useful if variables include measurements of different dimensionality, e.g. lengths, areas, and volumes
Arcsin	$X_i' = \text{Arcsin}(p^{-0.5})$ where $p = X_i/(\sum X)$	S	transforms samples so as to emphasize very rare and very dominant components
Normalization	$X_i' = X_i/[\sum(X^2)^{0.5}]$	S	generally used to transform samples into vectors of unit length

* Column indicates whether the transform is primarily used on variables (V) or samples (S)

a pool of samples, may be distinctly 'non-normal' (e.g. skewed) and benefit from a variance-altering transformation (e.g. log transform or power transform). Additionally, species present as no more than a minor faunul element may have little impact on the analysis, unless species numbers or proportions are standardized (for each variable, recalculating the value by subtracting its mean and dividing by its standard deviation).

Because many foraminiferal data sets are sparse (e.g. having many species present in low abundances in a few samples), researchers often eliminate rare species from the analysis to improve the analytical response. Traditionally, species present at abundances of less than 1 or 2% (sometimes only when low in more than 50% of the samples) are eliminated. Keep in mind that the analytical results will then say nothing about the eliminated taxa, or the portion of the fauna they represent.

Outliers are data elements which, for one or more reasons, seem at odds with the rest of the data (i.e. they do not lit the expected trend). Outliers exist for a variety of reasons: (1) errors in sampling, measuring, and recording of data, (2) greater than expected variability in a sampled value, (3) inclusion of one or more members of a 'different population,' and (4) incorrect expectations of relationships within the data. It is principally because they differ from the majority of the data that outliers are so often viewed as troublesome hindrances. Their variance from the data mean often gives the outliers unexpected influence in the outcome of analytical techniques. While the researcher may be inclined (and sometimes justified) in discarding such distracting elements, this is a potentially dangerous course. The outliers, by virtue of their difference, contain more 'information' than their counterparts, and to eliminate them is to discard this information. If a good case can be made that the outliers are different because of some *a priori* condition, then they may be discarded, *along with all other entities that meet the same criteria*. Otherwise, they

should remain in the analysis (with attempts made to minimize their distracting effects), or the analysis should be continued without them and their relationship to the final results stated.

One potentially confusing aspect of multivariate analytical techniques is the use of the terms 'sample' and 'variable'. As used here, 'samples' refer to entities which are conceptually composed of or described by other entities, the 'variables.' Thus, for a biogeographic study of foraminiferal assemblages, a sample might be the collection of recorded abundances of various species at a given location, and the variables would be the species. For a morphometric study of a single species, the sample might be a single specimen (or a population of specimens), and the variables would be the morphometric measurements. In our example data set, we have 38 foraminiferal assemblages from splits of washed, sieved, and floated sediment (containing at least 300 individual foraminiferal specimens, where possible) as samples. The 138 species present in these samples are the variables, and their values are recorded as counts of individual specimens for each species in each sample (ratio data). Due to the large and unwieldy nature of a 138-element variable list (many packaged programs have restrictions on the number of variables used in some analyses), and the observation that many of the species occur sparsely and have little correlation with any other species, we have reduced the variable list to the 77 species which show significant associations with at least one other species (following Arnold, 1983). Log transformation of data was chosen because species abundances are generally log-normal and because, philosophically, the difference between 0 and 1 individuals should be more significant than the difference between 100 and 101. Note that since the data set contained 0 values (for which the log transform is undefined), a constant, small value (smaller than the minimum positive value, e.g. 0.5) was added to each entry in the data set prior to log transformation. Thus a 0.0 value becomes −0.69. In addition to species abundances, we also have data on the depth, location, and sediment type at each sampling locality. These latter variables will be used to interpret the results of multivariate analyses of the species assemblages.

5.3   CLUSTER ANALYSIS

Cluster analysis (CA) is one of the most widely used and commonly understood multivariate analytical techniques in the foraminiferal literature. It segregates entities (samples, species, measurements) into 'naturally occurring' groups and quantifies the between-group relationships. It is difficult to peruse a copy of *Journal of Foraminiferal Research* or *Marine Micropaleontology* without seeing at least one example of the characteristic dendrogram (see Fig. 5.1) generated by most packaged cluster analysis programs. The spindles of the dendrogram track the entities in the clusters, while the linkage bars reflect the similarity of the clustered entities. Cluster analysis has been used to delineate biofacies (e.g. Ishman, 1996), species associations (e.g. Ishman and Domack. 1994), and morphometric associations (e.g. Saraswati, 1995). One caveat which must be remembered is that cluster analysis *always* produces clusters, whether or not any naturally distinct groupings occur in the data. It is most often used as an exploratory technique, to see what groupings might be present. To confirm the presence of any clusters observed, researchers resort to the quantification techniques discussed at the end of this section, or a comparison ('mapping') of the cluster analysis results with results of other multivariate techniques (e.g. factor analysis, principal components analysis, correspondence analysis, multidimensional scaling).

Almost exclusively, the varieties of clustering used with foraminiferal data fall under the heading of 'hierarchical agglomerative' clustering, meaning that they start with all entities in separate groups and proceed to cluster iteratively, by merging pairs of groups from previous iterations, until all entities are grouped into a single cluster. Analyses are referred to as Q-mode for clustering of samples (i.e. entities composed of several measurable parameters), or R-mode for clustering of variables (the measurable parame-

CLUSTER ANALYSIS DENDROGRAM

Re-scaled Cluster Dissimilarity

```
                     0         5        10        15        20        25
Sample depth sed     +---------+---------+---------+---------+---------+

664  675m OOZE
666  675m OOZE
1112 355m OOZE
1113 415m OOZE
514  148m SS-SLT
568  160m SS-SLT                                                   A
567  165m SS-SLT
1045 190m SS-SLT
1110 240m SLT-OOZE
111  116m SS-SLT
987  137m SH-SS
99   116m SS-SLT
1042 99 m SS-SLT
97   115m SS-SLT
104  110m SS-SLT
1048 125m SS-SLT
162  115m SS-SLT
101  109m SS-SLT
116  112m SS-SLT                                                   B
103  110m SS-SLT
110  115m SS-SLT
1043 135m SS-SLT
989  165m SS-SLT
1047 142m SS-SLT
516  114m SS
518  80 m SS
517  94 m SS
520  65 m SS
508  92 m SS
522  50 m SS
526  45 m SS
528  45 m SS
525  45 m SS
523  48 m SS
524  45 m SS
521  53 m SS                                                       C
509  108m SS
527  45 m SS
```

Figure 5.1 Dendrogram from Q-mode cluster analysis of samples from the Georgia–South Carolina continental slope using Pearson's coefficient and UWPGA method. Based on relative separation, three clusters (shaded) have been recognized. Note the relationship of the clusters to sample depth (A, deep; B, intermediate; C, shallow) and sediment type (A and B, finer-grained; C, coarse-grained).

ters). The choice of R- or Q-mode is a logical result of the kind of question being 'asked' of the data. If your interest is in similarity/dissimilarity among samples, then a Q-mode clustering of samples is indicated. Most implementations begin with conversion of the data to a matrix of similarities (or dissimilarities) among the entities to be clustered, and end with the production of the descriptive dendrogram. Variations on the basic format arise from differences in (1) the similarity (or dissimilarity) calculation used, (2) the means of choosing which entities to cluster at each step, and (3) the means of calculating similarities of entities to newly fused clusters.

Commonly chosen similarity measures include the Pearson's correlation coefficient (0-1.0) and euclidean distance (0-infinity). This choice can be important due to interaction between the nature of the data and the way similarity is calculated. Some indices of similarity, such as Pearson's correlation, are relatively immune to differences in the 'numerical size' of the entities being clustered, (i.e. whether the values are numerically larger or smaller than for other entities). Others, such as euclidean distance, change similarity values with changes in scale of measurement. Additionally, some data sets may produce similarity values between entities that have such small numerical ranges that interpretation of the dendrogram becomes difficult. Unless the worker is interested in exploring the numerical nuances of the various similarity measures, it is advisable to run several analyses with different indices, and discard, or at least distrust, any result that is fundamentally different from the others. Davis (1986), Sneath and Sokal (1973), and Sepkoski (1974) discuss various similarity measures available.

Most of the common clustering methods simply join the two entities with the highest mutual similarity at each iteration. One popular variant is Ward's minimum variance clustering method, which does not involve a similarity measure as such, but uses the data to calculate a sums-of-squares index E for all entities. At each step, a potential new cluster that yields the lowest total E value (for all the entities present at that step) is formed. This continues until a single cluster remains. Ward's method is often preferred because the dendrogram, when scaled to E, produces what appears to be exceptionally well defined clusters. This is primarily because E is a function of squared differences and is, therefore, nonlinear. A dendrogram scaled aginst the square root of E would be more comparable to the other methods. Note that Ward's method, because it uses no similarity measure (other than E, surrogate for variance), is susceptible to scale and measurement changes.

Among the variety of methods for calculating similarities for newly fused clusters, two methods, Unweighted Pair Group Method with Arithmetic averaging (UPGMA) and single linkage (SLINK), appear most popular. The former averages similarities of entities to new clusters (adjusting for the number of entities in each cluster), while the other takes the maximum similarity between the entity and any member of the new cluster. As expected, these different methods can produce dramatically different dendrograms, especially with regard to the levels of linkage between clusters.

Recognition of 'significant' clusters within a dendrogram is largely a subjective process. Practitioners most commonly attempt to define clusters based on relative spacing of linkages in the dendrogram. Clusters can be graphically designated by shading or by construction, on the dendrogram, of a 'phenon line,' marking a level of similarity (or dissimilarity) at which the clusters are presumed to represent meaningful aggregations.

If the aim of clustering is to explore or illustrate group structure in the data, then the appropriateness of the specific choice of method can be judged subjectively (i.e. do you see what you were looking for?). However, if the goal is to objectively quantify the 'success' of a given analysis, we require more rigor. Two quantification techniques are available. The cophenetic correlation value compares the between-entity similarity values in the original matrix with a similar set derived from the clustered results (described in detail in Davis, 1986). Values approaching 1.0 indicate less distortion of the

original similarities by the clustering process. More involved techniques use a Monte Carlo process (described in Milligan, 1996) to generate artificial, random data sets from the original data. Analysis of the artificial data provides a basis for quantitative comparison of the results of a given cluster analysis. Comparisons of various techniques (Milligan, 1996; Milligan and Cooper, 1986; Hubert and Arabie, 1985) suggest that the correlation coefficient generally outperforms euclidean distance and that Ward's method may show some superiority to UPGMA. SLINK methods, in general, fare poorly.

Recent examples of CA include delineation of species assemblages (Ishman and Domack, 1994; Chang and Yoon, 1995) and environmentally related biofacies (Whitehead and McMinn, 1997). A dendrogram for Q-mode CA (SPSS for Windows 7.5.1) of the example data set is shown in Fig. 5.1 with the clusters (shaded for identification) chosen on the basis of relative separation. Arnold (1983) presents both R- and Q-mode clusters of this data, using the data in presence/absence (1 or 0) form, and demonstrates that the Q-mode clusters thus formed are strongly related to sample depth. The analysis shown here uses fully quantitative data (counts rather than presence/absence) converted to natural logs and subsequently standardized. Sample similarites were calculated using Pearson's coefficient and the clusters formed using the UWPGA method. As you can see, the clusters display a relationship, albeit an imperfect one, with sample depth. The selection of the options presented here is based on approximately 15 different runs with a variety of data treatments, similarity coefficients, and clustering strategies, with varying success in producing depth-related clusters. While the results shown illustrate that the assemblages are related by their depths, the manipulation of the methodology necessary to achieve even moderately strong depth-related clusters suggests that depth is not the only factor influencing groupings in the data. For example, note that the clusters also tend to separate groups related by sediment type. We also note that those techniques which tend to minimize

the range of the variables, and make them numerically comparable, produce results most similar to that of Arnold (1983), perhaps because the presence or absence of a species indicates the environment better than its abundance.

5.4 EIGENVECTOR TECHNIQUES

5.4.1

Eigenvector techniques embrace a variety of analytical methods, including Principal Components Analysis, Factor Analysis, and Correspondence Analysis. All of these techniques attempt to portray/resolve the similarities or differences between entities (samples, species, etc.) in terms of placement in a multidimensional space. The dimensions of this new space are determined by converting the original or transformed data into some measurement of similarity between entities, and factoring the matrix of similarities into eigenvectors (mutually perpendicular axes defining the coordinate system of the new space) and eigenvalues (a measure of how 'important' each new axis is to the data). This factoring process is used to reduce the dimensionality of a multivariate data set, without losing important information, to the point that researchers can easily work with it. Although some of the techniques are most often used with species, and others with samples, all of these methods can be used in both R- and Q-modes (see discussion in David *et al.*, 1974; Klovan and Imbrie, 1971); the choice is less restrictive than for CA. With the calculation of loadings and scores, it is possible to derive information from the analytical results about the roles of samples and variables in the reduced dimensional space. Keep in mind that loadings address the relationships between the entities being factored and the new axes (e.g. for R-mode, loadings ⇔ variables; for Q-mode, loadings ⇔ samples), while scores represent the 'alternate entities' (R-mode, scores ⇔ samples; Q-mode, scores ⇔ variables). The differences between the various techniques discussed here are primarily due to the different assumptions

about the data and the different ways of data treatment.

5.4.2   Principal Components Analysis

Principal Components Analysis (PCA) is the simplest of the eigenvector analytical techniques. In PCA a variance/covariance matrix or a correlation matrix is factored, thus making this technique most suitable for R-mode investigations (note that calculation of an R-mode correlation matrix involves standardization of the variables). The process ideally will extract as many new dimensions as there were original entities in the data (e.g. factoring a matrix with 10 entities, you get 10 principal coordinates or factors). These new dimensions are mutually independent and each accounts for a decreasing share of the information in the original data (reflected by monotonically decreasing eigenvalues).

Most commonly, researchers are not interested in all of the new dimensions. The decision about how many dimensions to consider can be made in many ways. A common method is to plot the eigenvalue (or its log) versus its order (see Fig. 5.2 for an example, also known as a 'scree plot') and look for a 'natural break' in the decrease in eigenvalues with increasing rank.
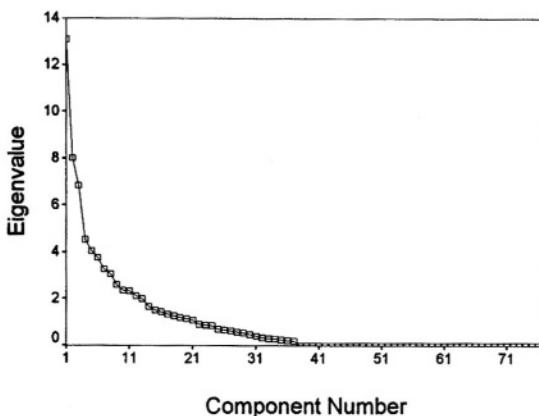
Figure 5.2 Scree plot showing eigenvalue against relative order of eigenvector (component) for principal components analysis of data discussed in text. Here, the first three PC's have substantially higher eigenvalues than the slope defined by the rest, suggesting that they hold more explanatory value.

Others choose to retain only those eigenvalues accounting for more variance than any original entity would have, if variance were distributed evenly (e.g. when factoring 20 species, only keep dimensions with 5% or more of the total variance). Keep in mind that as you reduce dimensionality, you lose information. Communality values (square root of sums of squares of loadings for retained dimensions) will help indicate when reducing dimensionality has effectively eliminated an entity from the analysis.

The new axes can be rotated in multidimensional space to increase their explanatory value. Rotations can be either orthogonal (maintaining the axes as independent) or oblique (allowing for inter-correlation). The only commonly used rotation is VARIMAX, an orthogonal rotation which maximizes the variance in factor loadings, thus having the effect of leaving each factor characterized by a few entities with high loadings.

There are a variety of ways in which PCA results can be interpreted. The principal components or factors can be viewed as new, 'synthetic' variables (R-mode), or new, 'endmember' associations of variables (Q-mode). Sometimes significant members of the original variables or samples have sufficiently strong loadings on a certain factor that the factor can be 'named' (e.g. the first factor in morphometric analyses often contains strong loadings from size-dependent variables, and is called the growth or size axis). One advantage of the new synthetic variables is their orthogonality; they are independent (i.e. uncorrelaled) to each other. Thus, if one axis describes size, the other axes are size-independent. The loadings can be used to characterize the original entities, or to explore relationships between subsets of entities. Naturally occurring groups of entities can be picked out on plots of loadings or scores. Lines or arcs of entities on loading or score plots reveal gradients of change. Often, plots of PCA loadings may display a highly curved or horseshoe-shaped arc. This is 'Kendall's horseshoe,' an artifact in the analytical process that can distort a simple (e.g. one-dimensional) gradient of change into a higher dimensional curve.

Recent examples of PCA in foraminiferal research include Mackensen *et al.* (1993b) and Harloff and Mackensen (1997); these use Q-mode PCA to differentiate ecologically significant benthic foraminiferal associations. Loubere (1996) uses PCA of benthic species abundance data to illustrate the differences between factoring correlation versus variance/covariance matrices (correlation equally weights all taxa, variance/covariance favors abundant taxa). Speijer *et al.* (1996) present results of both an R-mode CA and a PCA of Egyptian Paleogene benthic foraminiferal assemblages, giving a comparative view of the two techniques and showing how to incorporate the results of one in the other. Fig. 5.3 (after Speijer *et al.,* 1996) shows the stratigraphic distribution of sample scores, using the scores as synthetic sample descriptors which the authors have related to environmental variables.

Figure 5.3 Plot of sample scores (after Speijer *et al.,* 1996) for the first three PC's from an R-mode PCA of benthic foraminiferal species versus sample stratigraphic position. The PC's are being used as 'synthetic variables' with suggested environmental associations.

Table 5.2 Eigenvalues extracted using principal components analysis (example data).

Component	Eigen value	% of variance	Cumulative %
1	13.893	17.812	17.812
2	8.031	10.296	28.107
3	6.850	8.782	36.889
4	4.590	5.885	42.774
5	4.055	5.199	47.973
6	3.763	4.824	52.797
7	3.280	4.205	57.003
8	3.066	3.931	60.933
9	2.610	3.346	64.279
10	2.363	3.029	67.309
11	2.315	2.968	70.276
12	2.113	2.710	72.986
13	1.992	2.554	75.540
14	1.658	2.126	77.666
15	1.512	1.939	79.605
16	1.444	1.851	81.456
17	1.348	1.728	83.183
18	1.269	1.627	84.810
19	1.228	1.574	86.384
20	1.170	1.499	87.883
21	1.086	1.392	89.276

Note: components with eigenvalues < 1.0 omitted.

An R-mode PCA carried out on the example data set (using log transformed variables) yielded eigenvalues (and associated percentages of the total variance each accounts for) shown in Table 5.2. A scree plot of these eigenvalues (Fig. 5.2) shows a distinct drop after the first three components, suggesting that these three have substantially more explanatory power than the rest. A condensed table of VARIMAX rotated loadings (containing only those variables with high loadings on one of these first three components) is shown in Table 5.3. Note that many species, especially *Textularia conica* (TXT_CONI), *Textularia agglutinans* (TXT_AGGL), *Siphonaperta sabulosa* (SIPHON_S), *Reophax curtus* (REOPX_CU), *Eponides antillarum* (EPON_ANT), and *Calcituba decorata* (CATLUB_D) have high loadings on component one, the species *Amphistegina lessonii* (AMPHIS), *Cassidulina laevigata* (CASS_LAE), *Cibicides floridanus* (CIB_PSEU), *Glabratella lauriei* (GLAB_LAU), *Quinqueloculina jugosa* (Q_JUGOS), and *Rosalina bertheloti* (ROSA_

Table 5.3 Rotated principal component matrix (example data).

Species	Component 1	Component 2	Component 3
ACERV_IN	0.638	−0.375	−4.630E-02
AMPHIST	−1.623E-02	0.621	0.169
ASTRLINA	−0.581	−0.322	0.264
BIGEN_IR	0.595	−4.628E-02	6.716E-02
BOL_LOWM	−0.625	−0.461	4.297E-02
BUL_ACUL	−0.565	−0.337	−0.278
CALTUB_D	0.718	−0.504	7.535E-03
CASS_L_C	−0.579	0.189	−0.180
CASS_LAE	6.824E-02	0.529	−0.394
CIB_PSEU	3.803E-04	0.580	−0.547
CIB_RFLG	−0.133	−7.125E-02	−0.819
EPON_ANT	0.690	−9.299E-02	−2.276E-02
FISS_MAR	−0.512	−4.053E-02	4.325E-02
GLAB_LAU	0.105	0.604	−0.130
HANZ_CON	0.413	0.263	0.533
MELON_ZA	−0.273	0.334	−0.522
MIL_CIRC	0.360	−9.843E-02	0.503
NODOBC_A	0.563	0.296	0.328
NONLLA_A	5.480E-02	0.211	0.539
PLACPS_C	0.584	−0.447	8.983E-02
Q._JUGOS	6.614E-03	0.656	4.143E-02
REOPX_CU	0.701	0.142	5.469E-02
REUSSLA	0.289	1.515E-02	0.542
ROSA_BRT	−0.153	0.668	0.123
ROSA_FLD	−0.408	8.491E-02	0.578
SIPHON_S	0.739	−0.285	−1.543E-03
STILOSTO	−0.148	−8.637E-02	−0.815
MARTNOT	−0.104	4.071E-02	−0.791
TXT_AGGL	0.678	−0.171	0.392
TXT_CAND	0.643	−0.372	9.147E-02
TXT_CONI	0.836	2.850E-02	0.310
UVIG_PER	−0.372	0.405	−0.538
WEBNLA_C	0.671	−0.454	−4.151E-03

Extraction method: Principal Components Analysis.
Rotation method: Varimax with Kaiser normalization.

BRT), on component two, and especially, *Cibcides* sp. cf. *C. refulgens* (CIB_RFLG), *Rosalina floridana* (ROSA_FLD), *Stilostomella antillea* (STILOSTO), and *Martinottiella communis* (MARTNOT) on component three (a negative sign on the loading indicates that the species decreases as the component increases). A plot of sample scores in Fig. 5.4 shows a gradation of samples along PC1 with a separate grouping of points high on PC2. PC3 primarily accounts for two samples (1112 and 1113). A

plot of PC1 versus depth, shown in Fig. 5.5 shows a positive correlation, so that PC1 may be thought of as a depth component. The circles in Fig. 5.4a surround the clusters defined previously, demonstrating that the clusters A and C break up a continuum, while cluster B represents something different. Referral to a map of sample locations (Arnold, 1983) reveals that the samples scoring high on PC2 are substantially farther northeast along the slope than other samples at similar depths, and are typified by finer grained sediments. Thus, the analysis has picked up differences due to a variety of causes.

5.4.3   Factor analysis

Factor analysis (FA), *sensu stricto,* differs from PCA primarily in conceptualization of the data. In contrast to PCA, FA assumes that the information in the data is composed of a few factors common to all entities, mixed with factors unique to individual entities. The underlying common factors are not directly observable but are reflected in the observable entities. One implication of the factor analytic approach is that the number of underlying common factors may be known *a priori,* rather than approximated by looking at scree plots, loadings, or communalities.

A variety of methods exist for extraction of factors: principal components, principal factor, maximum likelihood, alpha, etc. Dillon and Goldstein (1984) conclude that (1) with communalities ~ = 1.0, all methods produce nearly identical results, and (2) with more variables, method choice is less important. Various studies (cited in Dillon and Goldstein, 1984) have suggested that the maximum likelihood method may be superior for very large numbers of samples (> 1500), while the alpha and image methods may be better for small data sets.

Like PCA, FA can be done in Q- or R-mode, the factors can be rotated either orthogonally or obliquely, and the results interpreted as discussed for PCA above. Recent examples of FA include an R-mode analysis of biometric data by Saraswati (1995), analyses of benthic species distribution data in relation to environment by
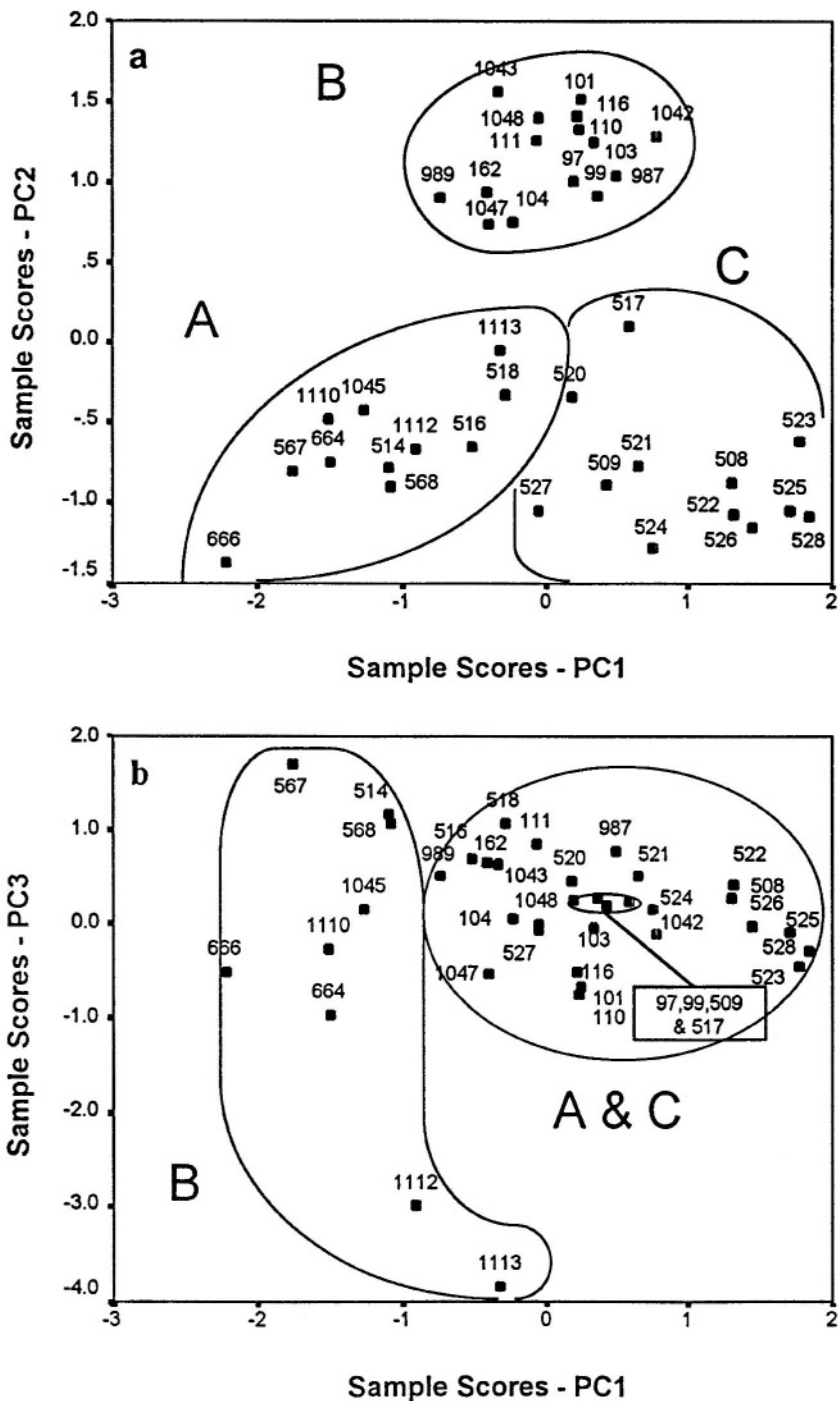
Figure 5.4 Bivariate plots of sample scores (first 3 PC's) form an R-mode PCA of the data discussed in the text. The circles enclosing groups of points map the three clusters shown in Fig. 5.1 onto the PCA. Note that PC1 contains a gradation of samples, with PC2 and PC3, separating out different subgroups.
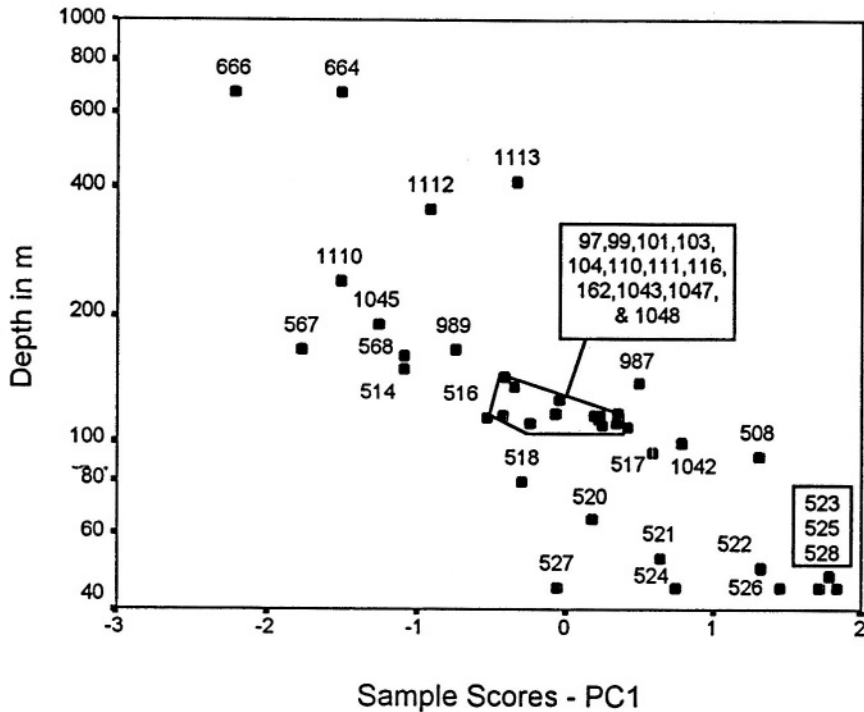
Figure 5.5 A comparison of PCA sample scores from PC1, as shown in Fig. 5.4, with sample depth. The obvious strong correlation suggests that PC1 may be thought of as a surrogate for depth.

Nigam (1987) and Jayaraju and Reddeppa Reddi (1996a), and an R-mode factor analysis of benthic foraminiferal assemblages in the northwestern Gulf of Mexico by Denne and Sen Gupta (1993).

5.4.4   Correspondence analysis

Correspondence Analysis, described by Davis (1986) and David *et al.* (1974), is similar to FA except that the data matrix is transformed into a matrix of conditional probabilities. This process allows for the use of data that are not ratio or interval type (e.g. enumerative data such as the counts of specimens in various species). The transformation is such that relationships between rows and columns in the transformed matrix are the same as in the original data; thus R- and Q-mode solutions are equivalent and are obtained simultaneously. Published results of correspondence analysis often show samples and variables plotted on the same set of axes, thus

enhancing interpretation of the results (provided the plots remain comprehensible) and reducing the number of figures necessary to illustrate the analysis. Recent examples of correspondence analysis include Widmark (1995) and Hermelin and Shimmield (1990).

5.5   MULTIDIMENSIONAL SCALING

Multidimensional scaling (MDS) is another data reduction technique that attempts to uncover 'hidden structure' in data. It requires a matrix of similarities (or dissimilarities), and can be used in either Q- or R-mode. Unlike eigenvalue techniques. MDS attempts to 'map' entities into a limited dimensional space such that the proximities between entities reflect their similarities. The process is iterative, involving changing the mapped locations of entities, and checking a calculated value of mismatch (between distances in the map and similarities) called 'stress.' Most

packaged varieties of MDS require specification of the number of dimensions for the map and a starting configuration. MDS can be either metric (assuming ratio or interval data and a precise function relating similarities to mapped distances) or nonmetric (assuming nominal or ordinal data and an unspecifiable monotonic relationship between similarity and mapped distance). Non-metric MDS can be superior to eigenvector techniques when relationships between entities are not linear, because nonmetric MDS does not assume linearity. Interpretation of the results is superficially similar to that for PCA, with mapped coordinates for the entities in each requested dimension (~ loadings) and correlations between map axes and entity characteristics (~ scores).

A good general description of MDS can be found in Dillon and Goldstein (1984), while discussions of applicability to paleontological data are in Shi (1993), Hazel (1977), and Millendorf *et al.* (1978). Despite its many advantages for foraminiferal research, MDS has seen less use than eigenvector techniques. Ishman (1996) uses a Q-mode MDS, CA, and PCA to analyze foraminiferal assemblages as indicators of North Atlantic deep water circulation patterns.

Application of Q-mode MDS to the sample data (log transformed) yields the two dimensional map shown in Fig. 5.6. The routine used was ALSCAL (SPSS for Windows 7.5.1). and the matrix of scaled distances was calculated from the data by the program using euclidean distance. A two dimensional solution was chosen for comparison to the results from PCA. Note that the pattern of sample locations is very similar to that from the PCA scores. The envelopes drawn are the clusters generated from CA. Again, MDS axis one seems highly correlated with depth while axis two separates geographically distinct groups of samples.

5.6 DISCRIMINANT FUNCTION ANALYSIS

Discriminant function analysis (DFA) is a technique for classifying entities into mutually exclusive *a priori* groups based on a set of independent variables. The technique operates by deriving linear combinations (discriminant functions) of the variables such that misclassification of the entities into the groups is minimized. Entities of unknown group affinity can then be classified using the discriminant function and a probability calculated for membership in each of the groups. This technique works best when the groups are well known and at least some of their members can be identified unequivocally. DFA shares many similarities with multiple linear regression, and it should be remembered that if the variables are highly intercorrelated, the list of 'discriminator' variables used in the discriminant function many not include all those expected.

Recent examples of DFA include Jennings and Nelson (1992), in which the technique is used to discriminate foraminiferal assemblage zones in Oregon tidal marshes. Martin *et al.* (1995) use DFA, along with CA and FA, to distinguish species assemblages in Gulf of California tidal flats. Ishman and Domack (1994) use DFA, CA, and PCA to identify benthic foraminiferal assemblages from the Antarctic Peninsula. For the sample data set, we have used DFA to distinguish between samples associated with coarse sandy sediment and those from finer grained sediments. Fifteen samples with obvious coarse sandy sediment were coded 1.0, and thirteen obviously fine-grained samples were coded 2.0. The remaining samples were left uncoded and were classified by the analysis. As shown in Table 5.4 the DFA achieved 100% correct classification of the coded samples with a function using only six of the species abundances (*Melonis zaandami* [MELON_ZA], *Quinqueloculina jugosa* [Q._JUGOS], *Rosalina bertheloti* [ROSA_BRT], *Rosalina floridensis* [ROSA_FLE], *Spiroloculina atlantica* [SPIROL_A], and *Martinottiella communis* [MARTNOT]). Figure 5.7 illustrates the distribution of all the samples on a plot comparing the sample discriminant scores with their depths. Note that the discriminant axis divided the samples into two groups, sand to the left, fine-grained to the right, and both groups falling in the 0–200 m range (possibly explaining why attempts to sep-
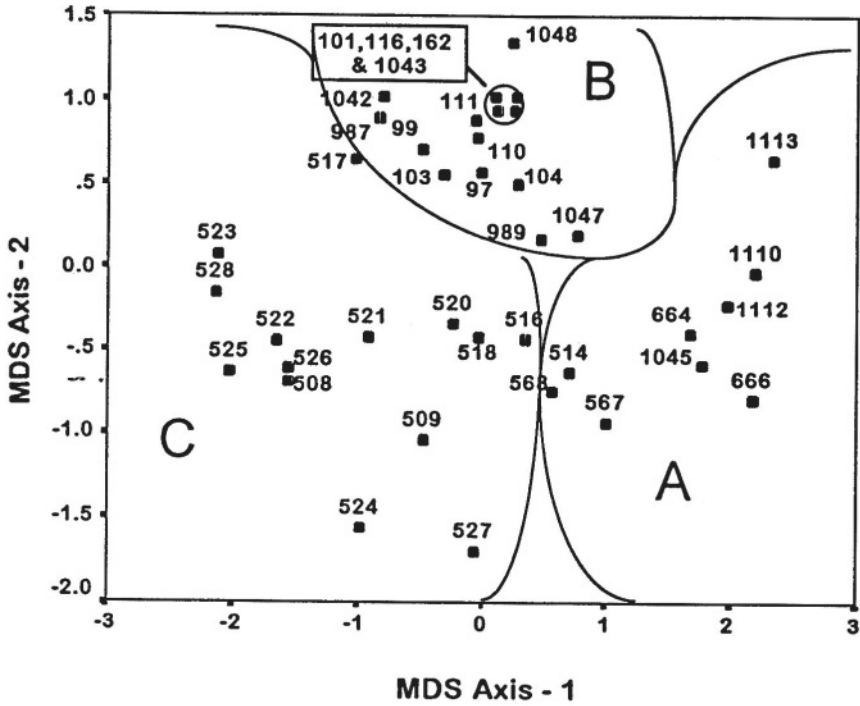
Figure 5.6 A two dimensional sample map of the data described in the text, produced by Q-mode MDS. The pattern of sample positions is very similar to that seen in Fig. 5.4 for PCA. The envelopes drawn map the clusters defined in Fig. 5.1.

Table 5.4 Discriminant function coefficients and classification results (example data).

Variable name	Standarized discriminant function coefficients
MELON_ZA	1.015
Q._JUGOS	1.056
ROSA_BRT	1.636
ROSA_FLE	1.097
SPIROL_A	0.512
MARTNOT	0.889

| | Code | Predicted group membership | | Total |
		1.00	2.00	
Count	1.00	15	0	15
	2.00	0	13	13
	Ungrouped cases	8	2	10
%	1.00	100.0	0.0	100.0
	2.00	0.0	100.0	100.0
	Ungrouped cases	80.0	20.0	100.0

arate these samples by depth alone were not successful). The deeper samples (not originally coded), although primarily classified by the DFA as sandy, do include one intermediate and one fine-grained sample.

5.7   REGRESSION ANALYSIS

Regression analysis is principally concerned with predicting the mean expected value of one variable ('dependent variable') from one or more explanatory variables ('independent variables'). The model for the predictive relationship is a linear function of the independent variables as shown below:

$$Y = b_0 + b_1 X_1 + b_2 X_2 + \dots + b_p X_p + e,$$

where Y = dependent variable, X = independent variable, b = regression coefficient (b_0 is intercept), e = error or residual.

Note that although the form of the regression model is linear, the relationship between the

Discriminant Scores from Function 1

Figure 5.7 A plot of discriminant function scores versus sample depth for the data described in the text (see Table 5.4 for coefficients and classification results). The samples were discriminated using sediment texture (coarse- vs. fine-grained), yielding two groups of samples at opposite ends of the function axis. Note that both these groups fall into the 0–200 m depth range (possibly explaining why attempts to separate the samples purely on depth were unsuccessful).

independent and dependent variables may be nonlinear. For example, any independent variable X_i can be replaced with X_i^2 or $\ln(X_i)$. The values of independent variables are assumed to be known precisely and the dependent variable is assumed to be normally distributed for any set of independent variables. In the common Ordinary Least Squares (OLS) approach, the coefficients (b's) are chosen so as to minimize the sums of squares of the error terms (e's). Packaged regression analysis routines not only estimate the coefficient terms (b's) but also the standard errors of the coefficients. Coefficients with large standard errors may be insignificantly different from 0.0 (checked with a t-test), and therefore contribute little to the prediction. In addition, an analysis of variance (ANOVA) for the entire regression will indicate whether the predictive equation represents a significant partitioning of variance in the dependent variable. The residuals (differences between the predicted and observed values of the dependent variable) should be inspected for heteroscedasticity (a

pattern in their variance) which would suggest an inappropriate choice in the form of the regression model. Because all of the coefficients have standard errors, the confidence limits for the equation as a predictor of the dependent variable are notably 'vase-shaped,' with 'tightest' confidence limits near the mean of each independent and larger limits near the extremes (i.e. the predicted values will be most precise near the means of the predictors).

If the independent variables are highly correlated (multicollinearity), then fewer than the expected number of independents is needed for an efficient prediction equation. Calculation of a regression equation with correlated independents can lead to instability in the coefficients (e.g. coefficients may change radically with the addition or subtraction of a single datum). Stepwise regression, a process that sequentially adds or deletes independents to produce the most efficient regression equation, solves the dilemma of selecting the most efficient subset of independent predictors.

Interpretation of regression results can take many forms. For example, the regression can be used to specify a trend, which can then be analyzed separately from the deviations (residuals). In foraminiferal research, multiple regression analysis is commonly used to predict physical and chemical environmental parameters from sample loadings in Q-mode PCA or FA (e.g. Giraudeau and Rogers, 1994; Mudie *et al.*, 1984), the regression equations then becoming transfer functions. This use of the procedure benefits from the orthogonal nature of the PC's such that no multicollinearity should occur. Other possible uses include trend surface analysis, where the independent variables record dimensions of a 'space' (e.g. map coordinates and/or depth and/or time), in which the dependent variable records the values of a presumably continuous function (e.g. an environmental variable or species density). The regression equation specifies a multidimensional 'surface' describing the regional trend in the dependent variable, while the residuals indicate local deviations from the trend. Both the regional trend and the pattern of local deviations may be of interest.

Table 5.5 shows the results of regression (SPSS for Windows 7.5.1) of sample scores for the previous sample data PCA against natural log of depth (regression against linear depth was also significant, but with substantially smaller R^2). The adjusted R^2 values show that almost 80% of the variance in depth can be predicted or explained using a 'transfer function' consisting of PC1 and PC3. The form of the transfer function is

$$\ln \text{depth} = 4.751 - 0.554 * \text{PC1 score}$$
$$- 0.274 * \text{PC3 score}$$

A comparison of true and predicted depth is shown in Fig. 5.8. Samples plotting above and to the left of a diagonal through the graph have positive residuals and have predicted depths higher than real, those to the lower right have negative residuals and under-predicted depths. Table 5.6 shows the results of a stepwise regression of the species abundance data against log depth. Here six independent variables (species) are included, yielding an adjusted R^2 of 0.939, almost 94% of depth variance explained. Fig. 5.9 shows a comparison of true versus predicted depths with much smaller residuals. Note that

Table 5.5 Transfer function regression model summary (example data).

Model summary

Model	R	R^2	Adjusted R^2	Std. error of the estimate
1	0.804	0.647	0.637	0.4149
2	0.897	0.805	0.794	0.3127

Dependent variable: LNDEPTH.

Coefficients

Model		Unstandardized coefficients		Standardized coefficients		
		B	Std. error	Beta	t	Sig.
1	(Constant)	4.751	0.067		70.588	0.000
	PC 1 scores	−0.554	0.068	−0.804	−0.8124	0.000
2	(Constant)	4.751	0.051		93.643	0.000
	PC 1 scores	−0.554	0.051	−0.804	−10.777	0.000
	PC 3 scores	−0.274	0.051	−0.397	−5.325	0.000

Dependent variable: LNDEPTH.
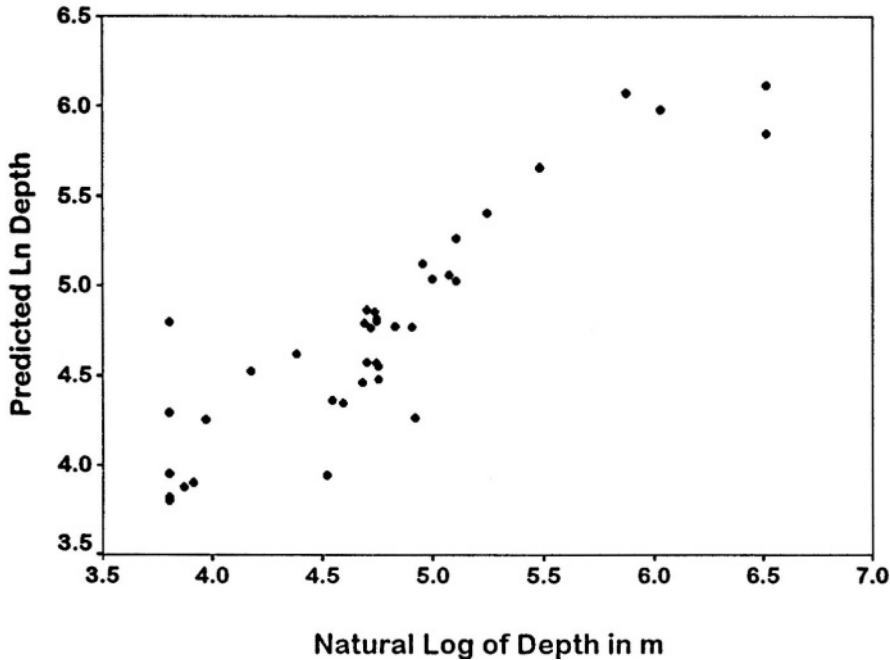
Figure 5.8 A plot of true sample depth versus depth predicted by a transfer function for the data discussed in the text. The transfer function was generated through linear regression of the natural log of sample depth on PCA scores. Adjusted R^2 = 0.794 (see Table 5.5).

although only six species' abundances were deemed sufficient for prediction of depth, other species may also be strongly depth-dependent.

5.8 ROADS LESS TRAVELED

There are a number of techniques in use in other areas of earth and life sciences which have potential for application to foraminiferal studies, but have yet to be commonly employed by researchers. Some of these methods suffer from a lack of inclusion in software packages, others from obscure backgrounds. Since they are not in common use, we will mention them only briefly, but the interested researcher may find value in some of these techniques.

Polar ordination is a data reduction technique developed by plant ecologists (Orloci, 1978; applied to fossil assemblages by Cisne and Rabe, 1978) which places entities in a limited dimensional space, the axes of which are defined by select entities from the original data. It can be operated in either Q- or R-mode, and interpreted much like PCA or MDS. It has the advantage of being less perturbed by outlier entities (those with little in common with the rest of the data), but is handicapped by a limited number of non-orthogonal axes. However, it has produced excellent results with ecological data, and has the distinct advantage that the endpoints of the axes are represented by 'real' entities, rather than by calculated associations.

Recurrent group analysis (Sen Gupta and Hayes, 1979) attempts to define groups of species which co-occur in a statistically significant number of samples. Working with presence/absence, it is somewhat similar to cluster analysis. Unavailable in common statistical packages, it has seen limited usage. Sen Gupta and Hayes (1979) used it for groups of species on the Georgia shelf and Grand Banks, and compared it to cluster analysis, finding that recurrent group analysis gave a better fit to species diversity

Table 5.6 Results of step-wise regression (example data).

Model summary

Model	R	R^2	Adjusted R^2	Std. error of the estimate
1	0.869	0.755	0.749	0.3453
2	0.920	0.846	0.837	0.2784
3	0.946	0.895	0.886	0.2327
4	0.957	0.917	0.906	0.2107
5	0.969	0.939	0.930	0.1823
6	0.974	0.949	0.939	0.1703

Coefficients

Model 6	Unstandardized coefficients		Standardized coefficients		
	B	Std. error	Beta	t	Sig.
(Constant)	5.109	0.073		70.224	0.000
MDS 1	0.349	0.046	0.608	7.530	0.000
EPON_TUM	0.484	0.052	0.440	9.218	0.000
NODOBC_A	0.101	0.029	0.206	3.516	0.001
STILOSTO	0.318	0.068	0.230	4.676	0.000
PLACPS_C	$-8.340E-02$	0.021	-0.216	-3.942	0.000
RCTOBOL	6.099E-02	0.026	0.107	2.384	0.023

Dependent variable: LNDEPTH.
Models 1–5 omitted for brevity.

gradients and identified patterns of group distribution that correlated with water depth and sediment type.

Kriging, developed in geology, is a method of analyzing regionalized data (data sampled at discrete locations, but with a continuous distribution over a spatial region). It can be used to estimate values of regionalized variates at unsampled locations, or to analyze the pattern of increase in variance between two observations with increasing separation distance. Having many of the same applications as regression (specifically, trend surface analysis), it differs in that the regionalized variate need not be modeled as a specific linear function. In addition, confidence limits are not as sensitive to the position within the region. Described in Isaaks and Srivastava (1989), kriging has seen little application in paleontological research.

5.9 CONCLUSION

For a researcher approaching quantitative analysis for the first time, or for one considering the expansion of a limited repertoire of techniques, the variety of different techniques and options available may initially seem overwhelming and undecipherable. In general, if the researcher believes that the data set contains natural groupings, and wishes to define these numerically, then cluster analysis or recurrent group analysis are recommended. If some or all of the members of the groups are known *a priori,* and the researcher wishes to classify unknowns or quantify the differences between the groups, then DFA is recommended. If the researcher is investigating underlying structure independent of groupings, then PCA, FA, correspondence analysis, MDS, or polar ordination are recommended. If the
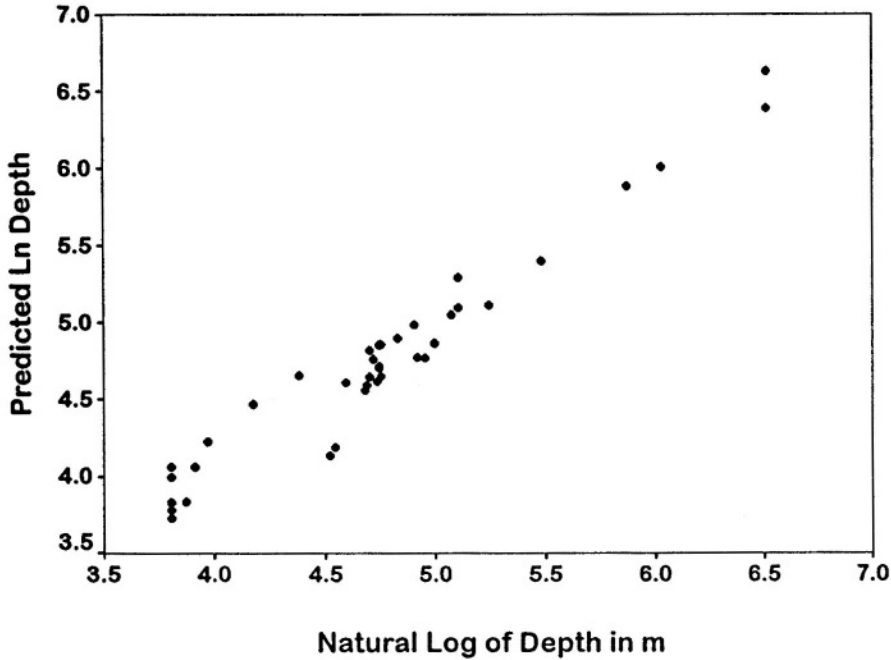
Figure 5.9 A plot of true sample depth versus depth predicted by a step-wise linear regression for the data discussed in the text. The procedure regressed the natural log of sample depth on species abundances, yielding a model involving six variables (species). Adjusted $R^2 = 0.939$ (see Table 5.6).

researcher wishes to use underlying relation-ships to predict values or compare prediction models with observed values, then regression analysis or kriging is recommended.

This chapter has provided only the briefest introduction to what techniques are available and in use in the field of foraminiferal research. The references cited, along with the software packages available, will give more detailed descriptions of specific methods. In closing, we leave the reader with a single caveat: Remember that no statistical technique or software routine, no matter how complex or expensive, can take the place of a deep understanding of the data and the processes being studied.

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PART II:
FEATURES OF
DISTRIBUTION

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6

Biogeography of neritic benthic Foraminifera

Stephen J. Culver and Martin A. Buzas

6.1 INTRODUCTION

Biogeographical studies (the distribution of
organisms, present and past, and the historical
and ecological processes that cause these distribu-
tions) are a natural extension of systematics. At
the highest level of the systematic hierarchy, King-
dom, we recognize a ubiquitous geographic distri-
bution of organisms. As we proceed downward
to the lower members of the systematic hierarchy,
discrete geographic distributions emerge. Recog-
nizing patterns of distribution and attempting to
explain them is the domain of the biogeographer.
However, the recognition of pattern depends
upon our definition of what constitutes pattern(s),
what systematic level we are examining, and at
what geographic scale. Likewise, explanation
requires a historical as well as an ecological per-
spective. These considerations, coupled with the
vast variety and numbers of organisms plus the
diverse interests of the investigators, insure a lack
of simplicity or unification of the subject.

At the species level, differences in distribution
with depth and latitude are readily apparent for
most benthic marine organisms, including the
Foraminifera. If we were to list desirable attributes
for an organism at the Class or Order level that

would ideally suit it for biogeographic studies at
the species level, we might list: 1, ubiquitous distri-
bution; 2, easily sampled: 3, high density; 4, many
species; 5, good preservation providing an excel-
lent fossil record; 6, large number of researchers;
and 7, many years of study. Curiously, the benthic
Foraminifera have all of these attributes and yet
they have received very little attention for biogeo-
graphic studies. North America is the exception
in that Culver and Buzas (1980, 1981a, 1982a,
1985, 1986, 1987) compiled and taxonomically
standardized all the existing data on the distribu-
tion of benthic Foraminifera around the margins
of the North American continent. We will use this
data set to gain some understanding of the bioge-
ography of neritic benthic Foraminifera, but first
we will briefly review two worldwide provincial
schemes.

6.2 GLOBAL BIOGEOGRAPHY

6.2.1 Cushman's faunas

Joseph Cushman's knowledge and experience
with Foraminifera led him to recognize general
distribution patterns for different groups (Cush-

man, 1948). For example, he noted that lagenids characterize continental shelves, miliolids (with some deep water exceptions such as *Pyrgo*) are most abundant in shallow warm-water, coral reef regions, while larger benthic foraminfera are essentially restricted to tropical waters less than 60 m deep. Cushman considered that temperature is the predominant controlling factor of benthic foraminiferal distributions. This led him to a global subdivision into cold-water and warm-water faunas (Fig. 6.1a, b: Cushman, 1948, map dated 1921).

The distribution of cold-water faunas is obviously relatable to cold oceanic currents (e.g. southern extension of cold faunas on the western sides of the North Atlantic and North Pacific; Fig. 6.1a). Cushman noted that although the Antarctic region has its own characteristic species, faunas there are very similar to those in the Arctic (species lists given in Murray, 1991b, suggest this is an over-simplification). Cushman also recognized the extension of cold-water faunas into the ocean basins, most of the information for this conclusion deriving from Brady's (1884) *Challenger* Report.

Warm-water faunas were recognized by Cushman (1948) to be less cosmopolitan; he drew four subdivisions but noted that there could be more (Fig. 6.1b). These are essentially shallow-water faunas as indicated by the extension of the West Indian fauna from Florida to Bermuda and across the Atlantic to the coast of Ireland. The Mediterranean fauna extends into the shallow margins of the Red Sea, and the Atlantic and Indian Ocean margins of Africa. Warm-water faunas around the islands of the Indian Ocean (East African fauna) were distinguished by Cushman from the generally more diverse East Indian fauna of the Pacific Ocean (Fig. 6.1b).

Cushman (1948) believed that although temperature controls benthic foraminiferal distributions, historical factors, such as Tertiary migrations, are of great importance in explaining modern distribution patterns. Cushman noted that the faunas of the Caribbean region are much more like those of Australia than of other tropical regions. Similarly, he pointed out that the cold-water fauna of the west coast of South America is more like that of northern Europe than of the much closer Pacific island groups. These patterns were attributed to earlier migrations rather than modern oceanographic conditions.

6.2.2   Boltovskoy and Wright's provinces

Boltovskoy and Wright (1976) concurred with Cushman's ideas concerning the importance of temperature and migrations in explaining the biogeography of neritic benthic foraminfera. They refined Cushman's map using the data published in many papers during the 1950s to 1970s and recognized 17 provinces, seven characterized by warm-water species, two by cold-water species, and eight by temperate-water species (Fig. 6.2). Boltovskoy and Wright (1976) noted that where enough data were available, division into subprovinces was possible but a subprovincial scheme was given only for South America (subsequently elaborated upon in Boltovskoy *et al.,* 1980).

There is great similarity between Cushman's and Boltovskoy and Wright's provincial schemes. West Indian, Mediterranean, East African, and Indo-Pacific provinces are recognized in both, but Boltovskoy and Wright distinguished Lusitanian and West African faunas from those of the Mediterranean. Similarly, they distinguished Panamanian and West Indian provinces. Cushman and Boltovskoy and Wright also recognized Arctic and Antarctic provinces but the greatest difference between the two schemes is in the temperate regions where Boltovskoy and Wright (1976) recognized eight distinct provinces. The pattern of shading on Cushman's map (Fig. 6.1a) suggests that he considered these temperate regions to be transitional between cold- and warm-water provinces (Cushman, 1948).

6.3   BIOGEOGRAPHY OF NORTH AND CENTRAL AMERICA

6.3.1   Background

Like Cushman (1948), Boltovskoy and Wright (1976) did not indicate in detail the criteria used
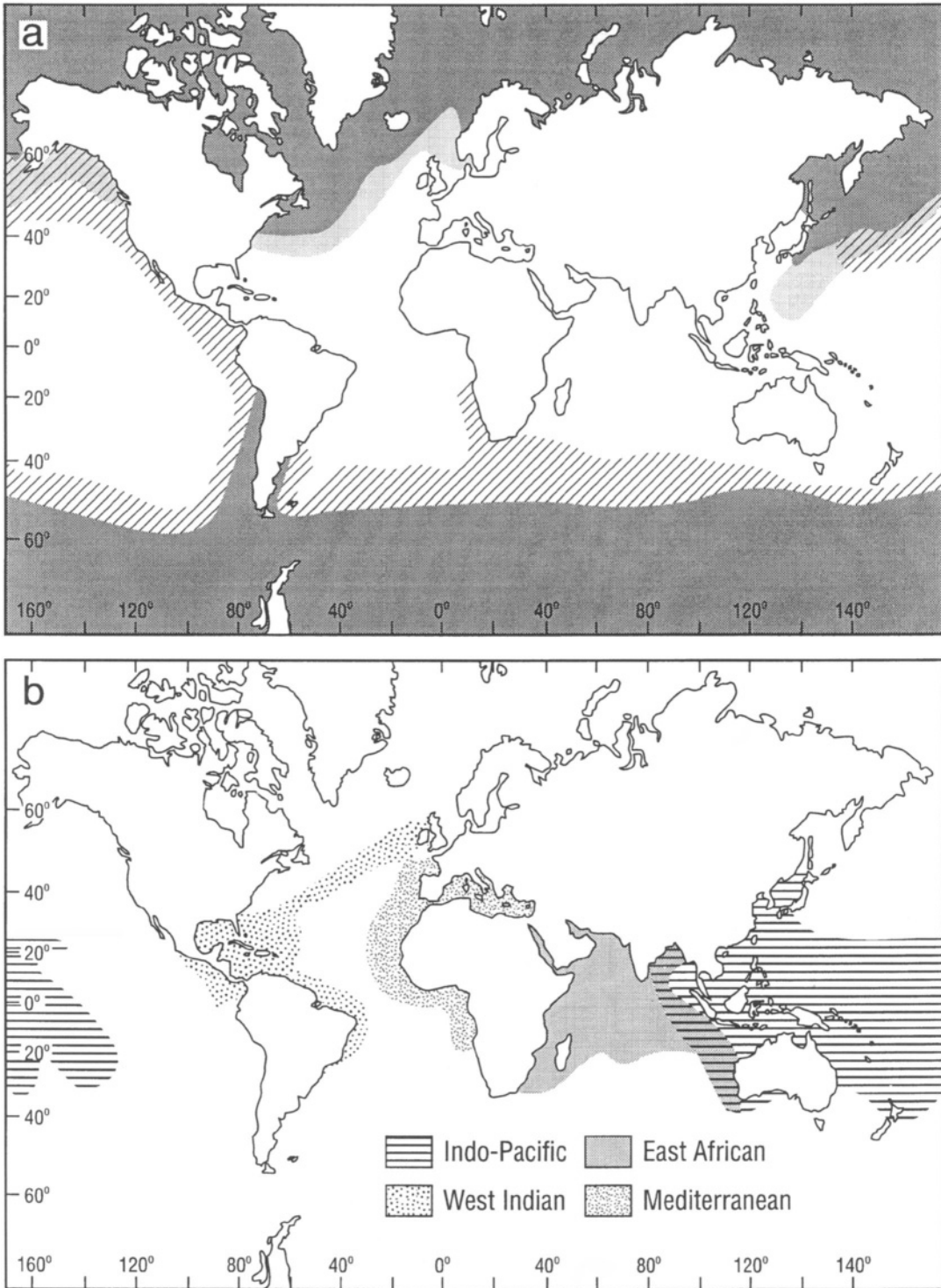
Figure 6.1 Distribution of (a) cold-water and (b) warm-water benthic foraminiferal faunas (after Cushman, 1948).
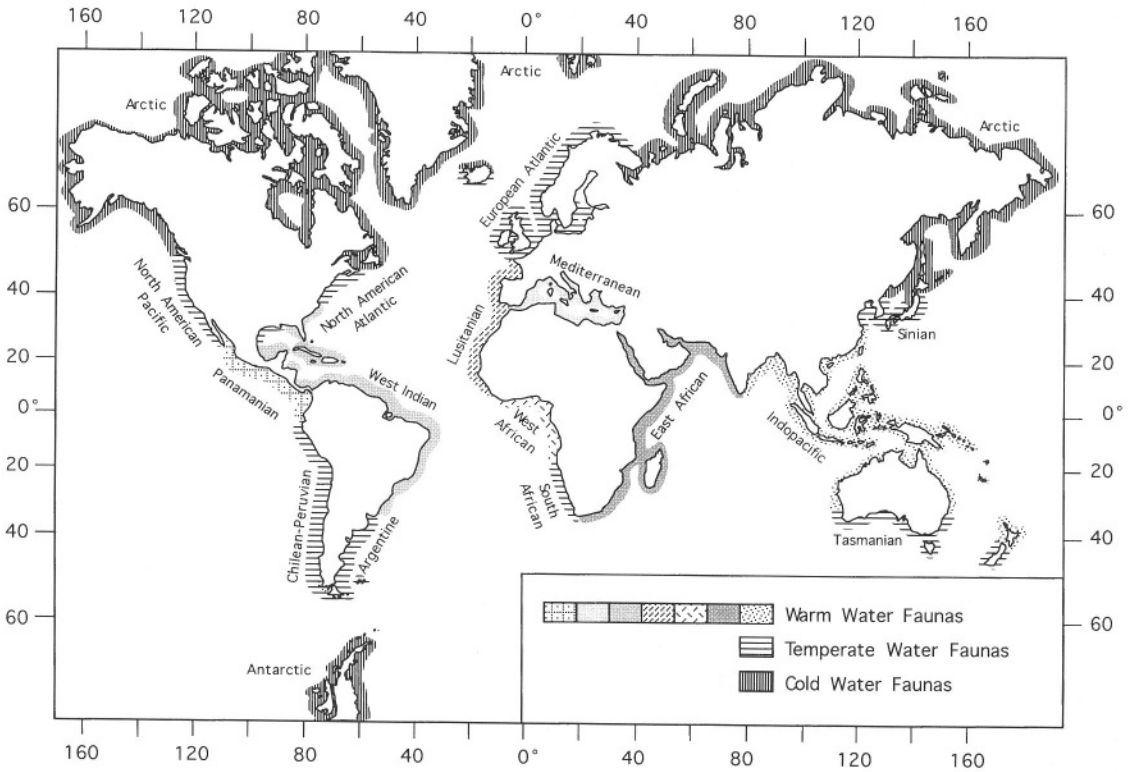
Figure 6.2 Benthic foraminiferal zoogeography of continental shelves (after Boltovskoy and Wright, 1976).

to distinguish provinces and subprovinces or to define the location of provincial and subprovincial boundaries. However, their provincial scheme is very similar to that produced by Hedgpeth (1957b) for macroorganisms of the littoral zones of the world. Boltovskoy and Wright (1976) did not consider this to be surprising, given the fact that similar controlling factors were involved. They did note, however, that differences could be best explained by differences in regional geological history.

Hedgpeth (1957b) was following the lead given by famous predecessors in the field of marine macrofaunal biogeography (e.g. Milne-Edwards, 1838; Dana, 1853; Woodward, 1856; Ekman, 1953). These workers classified the shallow seas of the world into realms and provinces based on the degree of endemism within the species inhabiting a province. But the amount of endemism necessary to recognize a province has varied greatly. Woodward (1856) considered

a province to be characterized by greater than 50% endemic species. Later workers (e.g. Kauffman and Scott, 1976) reduced this figure to 25 to 50% endemism (as low as 20% in practice), while Briggs (1974) considered 10% endemism to be sufficient.

When Culver and Buzas embarked on a project in 1978 to study the biogeography of modern benthic Foraminifera from the continental margins of North and Central America, they chose to identify provinces using the more flexible definition of provinces proposed by Valentine (1968, p. 257) namely, '... collections of communities associated in space and time.' They also chose to recognize provinces using the numerical technique of cluster analysis rather than relying on experience and/or visual examination of distributional data.

The amount of information on the distribution of modern benthic Foraminifera around North America is vast. Several hundred publica-

tions (Culver, 1980) contain relevant material, and the database has continued to grow. The majority of these data were compiled during the 1950s and 1960s in response to the pressure to locate oil and gas. It was realized that a knowledge of the distribution of modern Foraminifera would help interpretation of foraminiferal assemblages recovered from well-cuttings. Studies such as those by Phleger and Parker (1951), Parker (1954), and many others fulfilled this need.

Culver and Buzas constructed databases containing all of the published distributional data for all benthic foraminiferal species names ever recorded from the continental margins of North America. These data were published in volumes for the Atlantic continental margin (Culver and Buzas, 1980), the Gulf of Mexico (Culver and Buzas, 1981a), the Caribbean (Culver and Buzas, 1982a), and the Pacific continental margin from Alaska to Panama (Culver and Buzas, 1985, 1986, 1987). Data were also compiled for the Arctic margin of North America but remain unpublished.

Because the methodologies employed by authors over the years were quite variable (e.g. sampling equipment, sieve size, live or dead, absolute abundances or percent or presence-absence data, etc.), Culver and Buzas' compilations utilized presence-absence data. No information points were deleted. Some geographic locations were represented by only one species whereas others had scores of species. Where small areas had been intensively sampled, the data were combined so that a single locality represented all of those stations.

The problem with compilations is the inconsistency of the incorporated data. Utilizing a presence-absence approach ameliorates this problem but, without doubt, the most significant problem is taxonomic inconsistency. To address this problem, Culver and Buzas conducted an exhaustive process of taxonomic standardization. For example, by using the literature and extensive collections in the Smithsonian Institution, Washington, D.C., The Natural History Museum, London, and several other institutions, the 1303 species names used by authors

for species found on the Atlantic continental margin were reduced to 876. Similar reductions were made on the other continental margins. It is likely that no other foraminiferologist would agree with all of the taxonomic decisions that were made (all taxonomic changes were documented in the publications), but the resulting data set was standardized and, indeed, if errors were included (and they undoubtedly were), the scale of the data set meant that it, and the patterns that were subsequently recognized, were robust.

In addition to distributional data, Culver and Buzas (1980, 1981a, 1982a, 1985, 1986, 1987) provided maps showing the geographic and bathymetric distribution of the most commonly occurring species on the various continental margins. Cluster analysis (more elegant statistical procedures were not appropriate for such a heterogeneous database) resulted in the recognition of several provinces on each continental margin (Buzas and Culver 1980, 1990; Culver and Buzas, 1981b,c, 1982b, 1983).

Shallow-water provinces were similar to those recognized for other organisms, but depth-related provinces were also evident (e.g. Culver and Buzas, 1982b). Indeed, the faunal differences between shallow (<200 m) and deep (>200 m) provinces at the same latitude were greater than between adjacent shallow-water provinces (Culver and Buzas, 1981b, 1982b).

This succession of provinces with increasing depth was most evident on the passive continental margins of the Atlantic and the Gulf of Mexico. A similar pattern was present on the active Pacific margin but was less well developed, probably due to the relative narrowness of the continental margin and the more patchy distribution of data points. Culver and Buzas (1981b, 1983) related the depth-related provincial boundaries to water-mass boundaries and speculated (Buzas and Culver, 1982) that there may be as many provinces in the marine world as there are water masses impinging on the seafloor.

The next section will deal only with provinces on the continental shelves around North and Central America and will compare their config-

urations with those of provinces defined for macrofaunal data (see Sen Gupta 1972, for an earlier comparison).

6.3.2   Neritic provinces

Figure 6.3 diagrammatically indicates the eleven provinces that Culver and Buzas recognized in the shelf waters of North and Central America. Clear boundaries are evident along the generally north-south Pacific and Atlantic margins but the boundaries between the Arctic Province (1) and the Aleutian (2) and Atlantic Northern Inner Shelf Province (10) are not clearly defined. The southern extensions of the Panamanian Province (5) and Caribbean Province (= West Indian Province, 6) are detailed in Boltovskoy and Wright (1976). The entire width of the open continental shelf is the site of a single province around most of the continental margins, but outer shelf or upper slope provinces are present on the broad shelves of the Gulf of Mexico, and on the Atlantic margin north of Cape Hatteras, where slope waters impinge on the outer shelf (Culver and Buzas, 1981b, 1983).

The characteristic faunas of the eleven provinces are given in the various Culver and Buzas papers and, for the Arctic, in Vilks (1989), and need not be repeated here. However, it is interesting to compare the benthic foraminiferal provinces with those recognized for the benthic macrofauna around North and Central America. Valentine (1966) summarized the provincial schemes proposed by various mollusc workers for the Pacific shelf of North and Central America. Despite differences, all workers, including Valentine, recognized important provincial boundaries at the Strait of Juan de Fuca, Point Conception, and Cabo San Lucas (Fig. 6.3). In their study of isopods, Brusca and Wallerstein (1979) noted the same important boundaries, but also recognized a Cortez Province (in the Gulf of California and a Mexican Province from Tangola Tangola to Cabo San Lucas (Fig. 6.3). They also recognized a transitional zone between Cabo San Lucas and Punta Eugenio, a region recognized as the Surian Province by Valentine (1976) in a study of ostracod biogeog-

raphy. Valentine (1976) also recognized Oregonian, Californian, and Panamanian provinces and subprovinces within them. Major changes in foraminiferal faunas also occur at the Strait of Juan de Fuca, Point Conception and Cabo San Lucas (Fig. 6.3), but subprovinces recognized by Valentine (1976) and Brusca and Wallerstein (1979) are not evident in the foraminiferal data (Lankford and Phleger, 1973; Crouch and Poag, 1987; Buzas and Culver, 1990).

The Caribbean and Gulf of Mexico regions have also been subject to various provincial classifications based on macrofaunal data. Hall (1964), working with molluscs, included both areas in a single Caribbean Province, whereas other mollusc workers (Rehder, 1954; Warmke and Abbott, 1961) included the southern tip of Florida and the southern half of the Gulf of Mexico together with the Caribbean region in a Caribbean Province. The benthic Foraminifera of the shallow waters around the Caribbean islands and along the northern coast of south and Central America cannot be subdivided at this scale (Culver and Buzas, 1982a). Together with the carbonate substrate faunas of the Yucatan, southern Florida, and the Bahamas, they constitute a Caribbean Province. This is distinct in foraminiferal composition from the Gulf of Mexico Inner Shelf Province (Culver and Buzas, 1982b; Buzas and Culver, 1982).

Some macrofaunal workers have distinguished northern and southern shelf areas in the Gulf of Mexico and have assigned them to Carolinian and Caribbean provinces, respectively, with a boundary at Cabo Rojo (Fig. 6.3) (Hedgpeth, 1953). Foraminiferal distribution patterns in the Gulf of Mexico are largely concentric (Culver and Buzas, 1981c; Poag, 1981) and the faunas of the Gulf of Mexico Inner Shelf Province are as distinct from faunas south of Cape Hatteras (Fig. 6.3) (the macrofaunal Carolinian Province) as they are from those of the Caribbean Province (Culver and Buzas, 1982b; Buzas and Culver 1982).

The foraminiferal data agree with those for macrofauna in placing the carbonate substrate southern tip of Florida, between Cape Romano
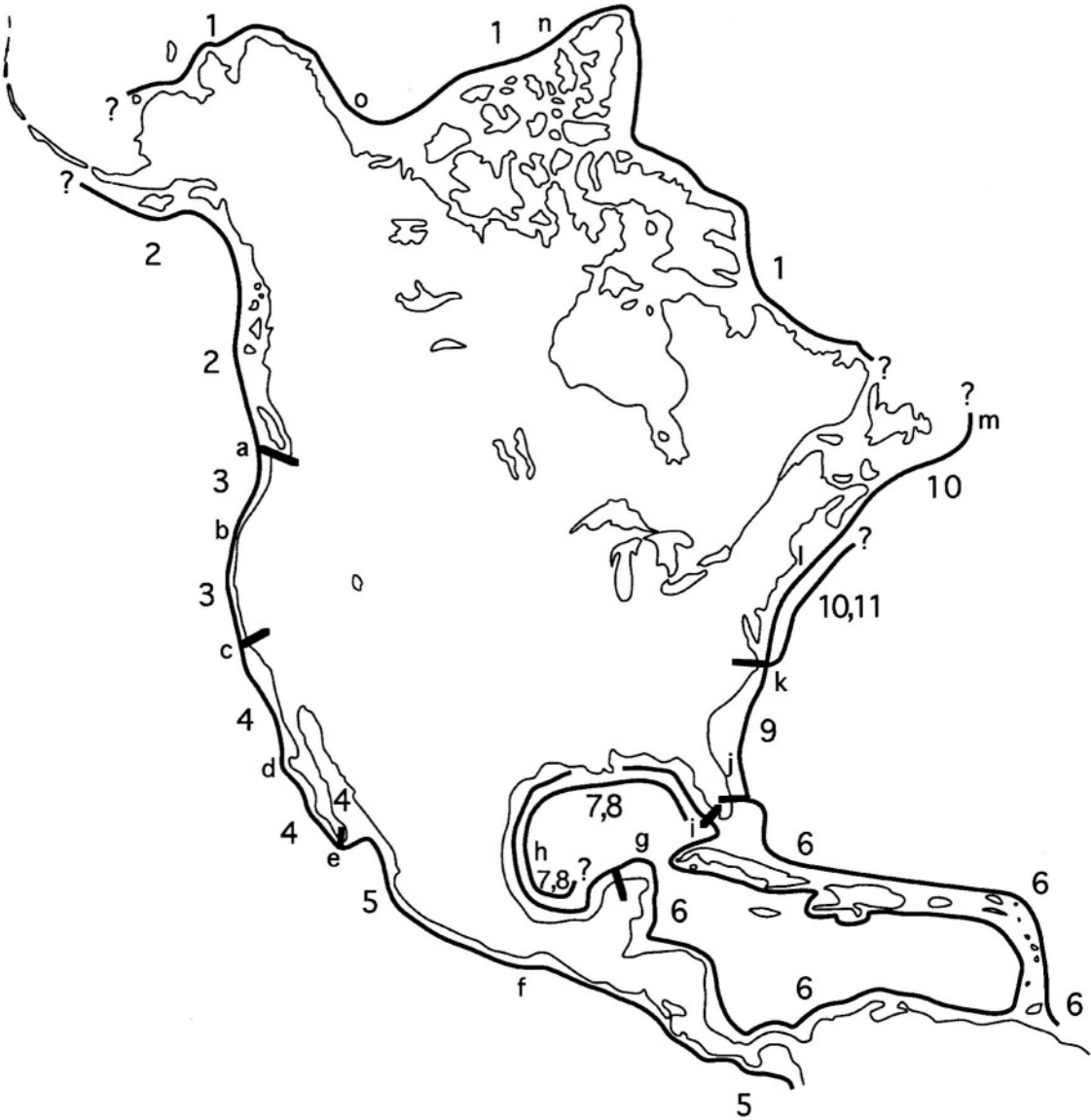
Figure 6.3 Benthic foraminiferal shelf provinces around North and Central America 1, Arctic Province; 2, Aleutian Province; 3, Oregonian Province; 4, Californian Province; 5, Panamanian Province; 6, Caribbean Province; 7, Gulf of Mexico Inner Shelf Province; 8, Gulf of Mexico Outer Shelf and Slope Province; 9, Atlantic Southern Shelf Province; 10, Atlantic Northern Inner Shelf Province; 11, Atlantic Northern Outer Shelf and Slope Province. Geographic locations: a, Strait of Juan de Fuca; b, Cape Mendocino; c, Point Conception; d, Punta Eugenio; e, Cabo San Lucas; f, Tangola Tangola (Puerta Angel); g, Yucatan; h, Cabo Rojo; i, Cape Romano; j, Cape Canaveral; k, Cape Hatteras; l, Cape Cod; m, Grand Banks; n, Axel Heiberg shelf; o, Beaufort Sea

and south of Cape Canaveral (Fig. 6.3), in a Caribbean Province. Between Cape Canaveral and Cape Hatteras, the distinctive foraminiferal assemblage comprises the Atlantic Southern Shelf Province (Fig. 6.3), equivalent to the Atlantic portion of the macrofaunal Carolinian Province (Hedgpeth, 1953). The shelf macrofaunas north of Cape Hatteras have been subdi-

vided into Virginian and Acadian (= Nova Scotian) Provinces with the boundary at Cape Cod (e.g. Dana, 1953; Hall, 1964; Maturo, 1968). Several foraminiferal workers followed this scheme (e.g. Cushman, 1948; Parker, 1948; Murray, 1973), but Culver and Buzas (1981b) did not make this distinction and recognized a single Atlantic Northern Inner Shelf Province stretching from Cape Hatteras to the Grand Banks off Newfoundland (Fig. 6.3). Several mollusc workers concur with this provincial classification (Coomans, 1962; Franz and Merrill, 1980).

The neritic environments of the Canadian Arctic Archipelago and northern Alaska are placed within the Arctic Province (Fig. 6.3). In review papers, Lagoe (1979) and Vilks (1989) noted that the foraminiferal faunas from water depths of less than 200 m were generally dominated by agglutinated Foraminifera, thus distinguishing them from faunas of the Aleutian Province and the Atlantic Northern Shelf Province. This pattern is not ubiquitous, however, and some regions, e.g. the Beaufort shelf (Fig. 6.3; Vilks, 1989) and the Axel Heiberg shelf (Schröder-Adams *et al.*, 1990) are dominated by calcareous species, and may exhibit quite high diversity.

At the beginning of this chapter, we described Cushman's (1948) and Boltovskoy and Wright's (1976) global provincial schemes for shelf Foraminifera which indicated temperature as the major controlling factor for species distributions, an opinion shared by Hedgpeth (1957b) and Murray (I991b). While acknowledging the important role of temperature as an environmental variable, it is worth noting that many provincial boundaries are located at headlands (Fig. 6.3) associated with oceanographic boundaries. Thus, many workers have related the large-scale distribution of shelf Foraminifera to water-mass distributions (e.g. Lankford and Phleger, 1973; Buzas and Culver, 1980, 1990; Culver and Buzas, 1981c; Crouch and Poag, 1987).

Figure 6.4 illustrates the relationship between water masses and benthic foraminferal provinces from shelf to abyssal depths in the Gulf of Mexico and on the Atlantic continental margin. The Gulf of Mexico Inner Shelf Province (Fig. 6.4) is associated with the surface mixed layer whose transitional boundary with the underlying Subtropical Underwater lies at 100 to 200 m, the depth limit of seasonal effects on water-mass characteristics (Phleger and Parker, 1954; Nowlin and Parker, 1974). The Gulf of Mexico Outer Shelf and Slope Province is related to several layered water masses (Fig. 6.4). Where these impinge upon the outer shelf and upper slope, changes in foraminiferal assemblages occur (Culver, 1988), but these are considered to represent biofacies variations within a province (Culver and Buzas, 1983).

On the Atlantic continental margin, the Atlantic Southern Shelf Province is related to Southern Shelf Water (Fig. 6.4). North of Cape Hatteras, the shelf is overlain by the much cooler Northern Shelf Water, and this is reflected in the significant change to the neritic foraminiferal assemblages of the Atlantic Northern Inner Shelf Province. Slope water overlies the slope but impinges on the outer shelf, and this overlies the Atlantic Northern Outer Shelf and Slope Province (Culver and Buzas, 1981b).

6.4   CENTERS OF ORIGIN AND DISPERSAL OF BENTHIC FORAMINIFERA

The concept of centers of origin for species has been extensively discussed in the literature of biogeography and evolution (e.g. McCoy and Heck, 1983). Although the Arctic (Hickey *et al.,* 1983) and the Antarctic (Zinsmeister and Feldmann, 1984) have been proposed as possible centers of origin, the tropics usually have this characteristic attributed to them (e.g. Durazzi and Stehli, 1972; Briggs, 1974; Pielou, 1979), with newly evolved species dispersing to the higher latitudes. Thus, on the Atlantic continental margin of North America one could hypothesise enhanced origination of benthic foraminiferal species in the Caribbean Province. Buzas and Culver (1986; 1989) examined this hypothesis by documenting the worldwide dis-

(a) Atlantic continental margin north of Cape Hatteras

NE   SW

CW

NSHW   GS   SAW

AT Northern
Coastal   AT   Northern   SW
Province   Inner   Shelf   GS
                      Province   WBUC

                                                                ⎰ ABW ⎱
                                                                ⎱ AABB ⎰

                            AT   Northern
                            Outer   Shelf   AT Northern   – –
                            and   Slope   Slope and Rise
                            Province   Province

(b) Atlantic continental margin south of Cape Hatteras

NE   SW

SSHW

                                              FC   AC
AT
Southern
Shelf   WBUC
Province
                      AT Southern Slope
                      Province   – – – ?

(c) Northern Gulf of Mexico continental margin

N   S

SML

GOM   STU
Coastal   GOM   Inner   OMW
Province   Shelf   AAIW
              Province   NADW
                                                         GBW

                  GOM   Outer
                  Shelf   and
                  Slope
                  Province   GOM Slope and Abyssal   – –
                                        Plain   Province

Figure 6.4 Profiles across continental margins of eastern North America, (a) northern Atlantic, (b) southern Atlantic, and (c) the northern Gulf of Mexico, showing the relationship between water masses and benthic foraminiferal provinces (not to scale); provinces in bold discussed in text. Water masses and currents: (a) CW, Coastal Water; NSHW, Northern Shelf water; SW, Slope Water; GS, Gulf Stream; SAW, Sargasso Water; ABW, Arctic Bottom Water; AABB, Antarctic Bottom Water; GOM, Gulf of Mexico; AT, Atlantic; (b) SSHW, Southern Shelf Water; FC, Florida Current; AC, Antilles Current; WBUC, Western Boundary Undercurrent; (c) SML, Surface Mixed Layer; STU, Subtropical Underwater; OMW, Oxygen Minimum Water; AIW, Antarctic Intermediate Water; NADW, North American Deep Water; GBW, Gulf Basin Water.

tribution of first reliable stratigraphic occurrences of all modern species recorded on the North American Atlantic continental margin. They found that modern species of benthic Foraminifera have originated in all parts of the world's oceans from the Cretaceous to the Pleistocene (Buzas and Culver, 1989). Possible concentrations of first occurrences in the Miocene of the Caribbean region were considered to be monographic effects. The Pleistocene was characterized by many more high-latitude occurrences but this, again, was considered to be due to one significant paper. Further, the apparent trend of more high latitude originations as climatic cooling occurred during the Neogene was believed to be the result of the distribution of outcrops of that age. Buzas and Culver (1989) concluded that the available data do not support a simple concept of a center of origin for modern benthic foraminiferal species from the North American Atlantic continental margin.

The data used to investigate centers of origin showed that first occurrences were often recorded in more than one place. This could be explained by poor stratigraphic control, but in the Pleistocene, where greater resolution is possible, several species were first recorded in Alaska and Maine in deposits of the same age. Buzas and Culver (1989) considered this to be the result of rapid dispersal, instantaneous in terms of our powers of resolution. Thus, this dispersal ability means that vicariance events, although important in some instances, such as the formation of the Isthmus of Panama, are probably factors of little importance to benthic foraminiferal biogeography.

The dispersal ability of continental margin benthic Foraminifera was further investigated by Buzas and Culver (1991). They showed that 53 of 878 species that currently occur on the North American Atlantic continental margin are ubiquitous around North and Central America even though they have no fossil record. Most of these are abundant and would have been found in the well-documented Cenozoic deposits around the North American margins if they had existed in the past. Buzas and Culver (1991) concluded that these taxa must have evolved recently and dispersed rapidly.

6.5   SUMMARY

Large-scale biogeographic distributions of benthic Foraminifera of the world's shelves exhibit a pattern that indicates a major controlling role for temperature at this scale. Cold-, temperate-, and warm-water groupings of provinces have been recognized around the world, with a greater number of provinces delineated in warmer regions. Modern provincial patterns, however, have also been influenced by differences in regional geological histories.

The continental margins of North and Central America have been subject to the most intensive biogeographic investigations, and eleven benthic foraminiferal provinces have been recognized in the neritic zone. Their distribution and boundaries can be closely related to the distribution and boundaries of major water masses. Thus, the provincial scheme for modern benthic Foraminifera is similar to that for modern shallow marine macroorganisms. The differences suggest that benthic Foraminifera may be somewhat less sensitive to the changes in the marine climate than other benthic organisms of the neritic zone.

No center or centers of origin can be identified for the modern benthic Foraminifera of the North American Atlantic continental margin. First stratigraphic occurrences are both temporally and geographically widespread, and suggest rapid dispersal.

6.6   ACKNOWLEDGMENTS

7

Biogeography of
planktonic Foraminifera

Anthony J. Arnold and William C. Parker

7.1 INTRODUCTION

7.1.1 A historical perspective

It is often said that nothing makes sense in biology
except in the light of evolution (Dobzhansky,
1973). It could equally well be said that little
makes sense in biogeography except in the context
of its historical development, since modern bioge-
ography reflects both organismal habitat prefer-
ences and the historical processes that have
culminated in modern distribution patterns.

Research on most modern plankton groups
has resulted in broad agreement among many
plankton biogeographers as to the disposition
of large scale provinces (e.g. Backus 1986;
McGowan, 1986). The frontal systems that
sometimes separate these provinces often show
steep environmental gradients that can corre-
spond to faunal transitions. However, even these
most conspicuous biogeographic provinces do
not always show a clearly-defined relationship
to physicochemical variables, and the search for
the factor(s) that explain the distribution of a
species or a group of species is rarely successful
(Backus, 1986). Such difficulties of finding con-
nections are usually attributed to the complexity

of interaction between controlling factors, but
historical considerations can also play a signifi-
cant role. Work on the planktonic Foraminifera
has made it increasingly clear that large scale
biogeographic features such as the global diver-
sity gradient and the latitudinally arrayed major
provinces owe their existence at least partly to
differential rates of speciation and extinction –
processes that are inherently historical in the
sense that they involve adaptation to antecedent
rather than present-day conditions. It is in pre-
cisely this sense that modern biogeography
cannot be separated from its evolutionary past.

Nonetheless, with rare exceptions, research on
plankton biogeography has focused primarily
on the relationship between species distribution
patterns and the physicochemical environment
they inhabit. Usually, delineating a modern
biogeographic province involves quantifying
species distributions along plankton tow tran-
sects, then using physicochemical properties of
the environment to extrapolate over larger
areas. However, when readily fossilized organ-
isms such as the planktonic Foraminifera are
involved, their stratigraphic record adds both
historical dimension and complexity to the
analysis; as a consequence, it becomes even more

essential to develop an understanding of the issue of scale – both spatial and temporal.

For example, it is often smaller-scale factors that mediate the evolutionary origins of species, even though larger-scale considerations may constrain their distribution. To the extent that allopatry and peripheral isolation play a role in the origin of planktonic species, the present-day provincial-scale geographic range of a given species is likely to be much larger than its range at its time of origin – and yet the adaptive circumstances of that species' time and place of origin may well dictate (and explain) its present distribution. Further, if the conditions for speciation arise only rarely – say, on a geological (rather than ecological) time scale – then the full diversity potential of a given province may not yet have been reached, and the question of equilibration time arises. For reasons like these, temporal and spatial scale are central issues and fundamental organizing principles in this chapter.

Before beginning any discussion of biogeography, it is important to be aware of the taphonomic and methodological factors that can influence basic data.

7.1.2   Taphonomy and methodology

7.1.2.1

Our perceptions of foraminiferal distribution and diversity are necessarily dependent on taxonomic philosophy, which can vary considerably. There are currently approximately forty-four recognized species of Recent planktonic Foraminifera, of which twenty-one are common in the world's oceans (Hemleben *et al.,* 1989), although some specialists recognize up to sixty-four for the total number (e.g. Saito *et al.,* 1981). Data on the patterns of distribution of living planktonic Foraminifera come from three main sources: plankton tows, sediment traps, and sediment-surface samples. Data derived from plankton tows are vulnerable to methodological difficulties relating to the mesh size used in plankton nets. Berger (1969) showed that there is an inverse relationship between the cube of the mesh size and the number of planktonic

Foraminifera trapped in the mesh, and provided a methodology for correcting samples to a nominal mesh size. The fact that reported abundances can vary by eight orders of magnitude, depending largely on the sampling gear used, indicates that care must be taken when making biogeographic abundance comparisons between plankton tow studies. In addition to absolute abundances, relative abundances and seasonal abundance variability also show a strong size dependency in plankton tows, which is reflected in diversity indices, multivariate statistical treatments, and even presence absence data (Ottens, 1991).

In general, the cold water aspect of a living fauna tends to be enhanced in the underlying sediments for two reasons. The first is an artifact of the dissimilar mesh sizes used in plankton tows versus the smaller size ranges commonly) included when examining coretop samples, since the smaller size fractions tend to have a cooler aspect (Berger, 1971). The second reason stems from differential dissolution susceptibilities between species and the resulting biases thereby introduced into our perceptions of fossil biogeography (useful summaries can be found in Rudimann, 1977, and Vincent and Berger, 1981). Many tropical species (as well as those that are enriched in the sediments due to spring upwelling) are relatively susceptible to dissolution; the differential removal of these species increases the cold water aspect of sediment-surface assemblages (Rudimann, 1977). The effects of differential dissolution are further complicated by variations in bottom topography in relation to the position of the lysocline.

Vertical mixing, current winnowing and sorting, and displacement by turbidites, among other taphonomic effects, can introduce additional bias into the biogeographic record; these are discussed in more detail by Bé (1977). Rudimann (1977), Orr and Jenkins (1977) and in chapter 16 of this book.

The relationship between abundance in the sediments and standing abundance in the water column is distorted significantly by a number of factors, not all of them taphonomic. Species with shorter generation times have proportionally

greater representation in underlying sediments (Berger and Soutar, 1967; Berger, 1970a, Berger, 1971). Current transport can displace living adult individuals outside the limits of their normal reproductive range (McGowran *et al.,* 1997).

7.1.2.2 Transfer functions

One of the most powerful tools used in the investigation of biogeographic and paleobiogeographic patterns is the transfer function. These functions relate species abundances to their life habitats (usually abundances in sediments are related to habitat conditions in the overlying waters), and the functions are normally applied to the problem of estimating environmental characteristics from species abundance data. Subject to several assumptions, any environmental parameter, say, temperature, can be predicted. Perhaps the simplest and most direct predictive equation was proposed by Berger (1969):

$$T_{est} = \frac{\sum P_i t_i}{\sum P_i}$$

where t_i, the optimum temperature preference of the ith species, is weighted by the species' proportional representation, P_i, yielding an average optimum temperature for the assemblage. This equation has been further refined (see Berger and Gardner, 1975; Vincent and Berger, 1981), but even in its simplest form it can yield surprisingly accurate results when used to predict average sea surface temperatures. However, this approach alone cannot account for complex interaction between temperature and other parameters that influence distribution, and requires an *a priori* understanding of the optimum temperature preferences of species.

A more widely used transfer function is based on empirically derived relationships between a spectrum of environmental parameters and species abundance data: it takes the form:

$$P_{est} = k_0 + k_1 A + k_2 B + k_3 C + k_4 D + \dots$$

where the k's are predictive coefficients (usually regression coefficients), P is an environmental parameter, say, temperature, and $A, B, C,$ etc. are variables, which may be actual species proportions, synthetic variables consisting of grouped proportions (e.g. characteristic polar, tropical, etc. species), or variables derived from multivariate analysis of species proportions. In this case, knowledge of the optimum environmental conditions for the species is replaced by a relationship usually derived from statistical regression.

Imbrie and Kipp's (1971) classic work on Caribbean temperature fluctuation, for example, used factor analysis to extract synthetic variables consisting of tropical, subtropical, subpolar, and 'gyre margin' assemblages, which show a partial correspondence to the large-scale latitudinal provinces discussed below. It is possible to apply these synthetic variables to the derivation of any environmental variable associated with the samples; they can also be used to estimate past environmental conditions (Imbrie and Kipp, 1971; CLIMAP 1976, 1981; Thunell *et al.,* 1994, among others). Useful reviews of the technique can be found in Hutson (1977), Sachs *et al.* (1977), and Vincent and Berger (1981).

Although the use of transfer functions has yielded excellent results, the technique must be used with caution. The predictive value of transfer functions based on recent sediment surface samples in a particular area is high when applied to recent environments in the same region, but complications arise when the function is applied to spatially or temporally distant samples. Relevant considerations include the following:

(1) The environmental preferences of extant species may not be the same wherever and whenever they occur. For example, some bipolar species can show different environmental preferences in different hemispheres. This could be because different limiting factors may act to control abundance in different settings. Additionally, species habitat preferences may have evolved through time, thereby diminishing the predictive power of transfer functions used to calculate past conditions based on present-day distributions.

(2) Present-day distributions may not have equilibrated. If they are still in a state of recovery

from recent environmental changes (e.g. a recent glacial phase or other shorter-term climatic pulse), then modern foraminiferal distributions (and their derived transfer functions) may not fully reflect either their historical habitat preferences, or their modern preferences. For example, the limiting factor in recovery time may be the presence of geographic barriers to repopulation rather than the ecological responsiveness of the species. Thus, continental positions (see below) can exclude species from occupying areas to which they would otherwise be adapted.

(3) Since these functions tend to be based on sea surface measurements and sediment samples recovered from depth, factors like changing seasonality and vertical depth distributions are not taken into account.

(4) Taphonomic effects such as preferential dissolution, winnowing, and diagenesis must be assumed to be negligible. To whatever extent these effects show temporal and spatial variation, it is not accounted for in transfer functions based on the distribution of modern faunas in surficial sediments (Vincent and Berger, 1981).

(5) In principle, there is nothing in the transfer methodology that prevents the prediction of an unlimited number of environmental variables from a limited amount of paleontological information ('transfer dilemma' of Vincent and Berger, 1981). This is partly due to covariation between environmental variables. Transfer function predictions may not be based on direct causal relationship between species distributions and the environmental variable being predicted. If the causal relationship is secondary or indirect, then that indirect linkage may change geographically or temporally even when the species' actual habitat preference is unchanged. This dilemma is a direct result of the methodology and is ultimately a reflection of the fact that correlation does not demonstrate causality.

(6) There may be some ancient environments for which there are no modern analogs, and which are therefore not predicted by transfer functions based on modern faunas ('transfer paradox' of Vincent and Berger, 1981). In particular, it is not valid to extrapolate beyond the limits of the parameters used to initially establish the transfer function.

(7) The modern species upon which the transfer function is based may not have sufficient historical range to allow application of the function to older samples, particularly samples that predate the first appearance of the most recently-evolved modern species that contribute to the transfer function.

Despite these problems, transfer functions remain a valuable tool in environmental reconstruction. However, it should not be forgotten that they are formulated to predict environmental characteristics from biogeographic distribution patterns rather than to address the reverse problem of explaining biogeographic distributions in terms of environmental parameters.

7.2   ECOLOGICAL FACTORS CONTROLLING THE DISTRIBUTION OF PLANKTONIC FORAMINIFERA

7.2.1

The tolerance limits of most species are not sharply defined. Instead, departure from optimal conditions causes a gradational reduction of organismal functionality, resulting in inhibition of reproduction, nutrient uptake, and growth, eventually leading to death. These effects can be both interdependent and nonlinear; for example, an organism may require optimal temperatures in order to tolerate extremes of hypersalinity (Odum, 1971; Hedgpeth, 1957a). For a general discussion of models dealing with the coupling between plankton and their physical environment, see Eckman (1994) and references therein. For specific correlations of modern species abundances with CLIMAP data on specific environmental factors, see Hilbrecht (1996).

7.2.2   Temperature

7.2.2.1   Direct control

As a result of the general observation that the most conspicuous planktonic foraminiferal distribution patterns are latitudinal, more research effort has focused on the influence of temperature than on any other single variable.

Some of the most convincing evidence for direct control of temperature over distribution comes from the experimental work of Bijma *et al.* (1990). Their results showed a correspondence between *in vitro* temperature tolerance limits and the known natural limits of their experimental species. Vital functions like food acceptance, growth, and reproduction were inhibited when natural temperature limits were exceeded, providing compelling evidence that temperature may be an important factor in controlling individual species distributions.

7.2.2.2   Temperature and the biogeography of coiling directions

Some species show a change in the dominance of coiling direction that appears to be temperature-dependent, although there is no known kinetic reason that one handedness should be preferred over another. Work on coiling direction has touched on such interrelated topics as stratigraphic applications (Cosijn, 1938; Vasicec, 1953; Nagappa, 1957; Bandy 1960), biogeography (Gandolfi, 1942; Ericson *et al.,* 1954; Bandy, 1959, 1960; Ericson, 1959), correlation (Ericson and Wollin, 1968; Robinson, 1969; Olsson, 1970; Hofker, 1972), evolution (Bolli, 1950, 1951, 1971), ecology and paleoecology (Vasicec, 1953; Ericson, 1959; Bandy, 1959, 1960; Loeblich and Tappan, 1964a; Bé, 1977; Boltovskoy, 1966b, 1969), and life history (Vella, 1974; Lipps, 1976, 1979) without explaining the nature of the relationship between temperature and coiling direction. The history of this literature is summarized in Bolli (1950, 1951), Loeblich and Tappan (1964a), Thiede (1971), Malmgren (1974), Kennett (1976), Boltovskoy and Wright (1976), Srinivasan and Azmi (1978), Lipps (1979), Vincent and Berger (1981), and Hemleben *et al.* (1989).

Recent work by Lohmann and Schweitzer (1990) provided concrete evidence that Lipps' (1976, 1979) focus on reproductive strategy might be appropriate, at least in the case of *Globorotalia truncatulinoides*. They discussed handedness-correlated variation with two factors in *G. truncatulinoides*: (1) the timing of descent from surface waters, and (2) the conse-

quent depth (especially in relation to the thermocline) at the time of gametogenetic calcification and reproduction. Specifically, a shallow thermocline seems to have a negative effect on the reproductive success of *G. truncatulinoides,* possibly due to interference from a correlated hydrographic gradient such as the pycnocline. Since sinistral individuals descend from the surface waters earlier in their life cycle, they are likely to descend to greater depths and, if the thermocline is too shallow, may find themselves below the depth at which seasonal overturn will return juveniles to the surface for another reproductive cycle. This selects against sinistral individuals, leaving an increase in the relative frequency of dextral individuals. Lohmann and Schweitzer point out that this is not a full explanation of the relationship between temperature and handedness, since the effect shows size-dependence even within samples (Thiede, 1971). Schweitzer and Lohmann (1991) showed a similar relationship between reproductive success and the depth of the pycnocline in menardiiform globorotaliids.

Lohmann (1992) suggested that the apparent biogeographic relationship between coiling direction and sea surface temperature may be an indirect result of the fact that the deepest mixing generally happens in late winter in most parts of the ocean, and is intensified at higher latitudes where temperatures are lower. He supports this hypothesis with the observation that handedness dependency persists in the Mediterranean where temperature and deep mixing are decoupled.

7.2.2.3   Temperature and the biogeography of pore size

Bé (1968) reported that porosity was highest in tropical and surface-dwelling species (Fig. 7.1). Scott (1972) suggests that this might imply a hydromechanical function for pores, since the reduced density and increased buoyancy that accompany increased porosity would retard settling rates in high-temperature low-density habitats; this inference is supported by experimental results of Bijma *et al.* (1990); also see
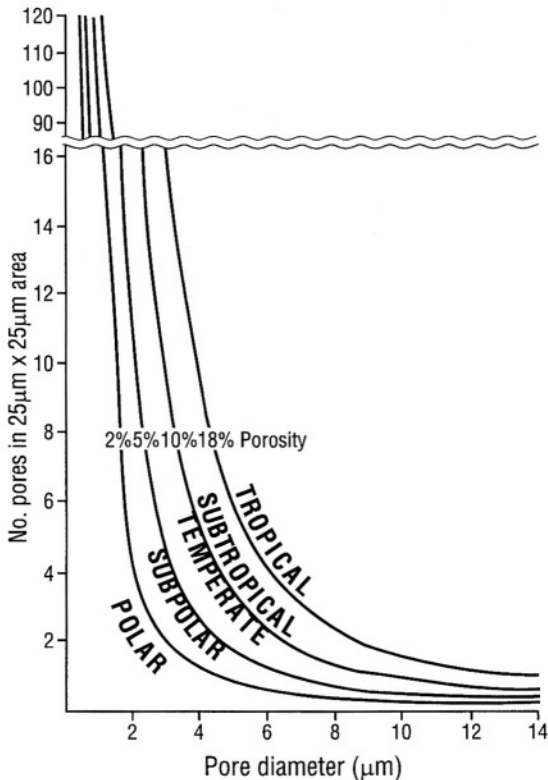
Figure 7.1 Pore concentration plotted against pore diameter for 22 living planktonic taxa. Horizontal lines indicate ranges of pore diameters (from Scott, 1972, after Bé, 1968).

7.2.3 Salinity

Planktonic Foraminifera are intolerant of brackish water. The lowest salinity in which living specimens have been captured is about 30‰ (Boltovskoy, 1976). The species most tolerant of hyposaline conditions in nature are reported to be *Globigerina bulloides, G. quinqueloba, Globaigerinita uvula, Globigerinoides ruber, Neogloboquadrina pachyderma* (f. *superficiaria*), and *Orbulina universal* these species have been recovered from waters having salinities of 30.5 to 31‰ (Bé and Tolderlund, 1971). *Neogloboquadrina dutertrei* is also associated with relatively low salinities, and shows abundance peaks during late Cenozoic episodes of Mediterranean sapropel deposition, which were probably caused by stagnation-induced glacial meltwater spillover from the Black Sea (Thunell *et al.*, 1977). Bijma *et al.* (1990) studied salinity tolerances of some planktonic species in laboratory culture and found that the *in vitro* salinity tolerance limits are greater than those found in nature, with *Globigerinoides ruber* showing the greatest tolerance range (22 to 49‰). They concluded that natural salinity variation in the open ocean is unlikely to exert significant control over the distribution of modern planktonic Koraminifera.

Kennett (1976) for additional discussion. Furbish and Arnold (1997) have investigated the functional morphology of hydrodynamical properties in spinose planktonic Foraminifera with specific attention to the determinants of settling velocity. Since there is a constructional constraint relating pore size and spacing to spine number, it follows that these characters may have a functional or constructional interrelationship. This possibility has not been investigated.

It is clear that temperature is not the only factor controlling species distributions. For example, even though temperatures in the deep sea are uniformly low, deep sea benthic taxonomic diversity is comparable to diversity levels on tropical shelves. Other factors must be considered.

7.2.4 Nutrients and geographic variation in abundance

In general, foraminiferal abundance patterns are similar to those of other groups that are believed to reflect primary productivity (Bé and Tolderlund, 1971; McGowan, 1971). Productivity is largely determined by photic levels and nutrient salts, especially phosphate, available to phytoplankton (Parker, 1960; Ryther, 1963; Berger, 1969). Although most research on planktonic foraminiferal abundance has shown correlations with phytoplankton productivity and nutrient levels (e.g. Hemleben *et al.*, 1989; Fairbanks and Wiebe, 1980; Ravelo and Fairbanks, 1995), there is evidence that the relationship may not be a simple one. For example, Oberhänsli *et al.* (1990) have shown that standing stocks can be highest where primary production is intermedi-

ate, suggesting the correlation may be nonlinear. Additionally, small-mesh tows correlate with phosphate levels while larger-mesh tows do not (Berger, 1969).

Quantitative comparisons of absolute abundances between studies are often problematic due to the variation introduced by sampling gear (see section 7.1.2.1). For these reasons, it is best to discuss abundances in relative terms. Abundances tend to be relatively lower in oligotrophic high-salinity central basin waters with weak circulation, such as are found in the North and South Atlantic and Indian Oceans; higher abundances tend, in general, to be found in major current gyres, equatorial and West Wind Drift, currents, upwellings, and frontal systems. Numerically, planktonic Foraminifera can range from 1.3 to 9.9% of the total zooplankton, ranking sixth in winter (after copepods, chaetognaths, tunicates, krill, and siphonophores, respectively) and third in summer, and sometimes achieving local dominance even over copepods. However, their small body size means the foraminiferal biomass contribution is less significant than their numerical abundance (Boltovskoy and Wright, 1976).

Some of the highest concentrations of Foraminifera are found in the North Pacific, north of the central water mass (Bradshaw, 1959; Berger, 1969; Bé and Tolderlund, 1971; Spindler and Dickmann, 1986), where plankton abundances are three orders of magnitude greater than those in the Sargasso Sea. Indo-Pacific abundances are a factor of two greater than those of the Atlantic ocean, although the relative pattern of accumulation rates are reversed, so that there appears to be a negative correlation between standing stock and shell deposition rates (Berger, 1969). Berger also noted that concentration maxima for small-mesh tows are found in high latitudes, while large-mesh tows show their concentration maxima at low latitudes, and suggested that this may be due to accelerated reproductive rates in areas of high productivity, which results in steeper size-frequency distributions. Regardless of the steepness of the size-frequency distribution, its exponential nature implies that there are many more juve-

niles than adults, and is consistent with the general expectation of high juvenile mortality and concave-upward survivorship curves.

The highest measured oceanic abundances (greater than 10^4 specimens per 1000 m³) occur in major current systems, boundary currents, divergences, and upwellings. Depauperate standing stocks (less than 10^3 specimens per 1000 m³) are found in central waters of oceanic basins and over continental shelves (Bé, 1977), although slope waters have been reported with 10^4–10^5 specimens per 1000 m³ (Cifelli and Smith, 1969). Some of the highest abundances reported $(4.7 \times 10^8$ per 1000 m³) have been of small, juvenile *Neogloboquadrina pachyderma,* probably living, recovered from melted Antarctic annual sea ice (Lipps and Krebs, 1974; Lipps, 1979; Spindler and Dickmann. 1986). and by Berger (1969) who reported abundances as high as 10^8 per 1000 m³ for small-mesh tows, although these abundances should not be compared due to differences in sampling technique discussed by Berger (1969). Berger (*op. cit.*), and Boltovskoy and Wright (1976) provide useful discussions of abundance variation.

7.2.5 Water depth and biogeography

Although there is considerable literature on the depth distribution of planktonic Foraminifera, the following discussion focuses on those aspects of depth distribution that influence biogeography of the group. Living planktonic Foraminifera have their maximum abundance in euphotic near-surface waters between 10 and 50 meters (Fig. 7.2), below which depth they show an approximately) exponential decline in abundance (Be, 1977). This pattern correlates with the abundance of nutrients, prey, and (for those with photosymbionts, e.g. *Globigerinoides sacculifer*) sunlight (Bijma and Hemleben, 1994). The depth habitats of individual species can seldom be defined within narrow limits because they show diurnal, ontogenetic, seasonal, and long-term variation that is beyond the scope of most studies to fully document. Bé (1977) considered three broad groups on the basis of their depth distribution. The first consists of shallow-water

FORAMINIFERA 125μ(f/m)
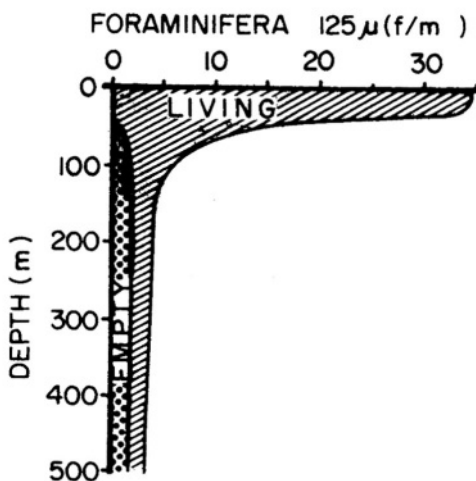
Figure 7.2 Abundance profile of planktonic Foraminifera in the Santa Barbara Basin, August, 1966 (after Berger, 1971).

species, primarily spinose forms including all species of *Globigerinoides* and several of *Globigerina.* These species tend to be thinner-walled and smaller than deeper-dwelling forms. Bé's intermediate water depth assemblage, whose species live predominantly in the 50 to 100 meter depth range, consists of both spinose (*Globigerina bulloides, Hastigerina pelagica, Orbulina universa, Globigerinella aequilateralis,* and *Globigerina calida*) and non-spinose forms (*Pulleniatina obliquiloculata, Neogloboquadrina dutertrei, Candeina nitida,* and *Globigerinita glutinata.*) Bé's deep water assemblage includes the spinose *Hastigerinella digitata,* which possibly is unique in that it may spend its entire life cycle below 1000 m. The remaining 12 species in Bé's deep water assemblage all live in the euphotic zone as juveniles but are found mainly below 100 meters as adults. These include two additional spinose forms, *Globigerinella adamsi* and *Sphaeroidinella dehiscens,* the non-spinose *Neogloboquadrina pachyderma* and *G. conglomerata* and all the species of *Globorotalia.*

Depth often shows a relationship to the distribution patterns of living planktonic Foraminifera, but depth-correlated factors such as temperature, salinity, dissolved oxygen, photic conditions, and nutrient levels are probably the direct controls over foraminiferal depth habitats.

In nearshore environments, however, the influence of depth can persist even when physico-chemical conditions are equivalent to an open marine setting. Planktonic Foraminifera are often undersized, and usually sparsely distributed in shelf waters; this is especially true of inner shelf environments on broad continental shelves where they may be entirely absent (Saidova, 1957; Lipps and Warme, 1966; Boltovskoy, 1976; Wang *et al.* 1985).

Bandy (1956) pointed out that the characteristic depth habitat of some species may preclude their survival in shallow waters. This could be due to a relationship between the life cycle and environmental gradients like the thermocline (Lohmann and Schweitzer, 1990; Schweitzer and Lohmann, 1991), the pycnocline, or the chlorophyll maximum (Hemleben and Bijma, 1994), rather than to the absolute magnitudes of temperature, salinity, and productivity in nearshore environments. In species that depend on seasonal overturn above the thermocline for successful completion of their life cycle, the depth of the thermocline – or even its existence where bathymetry intervenes in the shelf environment – may play a role in determining vertical and horizontal abundance and distribution. This is supported by Orr's (1967) finding that the intraspecific proportion of adult pregametogenic specimens of some species found in surficial sediments shows a discontinuity at depths that can be related to the species' life cycle.

If Orr's finding is the general case, then interspecific variations in shoreward distribution may be understood in terms of the bathymetry of their respective reproductive cycles. As Hemleben *et al.* (1989) have pointed out, historical changes in biogeographic distribution patterns cannot be fully understood until a fuller knowledge of foraminiferal depth habitats is developed. Of course, for extinct species, such knowledge must rely on the indirect evidence of bathymetry and light isotopes.

Although it is possible in principle to infer the vertical habitat distribution of planktonic Foraminifera from their light isotope composition (Savin and Douglas, 1973; Grazzini, 1976; Fairbanks *et al.,* 1980; Fairbanks, 1982; Deuser,

1987; Spero *et al.,* 1991; Sautter and Thunell, 1991; Spero and Lea, 1993; Ravelo and Fairbanks, 1992, 1995; Hemleben and Bijma, 1994; van Eijden, 1995), and ranked depth stratifications have been developed on that basis, it is also clear that ontogenetic changes in depth habitat and vital effects (including those of photosymbionts and gametogenic calcification) complicate the interpretation of isotopic data – a complication that is compounded when extrapolated into the fossil record (e.g. Shackleton *et al.,* 1985; Lohmann and Schweitzer, 1990; Corfield and Cartilidge, 1991; D'Hondt *et al.,* 1994; Kelly *et al.,* 1996; see also chapter 14).

Having enumerated the main factors influencing planktonic foraminiferal distributions, we will now discuss the effects they have on biogeographic patterns. This discussion is (somewhat arbitrarily) divided into large, meso-, and small-scale patterns.

7.3   LARGE-SCALE DISTRIBUTION PATTERNS

7.3.1   The global diversity gradient and latitudinal provinciality

7.3.1.1

Perhaps the single most conspicuous aspect of the Earth's biosphere is the global latitudinal diversity gradient, a gradient that embraces virtually all taxonomic levels. Wallace (1878) drew attention to the phenomenon, and Murray (1897) became the first to discuss latitudinal gradients in the planktonic Foraminifera. Since that time, eight large-scale biogeographic provinces have been identified that are symmetrically disposed about a ninth tropical province (Figs. 7.3, 7.4). Although various authors differ on the exact positions of provincial boundaries, and some have added details that reflect smaller-scale hydrography (e.g. McGowan, 1974; Hemleben *et al.,* 1989), the overall picture of latitudinal provinces and the diversity gradient that spans them is consistent with patterns seen in the remainder of the world's biota (McGowan,

1971). These large-scale patterns have been the central theme in most surveys of planktonic foraminiferal biogeography. The reader is referred to Bradshaw (1959), Bandy (1964), Belyaeva (1969), Bé and Tolderlund (1971), Boltovskoy and Wright (1976), Bé (1977), Bé and Hutson (1977), Lipps (1979), Olsson (1982), and Hemleben et. al (1989) for useful summaries. Pianka (1966) provides a useful general discussion of the phenomenon.

7.3.1.2   General features of latitudinal provinces

These nine large-scale provinces do not map systematically onto clearly defined physico-chemical oceanographic properties (Williams *et al.,* 1968; Backus, 1986), or onto planktonic surface-water distributions (Ottens, 1991), with the result that provinces are easier to describe than explain. Diversity shows a monotonic decrease from about 20 species (ten indigenous) in the tropical province to about 5 (one indigenous) in the polar regions, with few species being restricted to a single province (Fig. 7.3). Cold-water faunas are somewhat less diverse in the north than in the south, possibly because of the relatively restricted circulation in the Arctic (Bé, 1977).

The high-latitude provinces tend to be longitudinally continuous and faunally uniform due to a relative lack of continental barriers, but lower latitude provinces are interrupted, most conspicuously by the Americas, with the result that faunal differences are most pronounced between the low-latitude provinces of the Atlantic and the Eastern Pacific (Fig. 7.4).

Bé (1977) has drawn attention to the fact that the ratio of indigenous to total species found in these nine provinces is lowest in the transitional zone where only *Globorotalia inflata* is considered to be indigenous. This observation tends to characterize the transitional zone as an area of overlap between higher and lower latitude species distributions, and suggests that the number of large-scale functional ecosystems may be smaller than the number of provinces that can be delineated on the basis of foraminiferal distribution patterns.

Superimposed on this first-order provinciality is a second-order pattern that correlates most strongly with currents, frontal systems, and upwellings (e.g. Ottens, 1991), effects that are most strongly developed in the temperate through tropical provinces. Subtropical prov-

most strongly developed along western boundaries (Gulf Stream, and Kuroshio current in the north, Brazil Current, Mozambique-Agulhas Current, and East-Australian Current in the south) and it is in these areas that provincial distortion is most apparent (e.g. McGowran
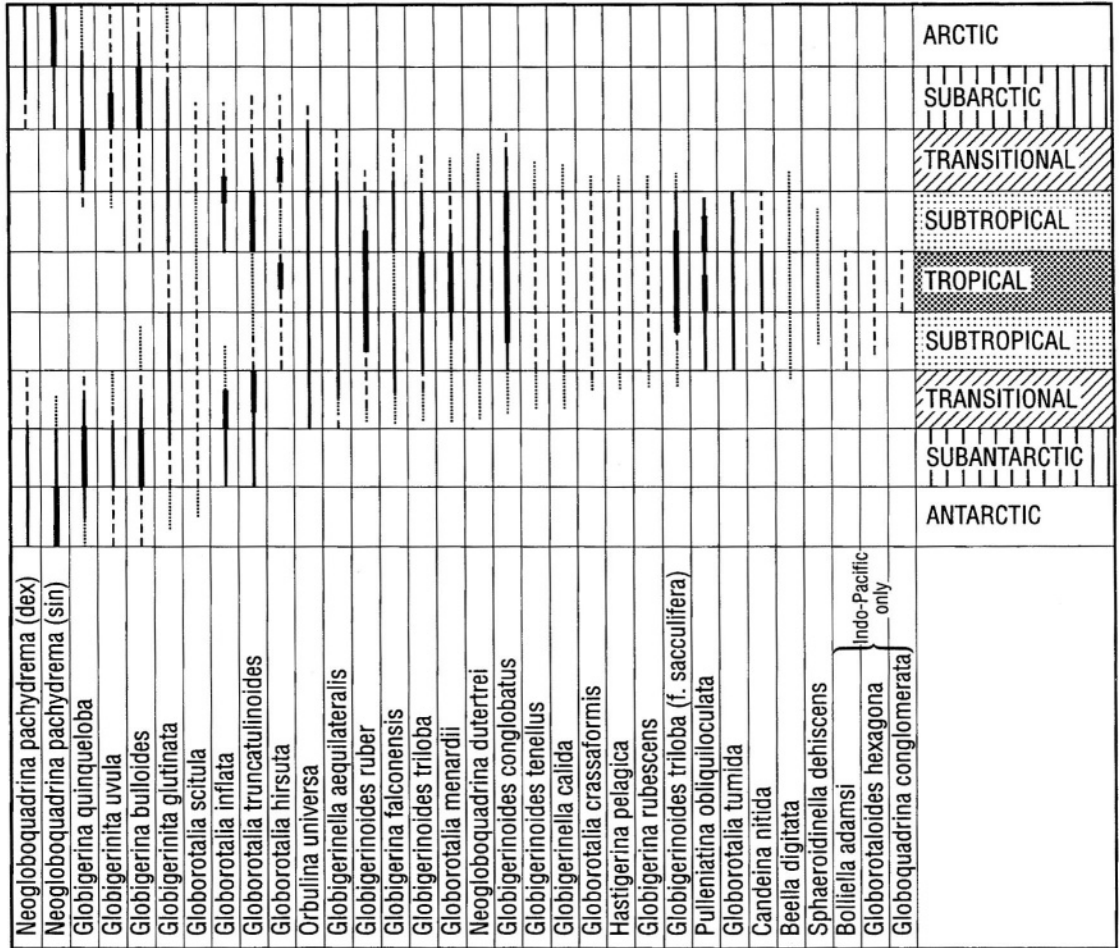
Figure 7.3 Latitudinal summary of planktonic foraminiferal species distributions. After Boltovskoy and Wright (1979) and Bé (1977).

inces, for example, tend to include a significant number of species (four of twelve) associated with upwellings and boundary currents. Current gyres also distort the latitudinal orientation of low-latitude faunal provinces by transporting equatorial species poleward in clockwise northern hemisphere gyres and in counterclockwise southern hemisphere gyres. These currents are

et al., 1997). Similarly, high latitude species are carried equatorward by the Labrador, Portugal-Canaries, Oyashio, Benguela, and California Currents (Fig. 7.5).

The geographic disposition and species composition of these provinces have been characterized in contexts ranging from broad latitudinal and provincial summaries (Figs. 7.3.
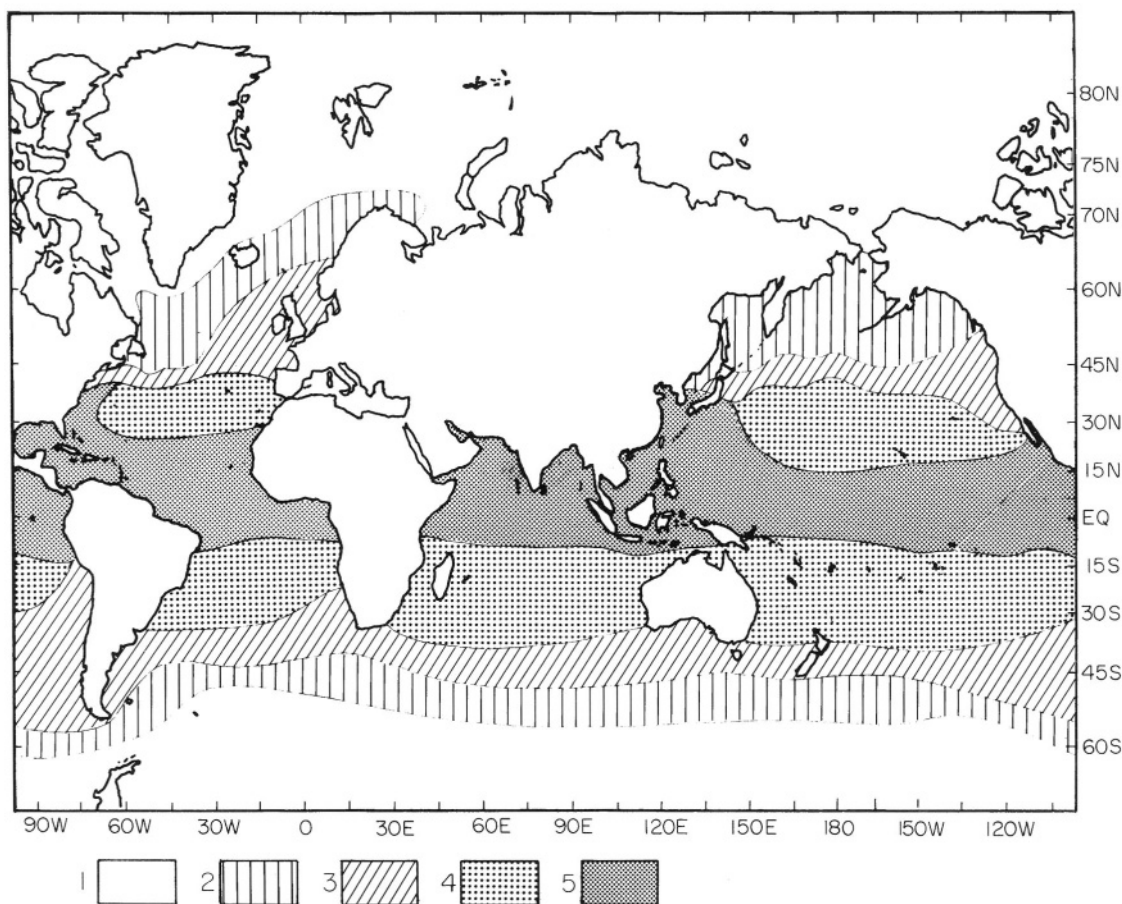
Figure 7.4 Biogeographic provinciality in modern planktonic Foraminifera. (1) Polar, (2) sub-polar, (3) transitional, (4) subtropical, and (5) tropical provinces. Note correspondence to Figs. 7.3 and 7.5. After Bé (1977).

7.4) to more detailed species-by-species documentation (e.g. Bé. 1977; Hilbrecht, 1996). The latitudinal character of these provinces and of the diversity gradient implies that temperature plays a dominant role in their disposition, although that role is probably indirect (Cifelli, 1971, but see Stehli *et al.,* 1969, 1972). Likely candidates for more direct influence would include temperature-correlated phenomena like productivity (Ortiz *et al.,* 1995) and the latitudinal distribution of hydrographic barriers to gene flow. Lipps (1979) listed six hypotheses that relate temperature, salinity, circulation patterns, water masses, ecosystem cores/ecotones, and environmental stability/predictability to planktonic foraminiferal provinciality, but concluded

that these hypotheses are more useful as tools in paleoecological inference than as explanations for foraminiferal distribution patterns.

7.3.2   The historical development of the global diversity gradient

7.3.2.1

Early classic works like those of Stehli *et al.* (1969) and Stehli *et al.* (1972) analyzed large scale biogeographic patterns from relatively restricted data bases. Recent workers such as Wei and Kennett (1983. 1986). Stanley *et al.* (1988). Norris (1991a), and Parker *et al.* (in press), have taken advantage of global compen-

dia like Kennett and Srinivasan (1983), Blow (1979), and Olsson *et al.* (1999) to relate paleobiogeography to macroevolutionary patterns of speciation and extinction as well as to morphology, life history, abundance, taxonomic affiliation, and paleoceanographic change.

It is clear that the well-developed global latitudinal diversity gradient seen in the Globigerinida has not been a static feature throughout the Cenozoic; rather, it is the continuing culmination of the last great iterative phase of the group's evolutionary history (Cifelli. 1969; Norris, 1991a). Latitudinal environmental gradients, and their consequent foraminiferal diversity gradients, were clearly much less steep in the early Paleogene (Olsson, 1982; Boersma and Premoli Silva, 1983, 1991; Olsson *et al.* 1999) but the speciation/extinction patterns that accompany this transition are not well understood.

7.3.2.2   The ecological role of temperature

Stehli *et al.* (1972) advanced the hypothesis that the latitudinal diversity gradient is driven by thermal control of two factors: greater ease of entry into low-latitude niches, and an equatorward increase in niche space. The latter factor could be related to intensified vertical stratification at low latitudes (Lipps, 1970), an equatorward increase in local upwelling (Stanley *et al.,* 1988), or to an equatorward gradient in the trophic resource continuum (Hallock, 1987). The effect of historical changes in temperature will be discussed in section 7.3.2.5.

7.3.2.3   Speciation and extinction rates

Stehli *et al.* (1969) discussed taxonomic survivorship, endemicity, and latitudinal diversity trends in Permian brachiopods, modern Bivalvia, and Cretaceous planktonic Foraminifera, and noted two striking patterns:

(1) a lack of endemic taxa at high latitudes (cold-water assemblages tend to be comprised almost exclusively of cosmopolitan species; Fig. 7.6); and

(2) turnover rates among low-latitude groups are higher than among high-latitude taxa (suggested by patterns of taxonomic survivorship).

In foraminiferal studies Stanley *et al.* (1988). Norris (1991a), Feldman *et al.* (1998), and Parker *et al.* (in press) confirmed the geographic pattern (1, above) in Neogene planktonic Foraminifera. Stehli *et al.* (1972) found indirect generic-level evidence of high turnover among low latitude Foraminifera, but was unable to find similar evidence at the species level, possibly because of a decoupling between species and higher-level taxic behavior (Arnold, 1982). Stanley *et al.* (1988), Norris (1991a), Feldman *et al.* (1998), and Parker *et al.* (in press) later confirmed a pattern (2 above) of higher species turnover among low-latitude Foraminifera.

The causes of these patterns were subsequently pursued by Wei and Kennett, (1986). Stanley *et al.* (1988). Norris (1991b. 1992). and Parker *et al.* (in press), who. in various combinations, examined the relationship between diversity and factors such as morphology (keeled vs. unkeeled, spinose vs. nonspinose), taxonomic affiliation (within-clade species turnover), geographic range (cosmopolitan vs. endemic), population size (dominance), patchiness (occurrence in upwelling), depth distribution, biology (symbiont relationships and life cycle), latitudinal occurrence (most poleward extent), and latitudinal variation in provinciality. Tracing patterns of causality among these factors despite extensive covariation has been a central issue in these works. The results tend to support Stehli's earlier work, and are further consistent with the expectation (Fisher, 1930; Wright, 1942) that the limited possibilities for genetic isolation in widespread, abundant cosmopolitan panmictic populations may retard microevolutionary rates and suppress speciation at high latitude.

7.3.2.4 Biogeographic change during speciation

Superficially, it would seem reasonable to expect that during lineage diversification, species would originate locally and then expand their biogeographic ranges into increasingly broad biogeographic provinces. However, on the average. Neogene speciation events tend to result in a
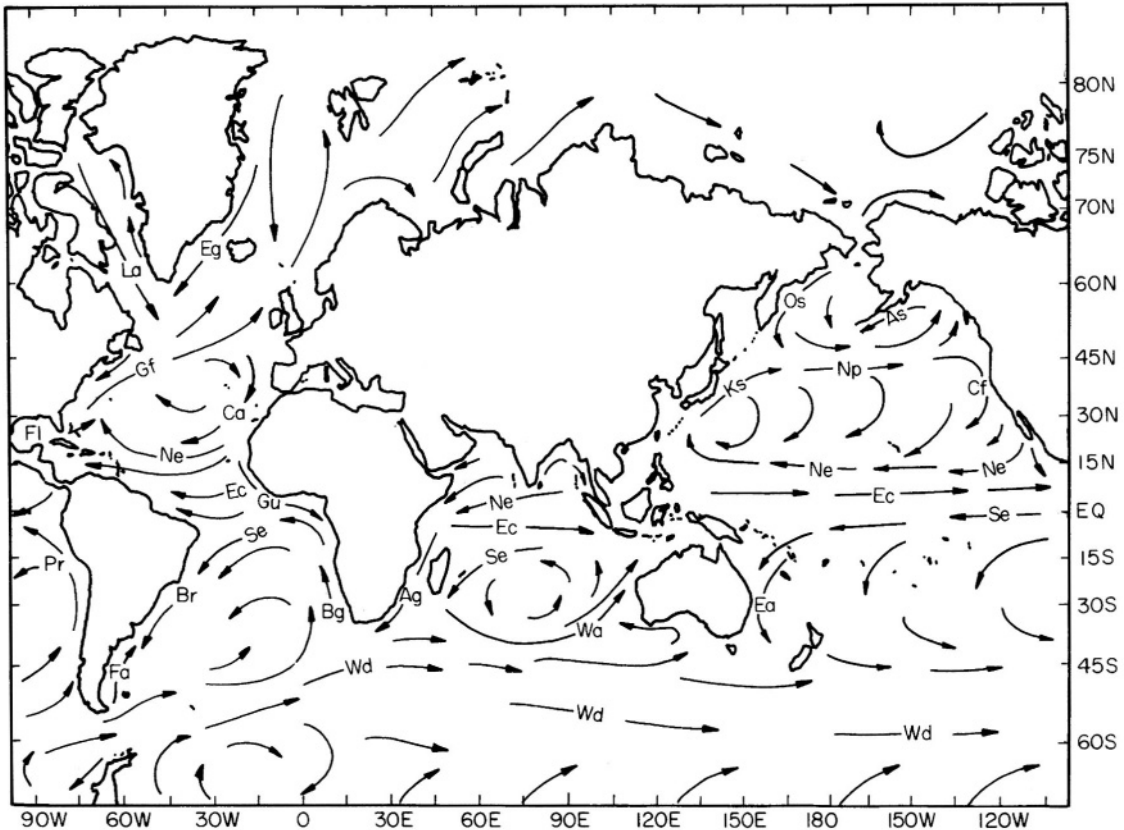
Figure 7.5 Generalized major surface circulation systems. Current abbreviations are Ag = Agulhas Current; As = Alaska Current; Bg = Benguela Current; Br = Brazil Current; Ca = Canary Curent; Cf = California Current; Ea = East Australia Current; Ec = Equatorial Countercurrent; Eg = East Greenland Current; Fa = Falkland Current; Fl = Florida Current; Gf = Gulf Stream; Gu = Guinea Current; Ks = Kuroshio; La = Labrador Current; Ne = North Equatorial Current; Np = North Pacific Current; Os = Oyashio; Pr = Peru Current; Se = South Equatorial Current; Wa = West Australia Current; Wd = Westwind Drift; The circum-Antarctic Polar Current, flowing from east to west along the coast of Antarctica, is not shown. After Kennett (1982) and Parker (1971).

statistically significant *reduction* in geographic range (Parker *et al.,* in press). This observation implies that the development of biogeographic patterns may proceed from relatively cosmopolitan ancestors that speciate by specializing and exploring increasingly geographically restricted niches. Indeed, it is established that the Cenozoic iterative diversifications did originate from relatively cosmopolitan, 'primitive' globigerine ancestors (Cifelli, 1969; Norris, 1991a). A tendency toward geographic specialization might be verified by examining changes in distribution patterns over the geologic history of species, but the existing comprehensive compendia on fora-

miniferal distribution patterns do not provide sufficient stratigraphic and geographic detail. However, Jenkins (1992) examined a restricted data set and found a pattern of retreat toward the tropics prior to extinction; if this pattern holds for pseudoextinctions, then Jenkins' pattern has general implications for the biogeography of evolution as well as extinction (see also Vermeij, 1989). Note that Hunter (1985), Hansard (1994), and Lazarus *et al.* (1995) have found cladogenesis to be accompanied by reduced abundances, although the generality of this observation and its biogeographic implications have not been assessed.
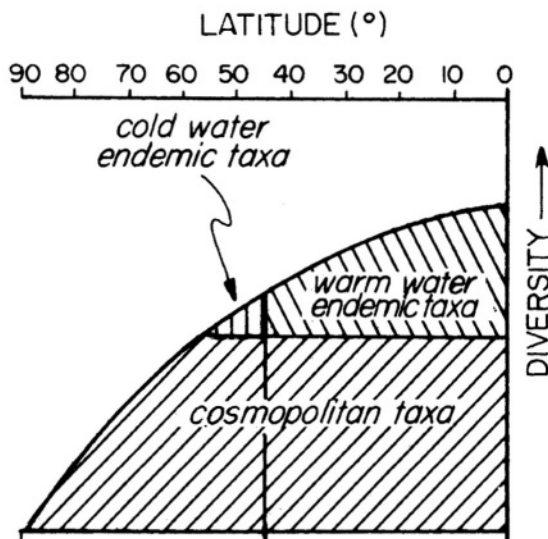
Figure 7.6 Diagrammatic depiction of the composition of warm and cold assemblages. Note that endemic assemblages are virtually absent at high latitudes, where assemblages consist almost entirely of cosmopolitan elements. This is true not only of planktonic Foraminifera, but of many other taxa as well. After Stehli *et al.* (1969).

7.3.2.5   Late Cenozoic cooling and latitudinal species distributions

For most of geologic time, global climates have been warmer than they are at present; the modern widespread cold-temperate and arctic regions developed as a result of Late Cenozoic cooling. If the world has been warm nearly everywhere for much of its history, then Darlington's (1959) classical view of low latitudes as centers of radiation may lose its meaning (Stanley, 1979). This suggests that an examination of Neogene cooling might be useful in understanding latitudinal provinciality. Thunell and Belyea (1982) have shown that Neogene Atlantic planktonic foraminiferal provinces shifted dramatically in the Middle Miocene and Late Pliocene during the development of the East Antarctic Ice Sheet and the initiation of the northern hemisphere ice sheets. At these times there were equatorward migrations of cool, high-latitude provinces and accompanying contraction of low-latitude provinces. Berggren and Hollister (1974) and McIntyre *et al.* (1972) noted that the polar front has swept back and forth during the

last 250 ky, alternately compressing and expanding the tropics at least six times. The exponential nature of rediversification during each recovery would tend to enhance the diversity gradient even if fractional (per-taxon) rates of speciation were latitudinally invariant. This is because (all other things being equal) a biota with larger initial diversity will have a faster rate of arithmetic growth, since diversification starts on a steeper part of the exponential growth curve (Stanley, 1979).

Stanley (1979) also emphasized that global cooling events might be expected to cause higher extinction rates among tropical species, a prediction that is consistent with many observed extinction patterns, and a prediction later verified in the Foraminifera (Stanley *et al.*, 1988). This model carries the corollary that the distributions of surviving low-latitude species should be compressed equatorward during cooling events (e.g. Thunell and Belyea, 1982), which in turn implies that subsequent recovery should be characterized by reradiation from the tropics, a process that could, in itself, maintain a latitudinal diversity gradient even if the number of niches were not latitude dependent. This is consistent with Jenkins' (1992) observation of equatorward biogeographic contraction prior to extinction.

Lipps (1970) emphasized the effect of sea surface temperatures at high latitudes on vertical and horizontal thermal gradients. Lipps proposed a model suggesting that during times of polar warming the absence of steep thermal gradients eliminates barriers that otherwise maintain species diversity through genetic isolation and allopatry; conversely, the potential for speciation would be greatest when the effectiveness of thermal barriers to gene flow is enhanced by strong localized thermal gradients caused by high-latitude cooling. Lipps' hypothesis implies that Stanley's (1979) 'crucible of speciation' may be the polar front or temperate region (where gradients would be steepest) rather than the tropics. Detailed information on the geographic distribution of stratigraphic first appearances might provide a means to test this hypothesis.

Lohmann and Schweitzer (1990) have pre-

sented evidence suggesting that the position of a different gradient, the thermocline, may play a key role in determining the differential reproductive success of subpopulations of *Globorotalia truncatulinoides.* Hemleben *et al.* (1989) have pointed out that the pycnocline and the chlorophyll maximum can play a similar role, and may act as barriers to gene flow during the speciation process. This raises the possibility that the lack of a well-developed thermocline characteristic of polar regions may be a key factor in suppressing speciation in those areas. It would then follow that equatorward movement of the polar front should suppress speciation over a broader area. Additionally, Wei and Kennett (1986) suggest that increased provinciality during the development of polar ice may drive the diversification process, especially in the globorotaliids; it is also established that latitudinal provincialization became more developed during times of polar cooling (Thunell, 1981).

7.3.3 Antitropicality and bipolarity

Most cool-water planktonic foraminiferal species, including *Neogloboquudrina pachyderma, Globigerina bulloides,* and *Globorotalia inflata,* occur in latitudinally delineated biogeographic provinces separated by equatorial water masses (Figs. 7.3, 7.4). This can also be true of morphotypes – specifically coiling direction – of some species (e.g. *Neogloboquadrina pachyderma, Globorotalia truncatulinoides*). Bipolarity has been the subject of investigation since the mid 19th century (Hooker, 1847), and in extant groups is usually considered to be the result of relatively recent Plio-Pleistocene cooling. The fact that the phenomenon can be detected as far back as the Early Jurassic does not require that present bipolarity is of ancient origin. However, the subfamilial level of differentiation in some living bipolar mollusca suggests the phenomenon may be the result of considerable evolutionary history (Crame, 1993). The question of whether bipolarity should be interpreted in a framework of vicariant evolution or dispersal history is deserving of closer scrutiny by foraminiferologists, for it is in this group that we have the stratigraphic and phylogenetic control to resolve the issue.

Hedgpeth (1957b) and Lipps (1979) have discussed several hypotheses to explain bipolarity, including submergence, a phenomenon in which extra-tropical cool-water species stay within their preferred thermal conditions by living in deeper waters at lower latitudes. The general form of this explanation appears to be valid in the analogous context of some antitropical plant species that are found in high altitude tropical settings (Thorne, 1972). Although submergence has been observed in *Globorotalia menardii* (Hemleben *et al..* 1989), *Globigerina bulloides, Globorotalia inflata,* and a few other cold-temperate and cold water species (Boltovskoy, 1971b), the phenomenon is unlikely to explain bipolarity, because other limiting habitat requirements (such as photic and nutrient levels) are not satisfied in the tropics where ideal thermal conditions may only be found in deeper water.

Bipolarity might also be the result of migration from more equatorial provinces into contiguous higher-latitude water masses, or the result of dumbbell allopatry during warming trends (McGowan, 1971; Lazarus, 1983). An additional hypothesis explaining bipolarity suggests it is a historical vestige of dissection of a previously continuous distribution by post-glacial warming in the tropics, with sufficiently frequent mixing between latitudinally disjunct populations to maintain genetic continuity (Bé, 1977; Bé and Tolderlund, 1971).

7.3.4 Continental positions

High latitude foraminiferal provinces tend to have lateral continuity. At lower latitudes, however, continuity is interrupted by land masses, particularly the Americas. The Pliocene closure of the Isthmus of Panama isolated Atlantic and Pacific tropical faunas and led to their independent faunal development. Today, *Globigerinella adamsi, Globoquadrina conglomerata, Globorotaloides hexagonus, Globorotalia menardii neoflexuasa,* and *Globorotalia theyeri* are confined

to the Indo-Pacific (see Vincent and Berger. 1981; Bolli and Krasheninnikov, 1977; Bé, 1977; Thompson *et al.*, 1979), and pink *Globigerinoides ruber* has disappeared from the Indian and Pacific Oceans (Thompson *et al.,* 1979). Additionally, coiling directions in *Pulleniatina obliquiloculata* cease to correlate between the Atlantic and Pacific basins after the development of the Isthmus of Panama (Saito, 1976).

In general, low-latitude species that evolved before the development of the Isthmus tend to show a more continuous circumglobal distribution than late-evolving species. For example, several descendants of *Globorotalia cultrata* that evolved after the Pliocene are restricted to the Atlantic basin (Vincent and Berger, 1981; Schott, 1935). *Globorotalia cultrata* itself disappears from the tropical Atlantic during glacial times (Schott, 1935; Vincent and Berger, 1981; Morin *et al.,* 1970), and populations only become reestablished in the Atlantic basin when the 18 C isotherm moves poleward of southernmost South Africa, thus allowing the species to circumvent the continental barrier at high southern latitudes. These repopulation events are discussed by Thompson *et al.* (1979), Ericson and Wollin (1968). and Schweitzer and Lohmann (1991).

7.4 MESO-SCALE DISTRIBUTION

7.4.1

Although large-scale foraminiferal biogeographic provinces are relatively simple and monotonous by comparison with similar-sized terrestrial provinces (McGowan, 1971), they are not devoid of small-scale structure. Research on regional and local-scale variation in distribution patterns has revealed them to be more than mere high-resolution details of the known large-scale patterns; instead, they arise from distinct smaller-scale oceanographic phenomena and have different implications for evolution, diversity, and biogeography. Thus, the key to understanding large-scale distribution patterns may not be found in comparably large-scaled phenomena, but in the cumulative effect of smaller-scale phenomena which themselves may show systematic latitudinal variation.

7.4.2   Genetic isolation

For example, Stanley *et al.* (1988) suggest that higher taxonomic turnover in globorotaliids is probably related to their generally discontinuous distribution, possibly because many are found in areas of (low to mid-latitude) upwelling and are symbiont-barren. Since smaller, more localized populations will have a greater likelihood of genetic isolation and greater vulnerability to localized change, sub-provincial ecological discontinuities are of particular interest for their potential influence on speciation, extinction, and turnover rates, and, a temperature-mediated latitudinal gradient in environmental patchiness might be a more immediate cause of low-latitude speciation rates than temperature itself.

Boltovskoy (1976) also presented an analysis of planktonic distribution patterns that contrasts sharply with the first-order global-scale latitudinal zonations. He focused on localized phenomena such as upwelling, peculiar hydrographic conditions, and complicated current gyres, belts, fronts, and tongues of converging water masses for his explanation of planktonic foraminiferal distribution patterns in the waters surrounding South America. While he does not deny the existence of larger scale global patterns. Boltovskoy contends that they are not, in themselves, an adequate framework for understanding the biogeography of planktonic Foraminifera. This perspective is reinforced by Wang *et al.* (1985), Ottens (1991), Ottens and Nederbragt (1992), and Hilbrecht (1996), among others; their work provides clear evidence that it is at this scale that faunal discontinuities are most readily related to hydrographic boundaries.

There are indications that Boltovskoy's focus on hydrographic detail may have critical explanatory value as our understanding of speciation in the plankton develops. One of the most problematic aspects of foraminiferal evolution is the mechanism of genetic isolation in the pelagic realm. Lipps (1970, 1979), McGowan (1971), Lazarus (1983), and others have noted the limited potential for allopatric speciation in large, panmictic populations of planktonic Foramini-

fera. In this regard it may be relevant that a significant number of species that Boltovskoy describes in his South American biogeographic studies are not among the widely recognized Recent species (e.g. *Globigerina diplostoma, G. juvenilis, G. radians, G. rosacea, G. subcretacea, G. trilocularis, Globigerinoides cyclostomus, G. suleki, Globorotalia canariensis, G. punctulata, G. seiglei,* and *Hastigerina involuta,* among others; Boltovskoy, 1976; see also Rögl, 1985). Boltovskoy mentions that many of these species are found only in restricted areas as isolated specimens, which raises the possibility that these areas may be the genetically isolated 'crucibles of speciation' discussed by Stanley (1979). Such areas might be expected to produce many short-lived species, most of which never become established on a global scale. Generally speaking, past micropaleontological awareness of species has been biased by a focus on their utility as tools for stratigraphic correlation; consequently, rare, restricted, and short-lived species have been frequently overlooked as isolated oddities. A closer examination of the biogeographic distribution of these 'oddities' may provide valuable clues in understanding mechanisms of speciation in the plankton, and the geographic distribution of these 'crucibles' may have biogeographic implications. Suggested avenues of research might include a comparative study of morphologic variability in these hydrographically distinct areas versus other areas in the open ocean, or a study of the stratigraphic continuity of these unusual forms in relation to the history of their restricted habitats.

However, even at this scale, it is not clear that hydrographic discontinuities are effective geographic barriers to gene flow. Ottens' (1991) study of various Atlantic fronts and currents found that the faunal boundaries between clearly-defined water masses coincided with intervening hydrographic frontal zones. These frontal boundaries were characterized by a high-diversity, low-equitability ecotonal fauna that shared species of both adjoining water masses. The highly gradational nature of these ecotones was supported by multivariate analyses suggesting that foraminiferal populations were more intergradational than the water masses they inhabited.

7.4.3 Directional currents

One question that arises in the context of meso-scale circulation patterns is the effect of directional advection/diffusion on the distribution of the species that inhabit transition zones. Olson (1986) draws attention to the question of how *Globorotalia inflata* maintains itself in the face of a net eastward flow in the south Atlantic – specifically, how individuals are recruited upstream to maintain the population against advection. Olson describes three smaller-scale mechanisms: westward transport by upstream movement of eddy fields, recirculation cells associated with western boundary currents, and the maintenance of a region of prolonged residence at the upstream extremity of the eastward advection.

7.4.4 The biogeography of foraminiferal genotypes

This field is just beginning to influence our understanding of the planktonic Foraminifera. It appears that intraspecific genotypic variation may be seen on roughly the same spatial scale as mesoscale hydrographic features; however, beyond drawing attention to the potential relationship with genetic isolation and speciation, it would be premature to speculate on the significance of this observation. Darling *et al.* (1998a) have examined various water masses for intraspecific variation in genotype; their preliminary results indicate significant patterns of genotype distribution within and between water masses. The implications of this finding for biogeographic studies has not been fully assessed, but Huber *et at.* (1997), Darling *et al.* (1998b), and de Vargas e*t al.* (1998) have discussed cryptic genotypic species within morphotypes previously believed to be monospecific. This implies that the traditional morphospecies concept may not be a fully adequate basis for understanding biogeographic patterns.

7.5   SMALL-SCALE PATCHINESS

Boltovskoy (1971a) provided an early quantification of the geographic scale of abundance variation; useful discussions can be found in Wiebe and Holland (1968), Boltovskoy (1971a) and Boltovskoy and Wright (1976). The phenomenon is probably too ephemeral to play a direct role in genetic isolation during the speciation process; however, Hemleben e*t al.* (1989) suggest that a significant portion of measured lateral patchiness may be due to diurnal vertical migration during sampling. Based on plankton tows, Boltovskoy reported abundance variation by a factor of 90 over distances as small as one nautical mile in the South Atlantic Ocean.

Recent work on patchiness in the plankton has been directed at the more general question of its underlying causes (Powell and Okubo, 1994; Abraham, 1998; Levin and Segel, 1976). Abraham (1998) has pointed out that turbulent stirring of plankton by nondiffusive advection is a likely explanation for patchiness. The concentration spectra of plankton tend to follow a power law over scales ranging from one to 100 km. Phytoplankton distributions are similar to the distribution of the physical quantities (especially, nutrient) that the phytoplankton are presumably tracking. Zooplankton concentrations however, are more variable over short distances- nearly as variable as they are at larger spatial scales. The difference, according to Abraham, can be accounted for by differing response times, i.e. longer-lived zooplankton may not reproduce quickly enough to closely track their nutritional resources. This might explain the closer correlation seen between productivity and foraminiferal abundances in small-mesh plankton tows noted by Berger (1969). Over their shorter lifetimes, juvenile specimens are likely to have experienced less advective transport, and therefore are more likely to reflect recent reproduction in resource-rich waters. Concentration spectra in the planktonic Foraminifera have not been examined quantitatively in the context of Abraham's model; nevertheless, there may be sufficient lifespan-dependent variation in response times between the long-lived genus *Globorotalia* and the shorter-lived *Globigerinoides* to test for consistency with Abraham's prediction.

On an extremely fine scale, Silver e*t al.* (1978) have presented evidence suggesting that the abundance and diversity of microplankton correlate with small-scale variation in the density of marine snow aggregates (fecal pellets, organic detritus, various exoskeletons, etc.). Some may even treat this snow as a substrate (Hilbrecht and Thierstein, 1996; see also Banerji, 1974).

7.6   TEMPORAL CONSIDERATIONS

7.6.1   Temporal patchiness

It is becoming clear that one means of achieving sympatric speciation in plankton may involve genetic isolation through intraspecific variation in the timing of the reproductive cycle. In species that time their reproduction to coincide with specific (but different) parts of the lunar cycle (e.g. Bijma *et al.,* 1990, 1994; Bijma and Hemleben, 1994; Erez *et al.,* 1991), or with seasonal overturn of the mixed layer (e.g. Lohmann and Schweitzer, 1990; Lohmann, 1992), we may find that their speciation rates, and hence their provincial diversity and distribution, may be influenced by geographic variation in the intensity of seasonal upwelling, or temporal variation in such factors as the depth of the thermocline, pycnocline, or chlorophyll maximum (see Wefer and Fischer. 1993; Williams *et al.,* 1981; Sautter *et al.,* 1991; Curry *et al.,* 1983, 1992).

7.6.2   Time scale and biogeographic patterns

7.6.2.1   The effect of recovery time

It may he fruitful to consider the time scale over which historical events might influence biogeographic patterns. It is likely that ecological restabilization after climatic change would appear to be virtually instantaneous when perceived on a geological time scale, however, it does not follow that biogeographic stabilization is beyond the resolving power of biostratigraphers. This is because ecological response time of the biota is

not the only determinant of biogeographic patterns. For example, evolutionary recovery plays a significant role, especially when extinction and speciation are latitude-dependent.

What is the time scale for evolutionary recovery in the plankton? The average censorship-corrected species duration is about 9.17 my for the Cenozoic planktonic Foraminifera and the expected and realized time to recover a stable species age distribution after the Cretaceous/ Tertiary extinction is about 15 my (Arnold, *et al.,* 1995b; Parker and Arnold, 1997; also *cf.* Stanley, 1990) After the post-Cretaceous recovery of a stable age distribution in Cenozoic planktonic Foraminifera, the mean species age fluctuates about an average of 5 my. With evolutionary recovery times of this magnitude, we should expect that the effects of late Cenozoic cooling are likely to exert a lingering influence over that component of biogeographic patterns that is influenced by speciation and extinction rate.

On a somewhat shorter climatic time scale, poleward retreat of Quaternary climatic belts and water masses in relation to southernmost South America has mediated the repopulation of the Atlantic basin by *Globorotalia cultrata* (Vincent and Berger, 1981; see discussion under 'continental positions' above). In this case the limiting factor in these repopulation events has been interaction between climatic belts and continental positions rather than ecological responsiveness of *Globorotalia cultrata.*

If recovery times can be constrained by factors with evolutionary or Milankovich time scales, it follows that the historical components of biogeographic equilibration deserve attention at time scales longer than those normally seen in plankton ecology studies. Endler (1982) provides a useful perspective on the relative importance of ecological and historical influences on diversity gradients.

7.6.2.2 Iterative evolution and the global diversity gradient

The repeated appearance of keeled morphotypes (Cifelli, 1969) is the most conspicuous manifestation of iterative evolution in the planktonic Foraminifera. Even though keeled globorotaliids tend to live at relatively low latitudes, their distribution may not be attributable to an eco-logical-adaptive (*sensu* Seilacher, 1970) relationship between keels and low-latitude habitats. There are two lines of evidence supporting this view. First, the ecological adaptive relevance of the keeled morphology is challenged by the fact that during the Cenozoic iterations similar morphologies developed in different environmental settings (Boersma and Premoli Silva, 1991). Second, other low-latitude morphotypes have similar speciation rates, so it is likely that the relationship between morphology and turnover rates is indirect.

These observations suggest the possibility of a constructional interpretation for the iterative evolution of keels, and for their nonpolar distribution; the larger number of steps required to reach a keeled morphology from globose ancestry virtually guarantees that keeled forms will tend to be evolutionary latecomers relative to their globose ancestors. Consequently, we should expect the buildup of diversity in keeled forms, *even when it occurs at random with respect to adaptation,* to be (a) late relative to that of globose forms, and (b) greatest and earliest where speciation rates are highest, namely in lower latitudes. Thus, iterative evolution in the planktonic Foraminifera may derive from iterative variance expansion rather than directed selection (see Gould, 1996, for a general discussion of variance-driven trends), and suggests that the key to understanding iterative evolution might be to learn why small globigerine forms survive mass extinction (Arnold *et al.,* 1995a).

7.7 CONCLUSIONS

There are several important unresolved issues in the area of modern planktonic foraminiferal biogeography. The large-scale latitudinally symmetrical faunal provinces do not appear to show a consistent relationship to comparably-scaled hydrographic features. The origins of these provinces are therefore likely to be understood by reference to other causal factors. The first of

these is the degree to which smaller-scale hydrographic features such as current, gyre, and frontal systems combine to play a role in determining larger-scale latitudinal distribution patterns. The second is the role historical processes – particularly, latitude-dependent rates of speciation and extinction, and the development of tectonic barriers – have played in establishing faunal provinces and the global diversity gradient. A number of additional factors, including depth habitats, bipolarity, pore size, coiling direction, and iterative evolution, are indirectly related to physicochemical characteristics of the foraminiferal habitat.

As our understanding of the basic governing principles of modern foraminiferal biogeography develops, it becomes easier to interpret the fossil record in the light of those principles. By the same token, modern distribution patterns, since they are partly the result of historical processes, cannot be fully explained without reference to their past development. We are so accustomed to hearing that the present is the key to the past that we sometimes forget that the past can also be the key to understanding the present. It follows that biogeographic studies of modern and fossil Foraminifera must necessarily proceed hand-in-hand.

7.8   ACKNOWLEDGMENTS

Symbiont-bearing Foraminifera

Pamela Hallock

8.1   WHAT ARE SYMBIONT-BEARING FORAMINIFERA?

Of approximately 150 extant families of Foraminifera, less than 10% harbor algal endosymbionts (Lee and Anderson, 1991a). Nevertheless, these families are responsible for much of the carbonate produced by the Foraminifera, because symbiosis is prevalent in tropical larger foraminifers and planktonic foraminifers, the two groups that are the most prolific carbonate producers. Globally, Milliman and Droxler (1995) estimated carbonate production at 5.7 billion tons per year, of which larger foraminifers produce about 0.5% and planktonic foraminifers produce about 20% (Langer, 1997).

Lee and Anderson (1991a), in their review of the biology of symbiosis in Foraminifera, listed four miliolid, three rotaliid, and five globigerinid families as hosts of algal symbionts belonging to three divisions and five classes of the algae. A few members of several families of smaller rotaliid foraminifers (e.g. Asterigerinidae) appear to host endosymbionts, but those relationships await study. In addition, members of several families are able to sequester chloroplasts, which are harvested from algal food, for days to weeks after ingestion (Lopez, 1979; Cedhagen, 1991; Lee and Anderson, 1991a). While this is not a true symbiosis, chloroplast sequestering does enable these protists to benefit directly from photosynthesis.

Algal symbiosis appears to have arisen independently in most of these lineages of Foraminifera, as well as in several now extinct lineages. Evidence for independent origins is strongest for the miliolid families and subfamilies. The ornamented Peneroplidae (Fig. 8.1.A) host symbionts belonging to the red algae (Division Rhodophyta) (Fig. 8.2.A), while the unornamented Peneroplidae (Fig. 8.1.B) and the Archaiasinae (Family Soritidae) (Fig. 8.1.C) host symbionts belonging to the green algae (Division Chlorophyta) (Fig. 8.2B). The Soritinae (Family Soritidae) (Fig. 8.1.D) host dinoflagellate symbionts (Division Chromophyta, Class Pyrrophyceae) (Fig. 8.2.C), and the Alveolinidae I Fig. 8.1.E) host diatom symbionts (Division Chromophyta, Class Bacillariophyceae). Among the planktonic Foraminifera (Fig. 8.3), both dinoflagellate (Fig. 8.2.D) and chrysophyte (Division Chromophyta, Class Chrysophyceae) (Fig. 8.2.E) symbionts are common. Recent isotopic studies (Norris, 1996a) indicate that within

globigerinid generic lineages, symbiosis may be independently acquired. The three rotaliid families, Amphisteginidae (Fig. 8.1.F), Calcarinidae (Fig. 8.1.G) and Nummulitidae (Fig. 8.1.H), all primarily host diatom symbionts (Fig. 8.2.F). Current phylogenies indicate that these families arose independently from smaller ancestors, but proof must await molecular-genetics studies. Nevertheless, evidence is strong that foraminifers are physiologically adapted to establishing symbioses (Lee, 1998), and that symbiosis can be highly advantageous under certain environmental conditions (e.g. Hallock, 1981a; Hottinger, 1982).

8.2   ADVANTAGES OF ALGAL SYMBIOSIS

The potential advantages of algal symbiosis to foraminifers lie in at least three major areas: a) energy from photosynthesis; b) enhancement of calcification; and c) uptake of host metabolites by symbiotic algae. None of these areas has been exhaustively studied, nor are they mutually exclusive. For example, both energy from photosynthesis and uptake of CO_2 or phosphatic waste products would presumably aid calcification.

8.2.1   Energy from photosynthesis

Hallock (1981a) mathematically explored the hypothesis that algal symbiosis provides host-symbiont units with substantial energetic advantages over similar organisms that lack endosymbionts. Organisms with the potential to both feed and photosynthesize have access not only to solar energy, but also to dissolved inorganic nutrients (nitrogen and phosphorus in forms

useable by organisms, i.e. NH_4^+, NO_2^-, NO_3^-, PO_4^{-3}) and to organic matter. In severely nutrient-deficient environments within the euphotic zone of the oceans (i.e. where there is sufficient light for net photosynthesis), the most significant concentrations of essential nutrients are in organic matter. Therefore, algal symbiosis enables the foraminifer to function as a primary producer that obtains nutrients by feeding. Hallock's (1981a) model indicated that algal symbiosis provides the host-symbiont system with several orders of magnitude energetic advantage over non-symbiotic competitors in nutrient-deficient environments. Thus, once acquired, algal symbiosis appears to give significant energetic advantage for specialization of the host to symbiosis, providing considerable insight into repeated episodes of evolution of probable symbiont-bearing foraminifers, as judged by the fossil record (Hallock, 1982, 1985, 1987; Lee and Hallock, 1987; Hallock et al., 1991a).

More recent research by Falkowski et al. (1993), Lee (1998), and others, indicates that the host must maintain control of fixed nitrogen supply to the symbiont, which reinforces recognition of the relationship between nutrient-deficient environments and algal symbioses. Because the photosynthetic process is limited by the availability of solar energy and CO_2, symbionts that are severely nitrogen limited but have plenty of sunlight can produce copious amounts of simple sugars and glycerol, which they release to the host. With its metabolic energy requirements met by this photosynthate, the host can use most of the proteins ingested in captured food for its own growth and reproduction. However, if the symbionts have access to abundant fixed nitrogen, they keep their photosynthate for growth and reproduction, causing physiological stress for the host.

Figure 8.1 Scanning electron micrographs of symbiont-bearing benthic foraminifers.
(A) *Peneroplis elegans* d'Orbigny from Conch Reef, Florida Keys, scale bar = 0.1 mm.
(B) *Laevipeneroplis proteus* (d'Orbigny) from Conch Reef, Florida Keys, scale bar = 0.2 mm.
(C) *Archaias angulatus* (Fichtel and Moll) from Conch Reef, Florida Keys, scale bar = 0.1 mm.
(D) *Sorites orbiculus* (Forskal) from Makapuu, Oahu, Hawaii, scale bar = 0.25 mm.
(E) *Alveolinella quoyi* (d'Orbigny) from Lizard Island, Great Barrier Reef, Australia, scale bar = 0.2 mm.
(F) *Amphistegina lessonii* d'Orbigny from the west Australian shelf, scale bar = 0.2 mm.
(G) *Calcarina gaudichaudii* d'Orbigny from Belau, Western Caroline Islands, scale bar = 0.25 mm.
(H) *Heterostegina depressa* d'Orbigny from the west Australian shelf, scale bar = 0.25 mm.
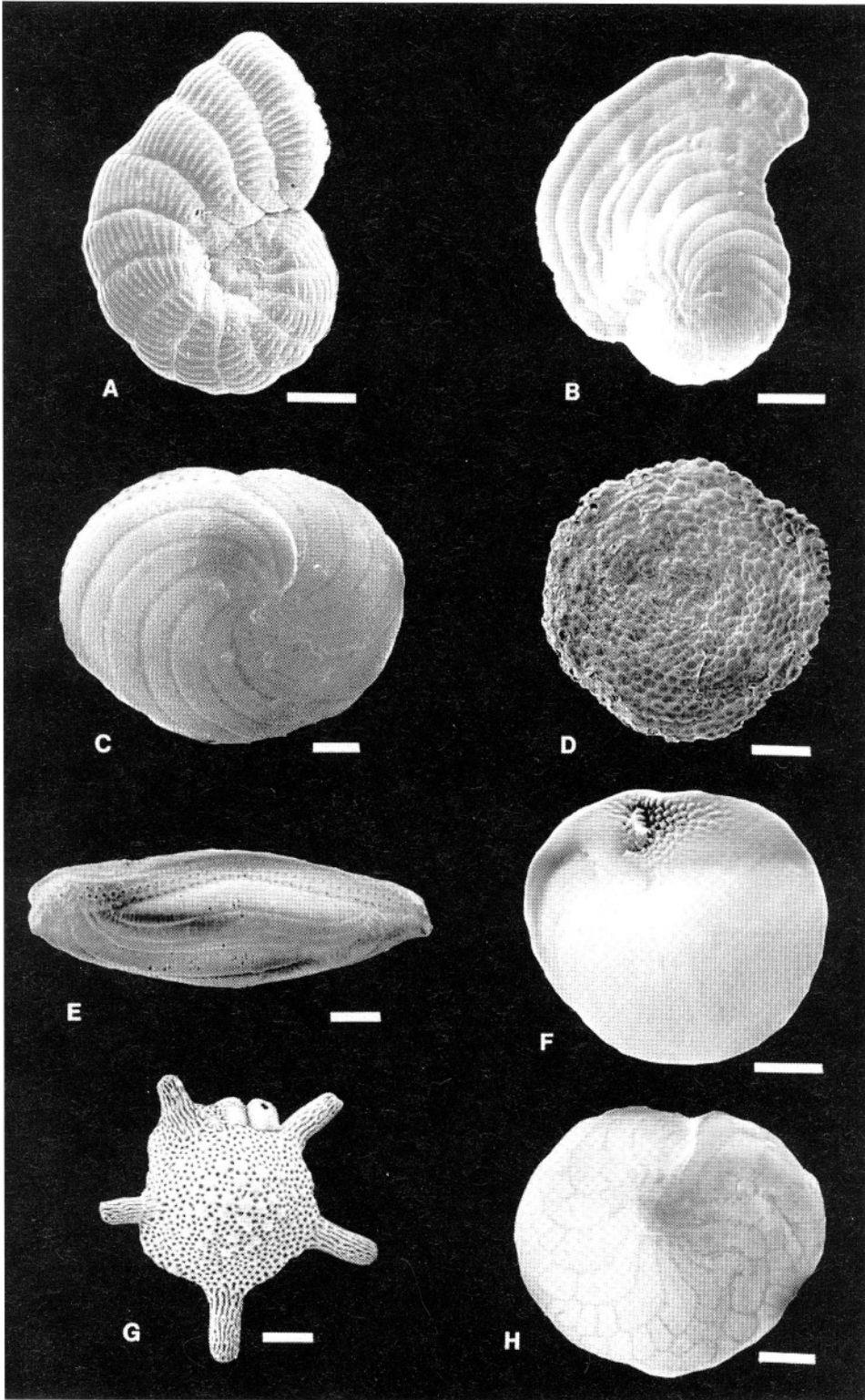
The actual roles of feeding and photosynthesis can differ substantially from theoretical predictions, and vary among the major taxa studied. *Amphistegina* spp. appear to behave most closely to model predictions; physiological studies indicate that ingested food primarily provides nutrients, while respiratory energy comes primarily from photosynthesis (ter Kuile *et al.*, 1987). In contrast, imperforate taxa such as *Archaias, Peneroplis,* and *Sorites* appear to be far more energetically dependent upon feeding and, in fact, the role of their symbionts is somewhat enigmatic (Lee and Anderson, 1991a). At the other extreme are some of the Nummulitidae and Calcarinidae, which lack primary and secondary apertures and have not been observed to feed on anything except their endosymbionts (Röttger *et al.*, 1984; Röttger and Krüger, 1990). Clearly this provides a mechanism for receiving proteins and phosphatic acids as well as carbohydrates from endosymbiosis, but does not explain how the host-symbiont unit uptakes essential nutrients. In culture, the foraminifer may be exposed to sufficient nutrients to sustain such a relationship, but in the natural environment, free-living algae should be far superior competitors for dissolved inorganic nutrients than are symbionts that are enclosed within a host organism. In theory, living on the host's nutrient wastes works only if the host is feeding. One possible explanation for this apparent enigma is that the nummulitids and calcarinids feed upon bacteria, as Lee *et al.* (1980) experimentally showed for *Heterostegina depressa*. Bacterial feeding can be easily overlooked. Members of both families produce organic attachment mechanisms (Röttger and Krüger, 1990) that Röttger (1973) originally described as rigid hyaline elastic sheaths. The composition

of these sheaths should be investigated, for they may provide additional clues to how these foraminifers get required nutrients. When provided with a carbohydrate-rich substrate, certain bacteria are much more efficient at extracting low concentrations of essential nutrients from the water column than are phytoplankton (Azam and Smith, 1991). If the sheaths are carbohydrate-rich, they may provide a substrate for 'farming' bacteria. The foraminifers could then either feed on the bacteria (e.g. Bernhard and Bowser, 1992), or uptake the nutrient wastes of the bacteria and the microplankton that come to feed on the bacteria. Observations of possible bacterial farming by foraminifers are relatively common (e.g. Langer and Gehring, 1993). Hallock *et al.* (1991b) also postulated that sediment-dwelling, flat-planispiral or discoid foraminifers may take up nutrients that are diffusing out of sediment pore waters, while utilizing sunlight from above.

8.2.2   Algal symbiosis and calcification

Because larger foraminifers with algal symbionts are such prolific calcifiers, conventional wisdom has long held that photosynthesis by the symbionts promotes calcification by splitting of bicarbonate (ter Kuile, 1991) and removal of CO_2 (Equation 8.1):

$$Ca^{2+} + 2HCO_3^- \Rightarrow CO_2 \text{ (to photosynthesis)}$$

$$+ CaCO_3 \text{ (calcification)} + H_2O \quad (8.1)$$
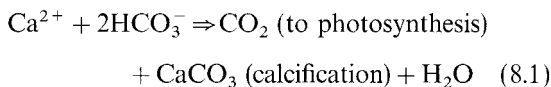
McConnaughey (1989c) and McConnaughey and Whelan (1997) have proposed the reverse interpretation. They postulate that lack of CO_2 limits photosynthesis in warm, shallow, alkaline aquatic environments and that calcification pro-

Figure 8.2 Algal symbionts in or isolated from foraminiferal hosts: (A) micrograph of a section through *Porphyridium purpureum* Hawkins and Lee isolated from *Peneroplis pertusus*, taken with a transmission electron microscope (TEM), P = chloroplast, scale bar = 1 μm; (B) TEM micrograph of *Chlamydomonas hedleyii* Lee *et al.* freshly extracted from *Archaias angulatus*, P = chloroplast, scale bar = 2 μm; (C) micrograph of '*Symbiodinium*'-like dinoflagellate symbiont isolated from *Amphisorus hemprichii*, taken with a scanning electron microscope (SEM), S = sulcus, F = hypocone flange, scale bar = 2 μm; (D) SEM micrograph of *Gymnodinium béii* Spero isolated from *Orbulina universa*, C = cingulum, S = sulcus, F = hypocone flange, scale bar = 2 μm; (E) TEM micrograph of unidentified chrysophyte algal cells in *Globoquadrina dutertrei*, P = chloroplast, scale bar = 1 μm; (F) SEM micrograph of *Nitzschia panduriformis* Grun isolated from *Calcarina hispida*, scale bar = 2 μm. Illustrations A, B, C, and F by J.J. Lee, D by H.J. Spero, E by Mary Downes Gastrich; D reprinted from *Journal of Phycology* (v. 23, p. 312) by permission.
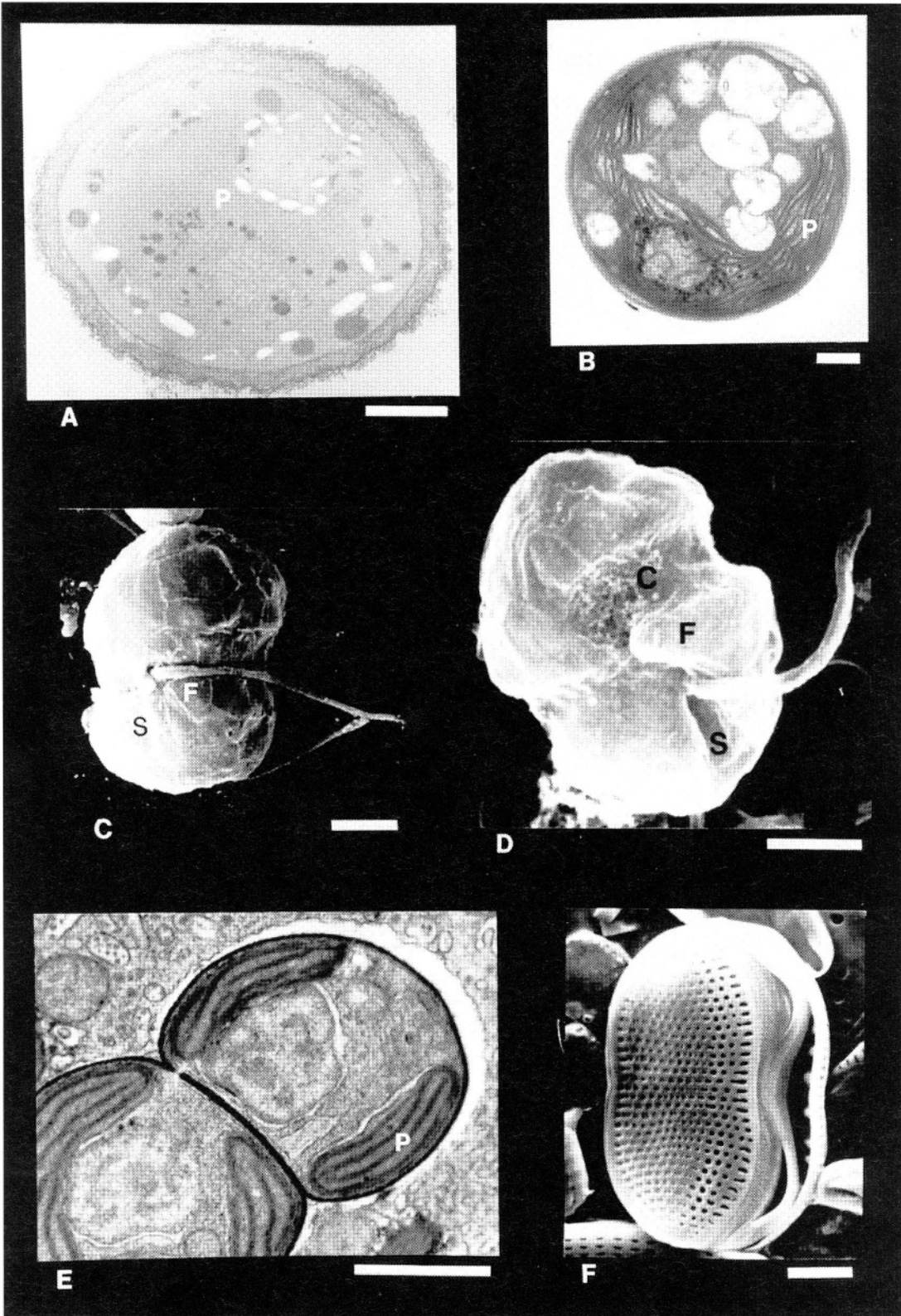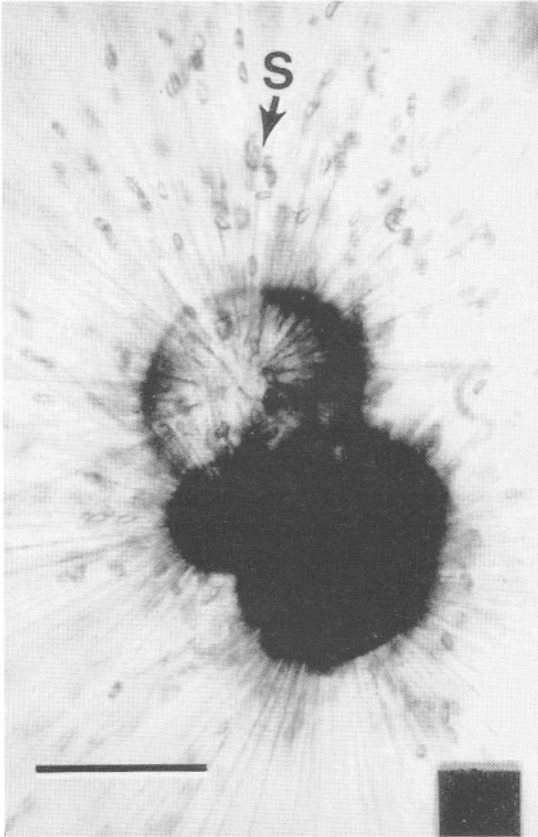
Figure 8.3 Light micrograph of a live *Orbulina universa* illustrating deployment of the dinoflagellate symbionts (S), on the spines of the host. Photo by H.J. Spero, reprinted from Journal of Phycology (v. 23, p. 310) by permission.

vides protons (equation 8.2) that make CO_2 readily available from the much more abundant bicarbonate ions (equation 8.3). That is, calcification:

$$Ca^{2+} + HCO_3^- \Rightarrow CaCO_3 + H^+ \tag{8.2}$$

promotes photosynthesis:

$$HCO_3^- + H^+ \Rightarrow CH_2O + O_2 \tag{8.3}$$
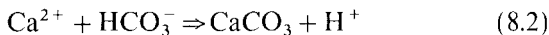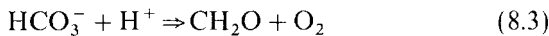
(CH_2O is a simplified expression for organic matter produced during photosynthesis, i.e. photosynthate). According to this hypothesis, the electron capture phase of photosynthesis provides ATP for active transport of Ca^{2+} and H^+ ions, promoting calcification and making bicarbonate ion a viable source of CO_2 for

the organic-carbon synthesis phase of photosynthesis.

Another link between photosynthesis and calcification may simply be the production of ATP, which can be used as an energy source for active transport within the cell. Erez (1983) found essentially normal calcification rates in perforate, symbiont-bearing foraminifers that had been treated with a herbicide that blocks the carbon fixation step in photosynthesis, but not the initial production of ATP. ATP provides the energy source for concentration of the inorganic carbon into internal reservoirs in the larger perforate taxa, and into vesicles in the imperforate species (ter Kuile, 1991). ATP may also provide the energy for removal of ions that can inhibit calcification, including NH_4^+, PO_4^{3-}, and Mg^{2+} (ter Kuile, 1991). Foraminifers with algal endosymbionts may use sunlight rather than food resources as the source of energy for ATP, thereby accounting for the significant enhancement of calcification by light (e.g. Duguay and Taylor, 1978; Duguay 1983; Erez 1983; ter Kuile 1991).

The organic matrix of the test is critical in initiating and directing calcification, particularly in perforate foraminifers (e.g. Hemleben *et al.,* 1977; Angell, 1979, 1980; Weiner, 1986; ter Kuile, 1991). The organic matrix also provides strength and flexibility to the test (Weiner, 1986). Lee (1998) discovered that the large, heavy tests of imperforate taxa such as *Marginopora* include substantial quantities of organic matter. Similarly, Toler and Hallock (1998) found that normal *Amphistegina* tests have substantial organic matter, but that the tests of individuals suffering from anomalous symbiont loss may be grossly deficient in organic matter, resulting in weakened and anomalously calcified tests. The organic chamber lining of the shell matrix of many foraminifers, which provides structural integrity to the test, is composed of glycosaminoglycans that are 99.5% polysaccharide and 0.5% protein (Weiner and Erez, 1984). Carbohydrate from photosynthate may be contributing to the organic matrix of the shell. This and other hypotheses concerning the role of the organic matrix in biomineralization are fertile topics for further research.

8.2.3 Uptake of host metabolites

Another postulated advantage of algal symbiosis, particularly for very large species, is the possible role of the symbionts in removal of host metabolites. Protists are dependent upon processes such as diffusion, active transport, and cytoplasmic streaming for transport of materials into, out of, and within the cell. The assumption behind the hypothesis of metabolic removal is that the larger the foraminifer, the greater the transport problem. Presumably, having intracellular symbionts could partially alleviate this problem. While there is very little evidence either to support or refute this hypothesis, a logical argument against it is that, while the symbionts might remove metabolites during the day, at night they produce their own metabolites, particularly CO_2, which would presumably exacerbate the need for water motion to supply oxygen and to remove carbon dioxide and other metabolites. However, the calcification process could benefit from metabolite removal, because NH_4^+ or PO_4^{-3} can interfere with crystal formation (e.g. ter Kuile, 1991).

8.2.4 Significance of algal symbiosis to ecosystems

Whatever the benefit to individual organisms, the advantage of such symbioses to ecosystems in nutrient-deficient environments is tremendous. Algal symbiosis is one of the major mechanisms that allows mixotrophic nutrition, that is, the ability to both feed and photosynthesize (Hallock, 1981a), in contrast to autotrophic and heterotrophic nutrition which allows one or the other. In ecosystems dominated by purely autotrophic and heterotrophic nutrition, food webs are based on autotrophic primary producers. There is typically a 90% or greater loss of energy and biomass to respiration with each heterotrophic link in the food web. Mixotrophic nutrition, in contrast, provides essentially 'free links' in the food web. That is, when a mixotrophic organism such as a larger foraminifer or zooxanthellate coral captures a unit of prey, the majority of the digestible organic matter in the prey can be used

by the host for growth and reproduction. Photosynthesis by the symbionts provides energy for the host's respiratory needs (Falkowski *et al.*, 1993). Thus, the biomass transfer from the prey to the mixotroph can potentially be far greater than the typical 10%. Prolific calcification, regardless of whether it promotes photosynthesis or is a byproduct thereof, provides substratum for whole ecosystems to develop and flourish. Furthermore, although the significance of mixotrophic nutrition in plankton communities is just beginning to be recognized (e.g. Stoecker, 1998), its contribution to recycled production in open-ocean communities appears to be significant. Perhaps most importantly, planktonic Foraminifera, many with algal symbionts, account for about 20% of global carbonate production (Langer, 1997), and thereby play a key role in marine geochemical cycles, whether the foraminiferal tests are dissolved in corrosive deep-sea waters or accumulate as foraminiferal ooze on the seafloor.

8.3 DISTRIBUTIONS OF BENTHIC FORAMINIFERS WITH ALGAL SYMBIONTS

Like most groups of organisms, the larger foraminifers exhibit higher diversities in the Indo-Pacific region than in the central Pacific, Gulf of Aqaba, and western Atlantic/Caribbean regions (Table 8.1). This is particularly true within the three larger rotaliid families (Hallock, 1988a,b). The Indo-Pacific Amphisteginidae (Fig. 8.1.F) and Nummulitidae (Fig. 8.1.H) each include five or six relatively well known and easily distinguishable species, as compared to one or two variable species in the Caribbean. The third rotaliid family, the Calcarinidae (Fig. 8.1.G), is restricted to the Indo-Pacific. Among the imperforate taxa, the Alveolinidae (Fig. 8.1.E), rhodophyte-bearing Peneroplidae (Fig. 8.1.A) and Soritinae (Fig. 8.1.D) are also more diverse in the Indo-Pacific than in the Caribbean. However, for taxa that have chlorophyte symbionts (Table 8.1), i.e. the unornamented Peneroplidae (Fig. 8.1.B) and the

Table 8.1 Comparison of selected symbiont-bearing benthic Foraminifera from Caribbean and western Pacific regions. The number in parenthesis is the number of species recognized for the genus in the particular area (adapted from Hallock 1988a).

Family (subfamily)	Symbiont Class	Western Pacific	Caribbean
Alveolinidae	Bacillariophyceae	*Alveolinella quoyi*	
		Borelis sp. (1–2)	*Borelis pulchra*
Peneroplidae	Rhodophyceae	*Dendritina* spp. (2)	*Dendritina* spp. (4?)
		Monalysidium sollasi	
		Peneroplis spp. (2)	*Peneroplis* spp. (2)
		Spirolina spp. (2)	*Spirolina* spp. (2)
	Chlorophyceae	*Laevipeneroplis malayensis*	*Laevipeneroplis* spp. (3?)
Soritidae			
(Archaiasinae)	Chlorophyceae		*Androsina lucasi*
			Archaias angulatus
			Cyclorbiculina spp. (3)
		Parasorites orbitolitoides	*Parasorites* spp. (2)
(Soritinae)	Pyrrophyceae	*Amphisorus hemprichii*	*Amphisorus hemprichii*
		Marginopora spp. (2)	
		Sorites spp. (2?)	*Sorites* spp. (2?)
Amphisteginidae	Bacillariophyceae	*Amphistegina* spp. (5–6)	*Amphistegina* sp. (1–2?)
Calcarinidae	Bacillariophyceae	*Baculogypsina sphaerulata*	
		Baculogypsinoides spinosus	
		Calcarina spp. (3)	
		Neorotalia calcar	
		Schlumbergerella floresiana	
Nummulitidae	Bacillariophyceae	*Assilina ammonoides*	
		Cycloclypeus carpenteri	
		Heterostegina spp. (2)	*Heterostegina antillarum*
		Nummulites venosus	

Archaiasinae (Fig. 8.1.C), the trend is the opposite (Table 8.1). In the Caribbean, this group is represented by five genera and ten or more species, as compared to the western Pacific, where there seems to be only two monospecific genera. Deciphering this anomaly may, in the future, provide insight into the paleoceanographic history of the Caribbean.

Depth trends of larger foraminiferal distributions are a key tool for paleoenvironmental interpretation (e.g. Hottinger, 1983, 1997; Hallock and Glenn, 1985, 1986). The most thorough studies to date on depth distributions of Indo-Pacific living larger foraminifers are those of Reiss and Hottinger (1984), Hallock (1984), and Hohenegger (1994), carried out in the Gulf of Aqaba, Belau (Palau, Western Caroline Islands), and Okinawa, respectively. Hottinger (1983) noted that the maximum depth for symbiont-bearing organisms in the Gulf of Aqaba is 130 m,

corresponding to 0.5% of surface light intensity. Figure 8.4 summarizes distributions of four modern larger foraminiferal families, illustrating trends in test shape with depth.

8.3.1   Larger rotaliid foraminifers

Larger foraminifers belonging to the Order Rotaliida share several important characteristics that enable them to effectively exploit an extensive depth range of euphotic habitats in warm, clear, nutrient-deficient seas (Hallock, 1988a,b). One characteristic is the ability to establish endosymbioses with several diatom species. This allows one species of foraminifer to exploit a substantial range of light intensities, which are contingent upon the photic requirements and limitations of several different diatom species (e.g. Lee and Anderson, 1991a). The flexibility of the endosymbiosis is complemented by the
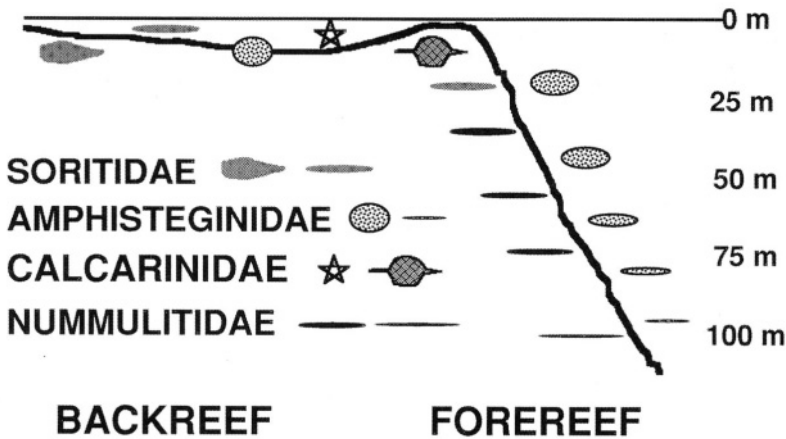
Figure 8.4 Cartoon representation of shape trends with depth in four families of symbiont-bearing benthic foraminifers.

structural characteristics of the perforate, hyaline, lamellar, low-magnesium calcite tests (Hallock, 1988a,b). Calcite secretion with the crystallographic c-axes perpendicular to the test surface, as observed by Towe and Cifelli (1967), provides the potential for the development of very transparent, hyaline tests which can transmit most available light energy. The lamellar structure permits thickening of the test wall through the life of the protist, which may be advantageous in shallow, high-light environments. In the Calcarinidae and Nummulitidae, the lamellar wall structure is modified into a canal system providing a variety of advantages that complement symbiosis (Röttger et al., 1984; Röttger and Krüger, 1990). In the Calcarinidae, in particular, the canal system permits the thickening and translucency of the shell, reducing light penetration and allowing individuals to live in the upper meter of brightly-lit tropical waters. The lamellar structure and canal system also allow for the complex spine systems in the calcarinids, thus providing anchoring and stability in high energy reef-flat and reef-margin environments (Röttger and Krüger. 1990).

Efficient precipitation and maintenance of low-Mg calcite tests do not require greatly elevated carbonate saturation states. Most of the larger rotaliid families arose during the early Paleogene, when atmospheric CO_2 concentrations were two or more times higher than present levels (e.g. Berner, 1994) and so sea-surface carbonate saturation levels were significantly lower. On the other hand, these foraminifers do not thrive under elevated salinities, with concomitant elevated alkalinity. The potential for crystal poisoning by Mg^{2+} should be investigated as the mechanism involved, since Mg^{2+} increasingly interferes with calcite precipitation as carbonate saturation state increases (Morse and Mackenzie, 1990).

(a) Amphisteginidae. The Amphisteginidae are the most studied of the symbiont-bearing families. The best known species are *Amphistegina lobifera* Larsen and *A. lessonii* d'Orbigny (Fig. 8.1.F) in the Indo-Pacific, and *A. gibbosa* d'Orbigny, the sibling species of *A. lessonii,* in the Caribbean. All three occur abundantly at depths less than 30 m, and are amenable to culture. Around some Pacific islands, *A. lobifera* and *A. lessonii* may be so abundant that they are major contributors to coastal sediments (McKee et al., 1959; Hallock 1981b). They live on firm substrates, both reefal and phytal, and may also occur in sandy substrates (Hohenegger, 1994). Generation times appear to be 3–6 months at depths < 30 m (Hallock, 1981c; Hallock et al., 1986b), but are probably longer in deeper habitats where there is less light energy. Generation times in *A. lobifera* are 6–12 months (Hallock. 1981c). Harney *et al.* (1998) and Dettmering *et al.* (1998) documented

trimorphic life cycles in *A. gibbosa.* That is, besides typical alternation of sexual and asexual generations, one or more schizont generations may occur between the agamont and gamont generations.

In the Indo-Pacific region, *Amphistegina* spp. exhibit a fairly straightforward depth zonation (Fig. 8.4) that is accompanied by shape trends (Larsen, 1976; Larsen and Drooger, 1977; Hallock, 1979). The shallowest-dwelling taxon, *A. lobifera,* is by far the most robust, with thickness-to-diameter ratios (t/d = minimum to maximum diameter) typically in excess of 0.6. These foraminifers predominate in shallow backreef and reef-margin environments at depths typically < 10m; *A. lessonii* somewhat overlaps *A. lobifera* in both range and morphology, though t/d ratios are generally 0.35–0.5, and optimum depths appear to be 10–30 m (Hallock 1984; Hohenegger 1994). Live *A. lessonii* can be found from the shallow subtidal down to depths of 100 m if water transparency is sufficient. They apparently do this by cryptic behavior at the shallow end of their depth range, thereby avoiding damaging light intensities, and possibly by utilizing symbiont species that are adapted to lower light intensities at greater depths (Lee *et al.,* 1980). *Amphistegina radiata* (Fichtel and Moll) is common at 20–50 m, and ranges to nearly 100 m in depth (Hallock, 1984; Hohenegger, 1994). *A. radiata* has a limited geographic distribution and does not occur in the central Pacific (e.g. Hawaii). Hottinger *et al.* (1993) reported a very small *A. radiata*-like form in the Gulf of Aqaba, living at somewhat deeper habitats than those found in the western Pacific. *A. bicirculata* Larsen is similar to *A. lessonii,* but has consistently lower t/d ratios of about 0.2–0.35 (Larsen, 1976; Hallock, 1979). Specimens are seldom found at depths < 30 m, and can be recovered live to depths > 100 m. *Amphistegina papillosa* Said is the deepest dwelling member of the genus, capable of surviving on the minimal light available at depths > 100 m (Larsen, 1976). Their tests are typically very flat, appearing almost paper thin, and have tiny papillae on test surfaces, the characteristic for which the species was named. The geographic distribution of *A. papillosa* appears to be similar to that of *A. radiata.*

In the western Atlantic and Caribbean, *Amphistegina gibbosa* is the predominant species of this genus. Whether it is the only species is controversial. Test morphologies are highly variable, and range between a form essentially indistinguishable from *A. lessonii* and the robustly plano-convex 'gibbose' forms for which the species was named. *A. gibbosa* has a wide depth distribution similar to, though generally slightly deeper than, that of *A. lessonii.* Live individuals can often be found at depths < 5 m on patch reefs and to 100 m on open carbonate-shelf environments, though their preferred depths appear to be ~ 15–40 m. Test shape is not as predictable with depth as it is in *A. lessonii* (Martin and Liddell, 1988).

(b) Nummulitidae. Habitats and geographic ranges of most species of Nummulitidae are incompletely known, because their occurrence in deep-euphotic areas (generally >30m) is beyond prudent SCUBA sampling depth (Fig. 8.4). These protists live on both firm and sandy substrates (Hohenegger, 1994). Some nummulitids lack true primary and secondary apertures; instead, they have canal systems that serve similar fundamental roles in locomotion, growth, excretion, reproduction and protection (Röttger *et al.*, 1984). The canal system permits the extrusion of pseudopodia from any point of the marginal cord. Trimorphic life cycles appear to be the norm in this group (e.g. Leutenegger, 1977a; Röttger *et al.,* 1990), and may partly account for the dearth of sexually-produced agamonts in most populations (Drooger, 1993). Agamonts are often distinctive, even without sectioning to confirm microspheric embryons, because these individuals typically grow to sizes substantially larger than schizonts and gamonts.

Heterostegina depressa d'Orbigny (Fig. 8.1.H) is the most widespread of all larger foraminiferal species, present in the Gulf of Aqaba and throughout the tropical and subtropical Indian and Pacific Oceans. It is the only larger rotaliid species that survived the oceanographic changes in the eastern tropical Pacific associated with the closure of the Central American Seaway

(Crouch and Poag, 1987). The Caribbean sibling species, *Heterostegina antillarum* d'Orbigny, appears to have diverged following the uplift of the Isthmus of Panama. *H. depressa* is the only nummulitid commonly found at depths less than 20 m, though its optimum depths are 20–60 m (Hallock, 1984; Hohenegger, 1994). Shallower-dwelling populations may be sustained primarily by successive asexual generations, while deeper dwelling populations appear to utilize sexual reproduction more commonly in their life cycles (Röttger *et al.*, 1990). Their very low light tolerances (Röttger and Berger, 1972) indicate that cryptic behavior may be necessary for them to survive at shallow depths. Individuals are amenable to culture, as demonstrated by the pioneering laboratory observations of Röttger (1972, 1973, 1974, 1976). Schizont reproduction occurs at about 6 months of age (Röttger and Spindler, 1976). Diameters at reproduction of *H. depressa* in culture range from about 2 mm for schizonts to 4 mm for gamonts to 7–14 mm for agamonts (Röttger *et al.*, 1986, 1990).

Assilina ammonoides (Gronovius) is superficially similar in appearance to *H. depressa,* but chambers of *Assilina* are not subdivided into chamberlets. This species is widely distributed throughout the Indo-Pacific, ranging from the Gulf of Aqaba (Hottinger, 1977; Hottinger *et al.,* 1993) to Hawaii in the central Pacific (Hallock, 1984). *Assilina* is common from 20–100 m, with an optimum depth of around 60 m. Though it can be found on firm substrate, it appears to prefer sand and muddy sand habitats (Hohenegger, 1994).

Nummulites venosus (Fichtel and Moll) is the only extant species of the name genus of the family. Individuals may be relatively lenticular and involute as juvenile and subadult agamonts, or even as adult schizonts and gamonts. Agamonts typically grow to much larger sizes than gamonts and schizonts. Hohenegger (1994) reported their depth range as 20–80 m, peaking in abundance at 40 m.

The two deepest-dwelling nummulitids, *Heterostegina operculinoides* Hofker and *Cycloclypeus carpenteri* Brady, have classic flat, thin, 'deep-euphotic' morphologies (Fig. 8.4). The latter species also differs from the other nummulitids in that the planispiral growth form develops into an orbitoid morphology early in life, so that adult individuals are large, thin disks with slightly elevated (thicker) central regions (Song *et al.,* 1994). Agamont generations of *Cycloclypeus* are apparently quite long lived, with test diameters exceeding 120mm (Koba, 1978). Gamonts and schizonts reproduce at considerably smaller sizes (Krüger *et al.,* 1996). Although the geographic distribution of *Cycloclypeus* is not well known, it appears to have a relatively restricted distribution in the Indo-Malay and far western Pacific. Another deep-euphotic species, *Heterocyclina tuberculata* (Möbius), has been reported from the Gulf of Aqaba and from the Indian Ocean (e.g. Hottinger *et al.,* 1993).

(c) Calcarinidae. The Calcarinidae, which live predominantly in shallow, high energy reef-flat and reef-margin environments (Fig. 8.4), include five genera: *Baculogypsina, Baculogypsinoides, Calcarina, Neorotalia,* and *Schlumbergerella* (Hohenegger, 1994; and personal communication). With the exception of *Neorotalia calcar* (d'Orbigny), which occurs in the western Indian Ocean region, the Calcarinidae are restricted to the Indo-Malay archipelago and western Pacific (Table 8.1), and are very important carbonate sediment producers in this region. Sediment production estimates, projected from known rates of production by *C. gaudichaudii* d'Orbigny (Fig. 8.1.G) from Belau, can approach those of reef-flat corals at 3–5 kg $CaCO_3$ m^{-2} yr^{-1} (Hallock, 1981b). In the Ryukyu Islands, the famous star-sand beaches are composed primarily of the shells of *Baculogypsina* (Hohenegger, 1994).

The elaborate calcarinid canal systems and spiny morphologies provide numerous points of contact with the external environment. Röttger and Krüger (1990) described an attachment mechanism in *Baculogypsina sphaerulata* (Parker and Jones) that consists of a durable, elastic organic cement, which enables individuals to adhere by a single spine to the algal substratum. This attachment mechanism allows calcarinids to thrive in high energy environments.

The very limited geographic distributions of the Calcarinidae indicate that their dispersal potential must be quite limited. However, factors contributing to the very widespread distributions of *Amphistegina lessonii* and *Heterostegina depressa* are no better understood. A study of biological and ecological factors associated with distributional patterns of larger foraminifers is long overdue.

8.3.2   Larger miliolid taxa

The imperforate foraminifers of the Order Miliolida construct porcelaneous-appearing tests of high-magnesium calcite. Distributions of imperforate taxa characterized by algal endosymbionts are not as well known as those of similar perforate taxa. In large part, this is because of taxonomic difficulties with miliolids, which are morphologically more plastic, and include many species that are superficially similar. From an ecological perspective, the larger miliolids can be discussed by the kind of symbionts they host.

Hallock (1988a,b) noted that the larger miliolids are most common in shallower habitats, and tend to have a more restricted depth range than the larger rotaliids (Fig. 8.4). The miliolid test structure includes a layer of randomly-oriented crystals, covered by a brick-like layer of crystals oriented with the c-axis parallel to the outer wall, resulting in a naturally opaque structure. To efficiently host algal endosymbionts, the shell wall over the chambers must be thinned (Hallock and Peebles, 1993). Thus, test structure may account for some of the distributional limitations on these foraminifers.

Test mineralogy may also provide other advantages and disadvantages, depending upon the environment. High-Mg calcite becomes increasingly easy to precipitate as the carbonate saturation state of the seawater increases (Morse and Mackenzie, 1990). This may partly explain the predominance of Archaiasinae in the western Atlantic and Caribbean (Hallock, 1988a,b). Oceanic salinities are 1–3‰ higher in the tropical Atlantic than in the tropical Pacific, contributing to higher alkalinity and degree of $CaCO_3$ saturation in the Atlantic (Broecker and Peng,

1987). The divergence of tropical ocean chemistries occurred during the Miocene and Pliocene with the emergence of the Isthmus of Panama. During this time, the porcelaneous, high-Mg-calcitic Archaiasinae became the predominant larger foraminifers in western Atlantic and Caribbean (Frost, 1977). In the Indo-Pacific region, localities with elevated salinities, such as the Persian Gulf (Murray, 1973) and Shark Bay, Australia (Davies, 1970; Logan and Cebulski 1970), are dominated by ornamented Peneroplidae. ter Kuile (1991) observed that external sources of bicarbonate are more important than enzymatic processes for calcification in imperforate Foraminifera, providing a clue to the success of these foraminifers in high alkalinity environments. Because high-Mg calcite is relatively weak, and the miliolid shell structure is not bilamellar, organic matter in the shell may provide necessary strength to the test.

The Alveolinidae are the only imperforate taxa known to harbor diatom symbionts (Lee *et al*., 1989). In modern seas, this family is represented by two genera and a few species. *Alveolinella quoyi* (d'Orbigny) (Fig. 8.1.E) appears to be geographically limited to the Indo-Malay and western Pacific regions. Its habitat includes fore-reef rubble and sands at depths from 5 to 50 m (Lipps and Severin, 1985; Severin and Lipps, 1989; Hohenegger, 1994). The much smaller *Borelis* spp. are circumtropical in distribution and can be found on reef rubble at depths to at least 30 m. *Borelis pulchra* (d'Orbigny) is one of only four symbiont-bearing foraminifers documented in the eastern tropical Pacific by Crouch and Poag (1987).

Two chlorophyte-bearing species have been reported from the Indo-Pacific (Table 8.1). *Parasorites orbitolitoides* (Hofker), a medium depth (10–60 m), sediment-dwelling species, occurs in New Caledonia (Debenay, 1986), off Okinawa (Hohenegger, 1994), on the Great Barrier Reef, and on the west Australian shelf (Hallock, unpublished observation). Cheng and Zheng (1978) described an unornamented peneroplid, which they called *Puteolina malayensis,* occurring abundantly around the Xisha Islands, Guangdong Province, China. Hallock (1984)

found a similar unornamented peneroplid on reef flats in Belau, Western Caroline Islands. Live specimens of both species exhibit the grass-green symbiont color characteristic of chlorophyte-bearing foraminiferal taxa. Loeblich and Tappan (1987) considered *Puteolina* to be a junior synonym for *Laevipeneroplis.*

Western Atlantic/Caribbean miliolid species with chlorophyte symbionts have been studied in detail by Lévy (1977, 1991) and by Hallock and Peebles (1993). The larger, internally-complex archaiasines include the *Androsina-Archaias-Cyclorbiculina* group distinguished by Levy (1977, 1991). *Androsina lucasi* Lévy was described from hypersaline reef flats in the Bahamas (Levy 1977), and is found very abundantly on dwarf-mangrove flats in the Florida Keys (Levy, 1991: Hallock and Peebles, 1993). *Archaias angulatus* (Fichtel and Moll) (Fig. 8.1.C) is abundant on shallow reef (Fig. 8.4) and open shelf sites (Hallock and Peebles. 1993). *Cyclorbiculina compressa* (d'Orbigny) can be found in shallow seagrass beds on the open shelf, but is more common on the reef margin at depths of 10–30 m (Fig. 8.4). Hallock and Peebles (1993) observed that chamberlet outer-wall thickness was distinctive in this group, with *Androsina* characterized by a relatively thick (up to 20 µm) wall, *A. angulatus* by an intermediate wall thickness ($\sim 6–8$ µm), and the deeper-dwelling *Cyclorbiculina* by the thinnest ($3–4$ µm) wall. Hallock and Peebles (1993) postulated that wall thickness was an adaptation to regulate light reaching the endosymbionts.

Lee *el al.* (1974) identified the chlorophyte symbionts of *A. angulatus* as *Chlamydomonas hedleyi.* Live specimens of *Laevipeneroplis proteus* (Fig. 8.1.B) appear to have the same symbionts (Leutenegger, 1984). Lee *et al.* (1979) described the symbionts of *Cyclorbiculina compressa* as *Chlamydomonas provasoli.* Lee and Bock (1976) reported that carbon gain by feeding was more than ten times greater than carbon fixation by photosynthesis in *A. angulatus.* Thus, the principal role that symbiosis appears to play is in enchanced calcification. Duguay (1983) reported that calcification rates varied with light intensity and were 2–3 times faster in the light than in the dark.

Parasorites is also common throughout the Caribbean, and occurs regularly in both soft sediment and reef-rubble samples taken at 10–30 m depth. Lévy (1977) called this genus *Broeckina,* and distinguished two species in the Bahamas: *B. discoidea* (Flint) and *B. orbitolitoides* (Hofker). A comparative study of the Indo-Pacific and Caribbean *Parasorites* and *Laevipeneroplis* is needed to clarify relationships within these genera. Several species of unornamented peneroplines (*Laevipeneroplis* spp., see Fig. 8.1.B). occur throughout the Caribbean in reef and open shelf environments.

Foraminifers that host red algae (Division Rhodophyta) as symbionts include extant members of the Peneroplidae with test-surface ornamentation, i.e. *Peneroplis, Dendritina, Spirolina,* and *Monalysidium* (Loeblich and Tappan, 1987). These foraminifers provide excellent opportunities for further study, particularly with reference to morphologic variability, habitat preferences, and physiology of their symbiotic relationships.

Hawkins and Lee (1990) and Lee (1990b) have studied the unique relationship between the rhodophyte symbiont, *Porphyridium purpureum* (Fig.8.2.A), and its foraminiferal host. Unlike other symbionts, the rhodophyte cell is not membrane bound within the host cytoplasm, and in that respect could be considered an organelle rather than a symbiont. In culture, *Porphyridium* cells are surrounded by a heavy fibrous polysaccharide sheath, but when the symbionts are located in a host, the sheath is reduced or absent. Lee and Anderson (1991a) suggested that sheath-fiber digestion by the host may be a mechanism of energy transfer from symbiont to host.

Hypersaline environments in Shark Bay, Western Australia, and the Persian Gulf are dominated by peneroplids. In Shark Bay, Davies (1970) and Logan and Cebulski (1970) reported low foraminiferal diversities with assemblages dominated by *P. planatus,* with a few other miliolid species, at salinities up to 70‰. Similarly, *Peneroplis planatus* (Fichtel and Moll), *P. pertusus* (Forskal) and a variety of miliolids dominate shallow-water, hypersaline habitats in the Persian Gulf (Murray, 1973).

Extant members of the subfamily Soritinae host dinoflagellate symbionts. Physiological studies by Lee and co-workers (Lee and Bock, 1976; Faber and Lee, 1991a) indicate that these foraminifers derive most of their carbon needs from their food rather than from their symbionts. So the benefit of the symbiotic relationship remains an open question. More recent observations by Lee *et al. (*1995, 1997) and Lee (1998) indicate that the soritine foraminifers, like the amphisteginids, do not require a particular species of symbiont, but rather one of a suite of acceptable symbionts. The physiology of the alga, which makes it capable of being a symbiont and recognizable as such by the host, appears to be more important than taxonomic identity. This relative flexibility of the symbiotic relationship is of obvious advantage to the host organism, which is dependent upon symbiosis but can accept any of several possible algal species rather than being dependent upon a single species of algae. Since the foraminiferal zygote must acquire symbionts following zygosis, the possibility of incorporating any of several potential symbiont species may increase the survival rates of sexually-produced individuals (Lee, 1998).

Taxonomic ambiguities hinder interpretation of literature reports of geographic ranges, depth distributions, and habitats of the Soritinae. *Marginopora* has been used in reference to both *Marginopora* and *Amphisorus* species, *Amphisorus* for both *Amphisorus* and *Sorites* species, and *Sorites* for both *Sorites* and *Parasorites.* The large, robust *Marginopora vertebralis* Quoy and Gaimard probably has a geographic and depth distribution similar to that of *Calcarina* spp. *Marginopora* can live on either firm or soft substrate (Hohenegger, 1994), attaching to algal thalli with an organic cement (Ross, 1972).

Amphisorus hemprichii Ehrenberg is intermediate in robustness, and has wide depth and geographic ranges. This species has been reported circumtropically, from the Gulf of Aqaba (e.g. Hottinger *et al.,* 1993) through the Indian Ocean and across the Pacific to Hawaii (Phillips, 1977), the eastern tropical Pacific (Crouch and Poag, 1987), and the Caribbean

(Lévy, 1977). It prefers firm substrates and can partially adhere to phytal substrates. *Amphisorus* (identified by Davies, 1970, as *Marginopora*) occurs in Shark Bay, Western Australia, at salinities up to 56‰ and temperature range of 14–38°C.

Several species of *Sorites* live on phytal substrates or in algal-bacterial mats that stabilize sandy substrates. These foraminifers can behave as vagile protists or as attached forms, as they can semipermanently attach to firm substrates by an organic cement (Röttger and Krüger, 1990). The type of surface and its shape may influence the growth and morphology of the foraminifer. Kloos (1980) noted that, in the Netherlands Antilles, living *S. orbiculus* (Forskal) appeared to prefer the seagrass *Thalassia* as substratum.

8.4   PLANKTONIC FORAMINIFERA WITH ALGAL SYMBIONTS

Compared with benthic Foraminifera, there are relatively few extant species of planktonic foraminifers (e.g. Kennett and Srinivasan, 1983). Yet these protists approach global distribution (e.g. Murray, 1991a) and, as previously noted, produce roughly 20% of the calcium carbonate fixed in the world's oceans each year (Langer, 1997).

Hemleben *et al.* (1989), in their comprehensive compendium on modern species, noted that 'The presence of algal associations with spinose planktonic Foraminifera is one of the most obvious features of living individuals' (p. 86). Algal symbionts include dinoflagellates, which occur in the Globigerinidae and the Hasterigerinidae, and chrysophytes, which are found in representatives of the Globigerinidae, Candeinidae, Pulleniatinidae, Hastigerinidae, and Globorotaliidae (Lee and Anderson, 1991a). As a general rule, symbioses with dinoflagellates appear to be obligative (Hemleben *et al.,* 1989); the exception may be the variety of dinoflagellates that can be associated with the bubble capsule of *Hastigerina pelagica* (d'Orbigny) (Spindler and Hemleben, 1980). On the other

hand, symbioses with chrysophytes (Fig. 8.2.E) appear to be facultative, since both Gastrich (1988) and Hemleben *et al.* (1989) reported that individuals of some species reported to host chrysophyte symbionts commonly lack symbionts during winter months.

Spero (1987) isolated and described the dinoflagellate symbiont in *Orbulina universa* d'Orbigny as *Gymnodinium béii.* (Figs. 8.2.D, 8.3). This symbiont occurs in several other species (Lee and Anderson, 191la), and may be the only dinoflagellate species to establish symbioses with planktonic foraminifers (Gast and Caron, 1996). In their hosts, *G. béii* individuals are small (5–10 μm) and coccoid; 10^3 to 10^4 symbionts may occur in a single host cell (Spero and Parker, 1985). When isolated from the host and incubated in culture, these dinoflagellates develop flagellated gymnodinoid morphologies (Fig. 8.2.D; Spero, 1987). When the planktonic foraminifers reproduce, releasing flagellated swarmers, algal symbionts are either lysed, digested, or released into the environment (Hemleben *et al.*, 1989). Early in their life, the juvenile foraminifers must encounter and incorporate symbionts (Hemleben *et al.*, 1989), indicating that suitable dinoflagellate populations are free-living in the water column.

As discussed earlier, the potential advantages of algal symbiosis include energy from photosynthesis, enhancement of calcification, and uptake of host metabolites by symbiotic algae. This certainly applies to planktonic as well as to benthic foraminiferal symbioses (Hemleben *et al.,* 1989; Caron and Swanberg, 1990). The host deploys its symbionts outside the test along the spines within the rhizopodial network during the day (Fig. 8.3), and withdraws them into the cytoplasm within the shell at night; light reception by the symbionts triggers deployment (Caron *et al.,* 1981; Bé, 1982). This diel cycle appears to allow maximum exposure of the symbionts to light during the day. By bringing the symbionts inside the test at night, they are made less vulnerable to micrograzers and are given enhanced exposure to host metabolites. This behavior may also provide the opportunity to harvest symbionts according to the host's nutri-

tional needs (Hemleben *et al.,* 1989). Symbiosis appears to aid calcification in these foraminifers (Bé *et al.,* 1982).

Algal symbiosis has possibly provided an important energetic advantage in the adaptation of planktonic symbiont-bearing foraminiferal lineages to low nutrient environments, especially in subtropical and tropical oceanic environments (Hallock *et al.,* 1991a; Norris, 1996b).

8.5 LARGER FORAMINIFERS AND GLOBAL CHANGE

Rapidly increasing human populations are altering the Earth's environments in unprecedented ways, or at least at unprecedented rates. Major categories of anthropogenic change include increasing concentrations of greenhouse gases, which influence climate and ocean chemistry; increasing input of anthropogenic nutrients to aquatic systems; and ozone depletion, which increases the intensities of biologically damaging ultraviolet radiation penetrating the surface waters of the oceans. How will these changes affect foraminifers with algal symbionts? Can the histories of symbiont-bearing foraminifers aid scientists in predicting consequences of global change (Fig. 8.5)?

Greenhouse gas-induced global warming may actually be advantageous to many foraminifers with algal symbionts. Warm episodes in the geologic past expanded habitats for both symbiont-bearing planktonic and larger benthic foraminifers, as subtropical belts expanded into higher latitudes, and as sea level rose and flooded continental shelves.

Increasing atmospheric CO_2 also strongly affects ocean chemistry, with predictable effects on photosynthesis and calcification. It is a paradox of carbonate geochemistry that higher concentrations of atmospheric CO_2 actually promote dissolution of $CaCO_3$. At the same time, higher CO_2 concentrations means that calcification is less important as a source of CO_2 for photosynthesis in aquatic systems (McConnaughey 1989c). Doubling to tripling of current CO_2 levels, as are predicted for the 21st century
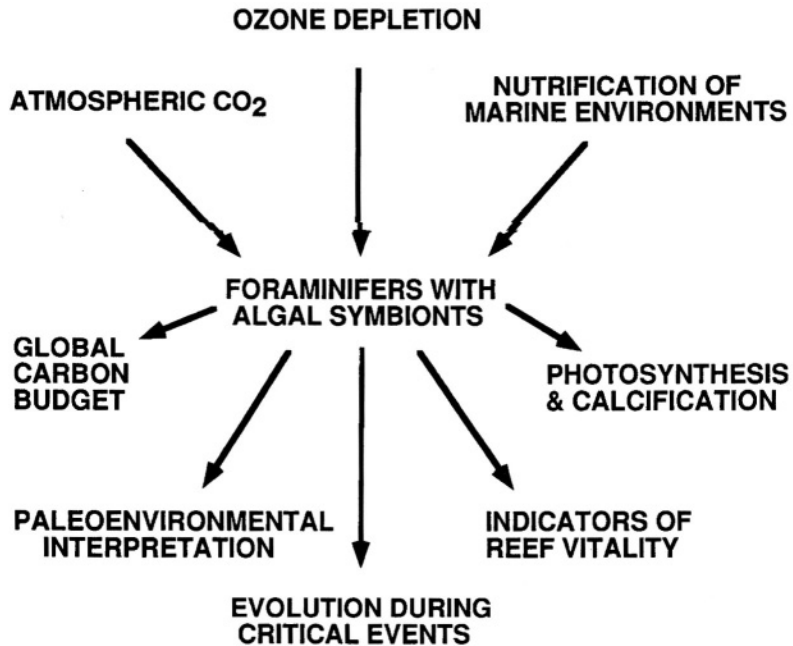
Figure 8.5 Some of the fields that may benefit from research on the response of symbiont-bearing foraminifers to anthropogenically-induced global change.

(e.g. Watson *et al.,* 1990), will lower carbonate saturation levels in surface waters of the oceans. The last time atmospheric CO_2 levels were so high was in the Eocene (Berner 1994), when larger rotaliid foraminifers, coralline algae and bryozoans were the dominant producers of shallow-water carbonates. Will these taxa again replace the aragonitic corals and calcareous green algae as the predominant shallow-water carbonate producers?

Human activities have doubled the rates at which fixed nitrogen is entering terrestrial ecosystems, and a substantial proportion of that nitrogen is washing into aquatic systems (e.g. Vitousek, 1997). The consequences for coastal systems are a spectrum of effects, from 'nutrification' which promotes change in benthic community structure (e.g. Birkeland, 1988; Hallock *et al.,* 1993a; Cockey *et al.,* 1996) to 'eutrophication' which can create or expand 'dead zones' in bays, estuaries and deltas, as has been observed in the Mississippi River delta (e.g. Turner and Rabalais, 1994; Rabalais *et al.,* 1996; Sen Gupta *et al.,* 1996).

Influx of nutrients is a serious threat to benthic communities dominated by algal symbiont-bearing organisms. Cockey *et al.* (1996) compared foraminiferal assemblages from sediment samples collected along transects off Key Largo, Florida, in 1991–92 with assemblages in samples collected in the same area in 1961 (Rose and Lidz, 1977). Assemblages had changed from 60–80% dominance by symbiont-bearing taxa in 1961 to dominance by smaller rotaliid and miliolid taxa by 1992. These changes are consistent with reported declines in populations of reef-building corals on Florida Keys reefs (Dustan and Halas, 1987; Porter and Meier, 1992), and with nearshore nutrient loading reported by Szmant and Forrester (1996). What Cockey *et al.* (1996) found appeared to be classic community shift in response to nutrification (e.g. Alve 1995a).

Many researchers and scientific agencies do not consider ozone depletion to be a problem for tropical marine communities, because intensities of biologically damaging ultraviolet (UVB) radiation are high and seasonally variable at

lower latitudes (Frederick *et al.*, 1989), and because there is the misconception that UVB only penetrates a few meters into seawater. Unfortunately, at least subtropical shallow-water communities may be vulnerable. Strato-spheric ozone depletion has increased biolo-gically damaging ultraviolet radiation to the degree that pre–1960s summer solstice inten-sities are now experienced throughout summer months at subtropical latitudes (Shick *et al.*, 1996). Furthermore, major volcanic events such as the El Chichon eruption in Mexico in 1982 and the Mt. Pinatubo eruption in the Philip-pines in 1991 inject SO_2 molecules into the stratosphere that provide additional substrate for chlorofluorocarbons to attack ozone mole-cules. The Mt. Pinatubo eruption resulted in an approximately 4% increase in ozone depletion (Randel *et al.*, 1995), so that UVB intensities in the early 1990s were as much as 15% higher than intensities in the 1960s. The idea that UVB does not penetrate to any significant depths in marine waters is only partly correct. Indeed, UVB is rapidly absorbed by waters with signifi-cant amounts of plant pigments or refractory organic compounds ('tannins') of terrestrial origin (Bricaud e*t al.*, 1984). However, clear, nutrient-deficient oceanic waters generally do not contain significant concentrations of either phytoplankton or tannins, and as a result, sig-nificant doses of UVB can penetrate tens of meters (Smith and Baker, 1979; Gleason and Wellington, 1993).

There is substantial evidence that *Amphisteg-ina* populations are suffering damage from increasing UVB. Beginning in summer 1991. following the Mt. Pinatubo eruption, *Amphi-stegina* populations in the Florida Keys began to exhibit visible loss of algal endosymbionts (Hallock *et al.*, 1993b). Subsequent sampling along both the east and west coasts of Australia, as well as at several Pacific and western Atlantic localities, revealed that this previously unknown malady was widespread in *Amphistegina* popula-tions in the 1990s (Talge *et al.*, 1997). Monitor-ing of populations in the Florida Keys between 1992 and 1996 revealed that symbiont loss began to increase each March to summer maxima in June or early July, with partial pop-ulation recovery by late summer each year. This pattern indicates a relationship to the solar light cycle, which peaks with the summer solstice in the Florida Keys, and not to the seasonal tem-perature cycle which peaks in August or Septem-ber (Hallock *et al.,* 1995: Talge *et al.,* 1997: Williams *et al*., 1997). The kinds of damage exhibited by the afflicted foraminifers are also consistent with UVB damage, which typically influences photosynthesis, protein synthesis, DNA, and behavior in protists (e.g. Hadar and Worrest, 1991). Talge and Hallock (1995) reported progressive cytoplasmic damage that begins with deterioration of symbiont chloro-plasts, then digestion of the symbionts by the host, and finally autolysis of the host cytoplasm. Afflicted populations exhibited incidences of shell breakage of 15–40%, compared to 5% observed in populations prior to the event (Toler and Hallock, 1998). Reproduction was pro-foundly affected (Hallock *et al.,* 1995; Harney *et al.,* 1998), with schizont broods exhibiting a variety of new morphologies, including encrust-ing forms. Experimental research is needed to substantiate or refute the hypothesis that biologically damaging UV radiation is causing symbiont loss and associated symptoms in *Amphistegina* (Hallock *et al.*, 1995). A parallel concern is whether planktonic foraminifers are also being affected.

8.6 REMARKS

Research on the biology and ecology of modern foraminifers with algal endosymbionts has an exciting future. Anthropogenically-induced changes in the atmosphere and ocean chemistry will most certainly influence these foraminifers. Both field studies and laboratory experiments hold great promise for providing insights into mechanisms ranging from the role of photosyn-thesis in calcification to coral-reef decline to the global carbon budget (Fig. 8.5).

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9

Foraminifera in marginal marine environments

Barun K. Sen Gupta

9.1 INTRODUCTION

Marginal marine habitats, ranging from coastal marshes to inner parts of continental shelves, are usually areas of high organic productivity and relatively high environmental variability. Numerous species of benthic Foraminifera, both eurytopic and stenotopic, have adapted to these environments. Many of these taxa are so characteristic of marginal marine habitats that their abundance in sediment samples immediately brings to the mind of the specialist words such as brackish, coastal, littoral, shallow-water, marsh, estuarine, and reefal. This chapter looks into the common features of distribution of such foraminiferal species and assemblages, and into the limits of their restriction to particular marginal marine habitats. For convenience of description, the foraminiferal distribution is considered mainly under three major environmental headings – coastal marshes and mangrove stands, estuaries and lagoons, and open inner shelves, although they may not be easily separable from each other. The treatment is unequal; more attention is given to brackish-water environments than to those of normal marine salinity.

9.2 COASTAL MARSHES AND MANGROVE SWAMPS

Two groups of vegetation are common in intertidal zones of wet coastal areas (Fig. 9.1). The first, a group of grasses, mainly prevalent in temperate zones, forms salt marshes; the other, a group of trees, at places intermingled with marsh vegetation, is characteristic of mangrove swamps (mangals) of the tropics or the subtropics (Chapman, 1977). Some of the plant genera in either group, e.g. the marsh grasses *Salicornia*, *Spartina*, *Juncus*, *Arthrocnemum*, and *Plantango*, and the mangrove trees *Rhizophora*, *Avicennia*, and *Acrostichum*, are widespread in both the northern and the southern hemispheres. These remarkable distributions of the plants are probably related to ancient biogeography, but the main areas of salt marshes and mangrove swamps are on coasts protected from strong wave action, or at major river mouths (Chapman, 1977).

9.2.1 Salt marshes

The macro-environment of a given salt marsh may seem uniform, but a variety of habitats is available to smaller organisms (Teal, 1996).
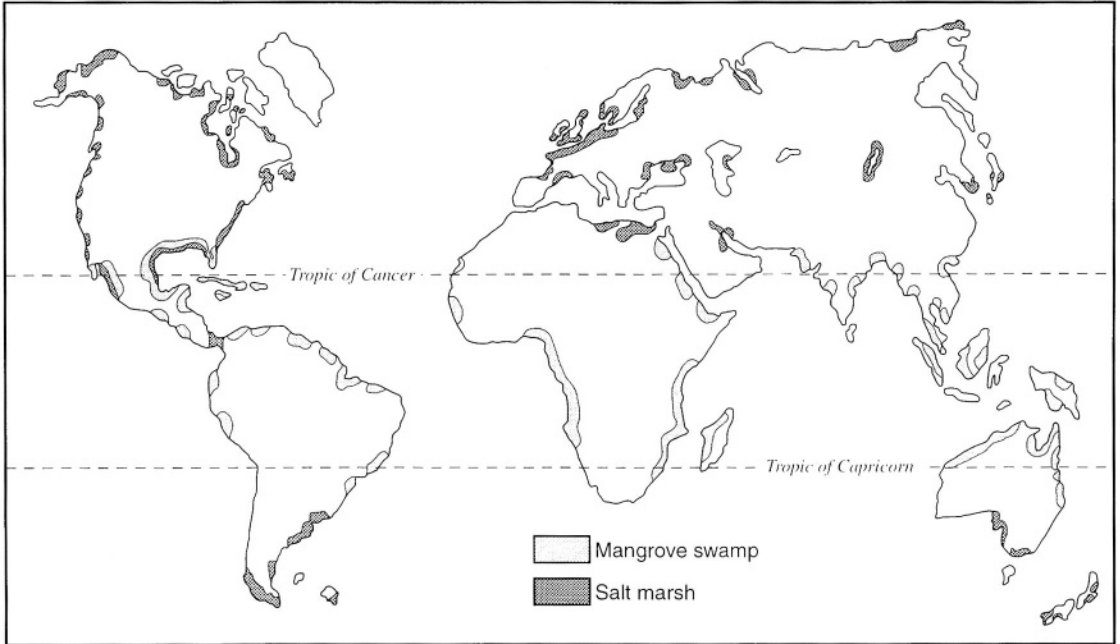
Figure 9.1 Principal areas of salt marshes and mangrove swamps. Modified from Chapman (1977).

Bradshaw (1968) suggested that the following factors are beneficial to Foraminifera living in marsh habitats: (a) lowering of temperature in shade provided by larger and smaller marsh vegetation such as grass, algal mats, and algal clumps; (b) protection from desiccation provided by algal cover; and (c) availability of diatoms and other algae as food. There is no reliable evidence that a particular kind of marsh grass would support a particular kind of foraminiferal assemblage (see Hayward and Hollis, 1994).

There are problems with measurement of total productivity in salt marshes (Long and Mason, 1983), but a consensus exists that the productivity is very high (e.g. Chapman, 1977; Valiela, 1995). This ecosystem is marked by abundant dissolved nutrients, energy-rich reduced compounds, and particulate matter; in some situations, it may be the source of over 40% of the dissolved nitrogen in the less eutrophic, near-shore sea water (Valiela, 1995). The bulk of the primary production is provided by marsh grasses, but a substantial proportion is con-

nected to intertidal algae (Odum, 1971; Long and Mason, 1983).

The inorganic sediment of coastal salt marshes is derived from both terrestrial and marine sources, whose relative importances depend on factors such as the amount of river transport, strength of tidal flow, and wind effects. In addition, accumulating organic debris may eventually be preserved as peat and calcareous shell material. The organic-matter content of the sediment is highly variable even in the near-surface part, e.g. 50% in a Delaware or Massachusetts *Spartina* marsh and 9% in a Morecamb Bay (England) *Puccinellia* marsh (Howes *et al.,* 1981; Long and Mason, 1983). The substrate is anoxic a few centimeters below the surface, except where extensively burrowed (Bertness, 1985).

The grain size of most surficial marsh sediment is fine, because of low current velocities that are further diminished by the baffle of abundant vegetation. The finest sediments are deposited at the landward limit of the tidal excursion, or at the shallow edge of the estuary (Phleger,

1977; Chapman, 1977). The baffle effect of marsh grass on the settling rate of suspended sediment is reflected in the fact that the highest sedimentation rates are frequently at the lowest level of continuous vegetation, and not at the lowest level of the marsh (Adam, 1990). A pure sand substrate is usually too mobile for marsh grasses to take hold, but salt marshes are common on sandy silt substrates (Chapman, 1977). Drainage is poor in salt marsh substrates, except near tidal channels and where animal burrows are abundant (Phleger, 1977). The salinity of substrate pore waters is dependent on several factors, one of which is the ground elevation. In the often-submerged lower salt marsh, salinity is relatively constant and close to that of the flooding water. In the upper marsh, however, the pore-water salinity can be highly variable. Episodes of tidal flooding are infrequent, and in the interim, rainfall may cause a reduction of pore-water salinity. On the other hand, during periods of desiccation, this salinity may increase significantly through evapotranspiration, which may lead to the formation of a saline crust at the surface. In marsh substrates, pore-water salinity higher than that of sea water is not uncommon (Adam, 1990).

Foraminiferal zonation. A suite of widespread agglutinated taxa is generally regarded as typical of coastal salt marshes (Phleger, 1970; Murray, 1971; Phleger, 1977). It includes *Ammotium salsum, Arenoparrella mexicana, Jadammina macrescens, Miliammina fusca, Tipotrocha comprimata,* and *Trochammina inflata* (Fig. 9.2). In addition, a few well-known euryhaline calcareous species, such as *Ammonia beccarii* and *A. parkinsoniana,* are commonly present. Careful examinations of the distributions of these and other marsh species of Foraminifera reveal that low-marsh assemblages can be distinguished from high-marsh ones on the basis of species dominance. For example, along the Atlantic coast of North America, where marshes are extensive and the Foraminifera well recorded, the following species are usually dominant in the three parts of a typical salt marsh that are recognized by their elevations above the low-tide mark: (1) high marsh: *Jadammina*

macrescens, Tipotrocha comprimata; (2) middle marsh: *Trochammina inflata*; and (3) low marsh: *Elphidium williamsoni, Miliammina fusca, Ammonia beccarii* (or *A. parkinsoniana*), *Haynesina germanica* (Murray, 1991b). In a particular marsh, however, the distribution may be much more complex than suggested by the above scheme, because of the complex interplay of biotic and abiotic factors.

The common features and the inherent variability of marsh foraminiferal assemblages are both illustrated by data from three marsh areas along the U.S. Atlantic coast, the first two (Maine and Massachusetts) from between 41° and 45°N latitudes, the third (Georgia) at 31°25N. In these zonal schemes, absence or paucity of some species may be as important as the presence or abundance of some other.

(a) The relationship between surface elevation and the composition of the foraminiferal assemblage in the extensive salt marshes of the Maine coast was studied by Gehrels (1994) along six transects, two of which are shown in Fig. 9.3. The foraminiferal zonation was found to be similar to that reported from the Canadian maritime provinces by Scott and Medioli (1978, 1980a). Using Scott and Medioli's numerical designations of zones, the diagnostic features of the zonal assemblages in Maine are as follows: (1) Zone 1A: 'almost pure' *Jadammina macrescens* forma *macrescens* assemblage; (2) Zone 1B: additional high-marsh species, e.g. *Tipotrocha comprimata, Trochammina inflata,* and *Haplophragmoides manilaensis*; (3) Zone 2A: *Miliammina fusca* replacing *Tipotrocha comprimata* and *Haplophragmoides manilaensis*; (4) Zone 2B: strong dominance of *Miliammina fusca* and appearance of *Ammotium salsum* and calcareous species (Gehrels, 1994).

(b) In the Great Sippewissett Salt Marsh, Massachusetts, *Trochammina inflata* and *Jadammina macrescens* are abundant in all marsh habitats and at all elevations, with *J. macrescens* forma *polystoma* becoming more abundant in high-salinity areas of outer marshes (Scott and Leckie, 1990). A vertical zonation of surface-sediment Foraminifera (related to salinity and ground elevation) in the inner marshes is seen
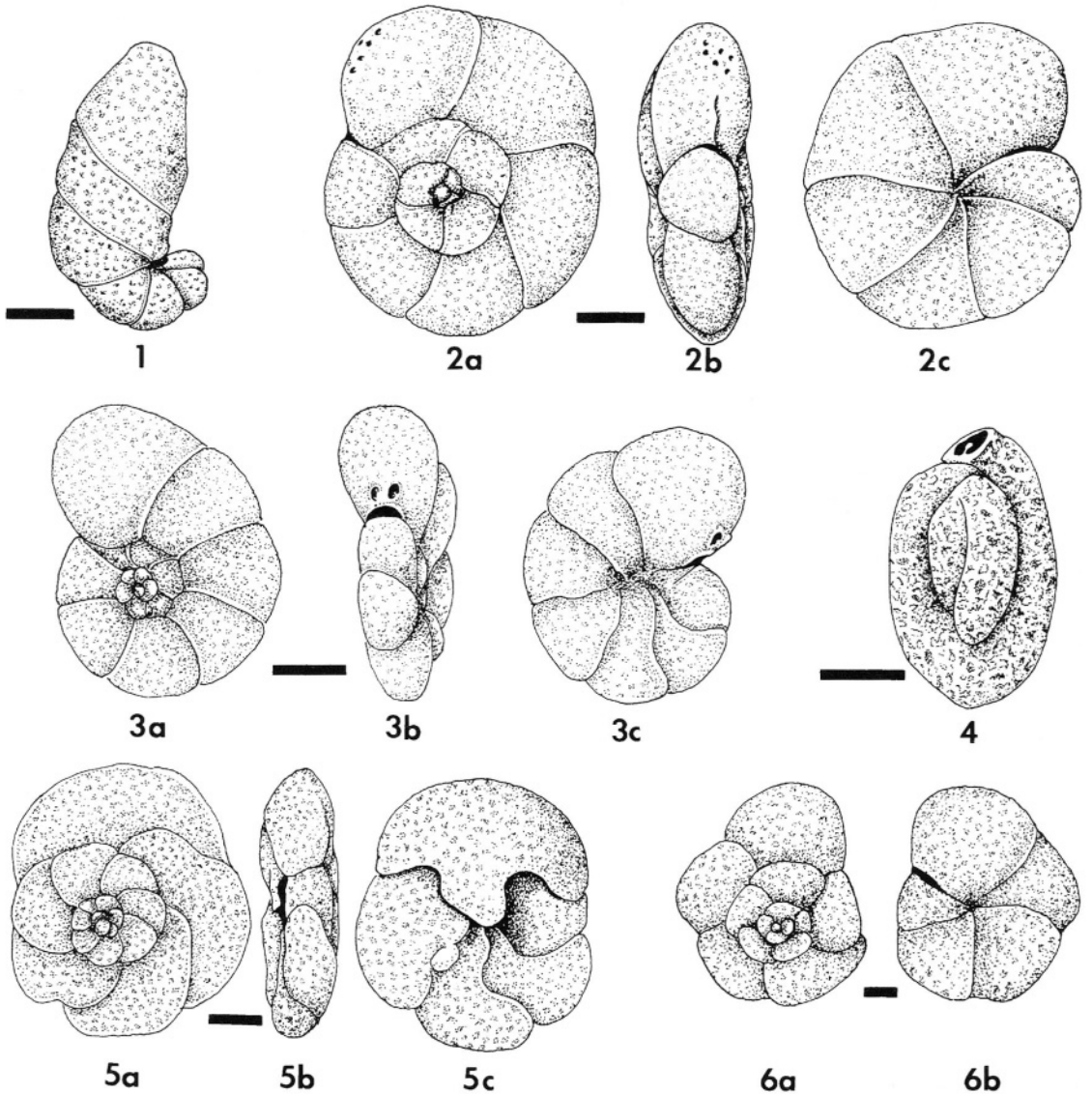
Figure 9.2 Widespread agglutinated Foraminifera of salt marshes: 1, *Ammotium salsum* (Cushman and Brönnimann); 2a,b,c, *Arenoparrella mexicana* (Kornfeld), dorsal, edge, and ventral views; 3a,b,c, *Jadammina macrescens* (Brady), dorsal, edge, and ventral views; 4, *Miliammina fusca* (Brady); 5a,b,c, *Tipotrocha comprimata* (Cushman and Brönnimann), dorsal, edge, and ventral views; 6a,b, *Trochammina inflata* (Montagu). Scale bars = 0.1 mm. Redrawn from Brady, 1884 (6); Cushman and Brönnimann, 1948 (1); Saunders, 1958 (2, 4, 5); and Haynes, 1973 (3).

in the distribution of a number of less common species. The high-marsh zone (mean high water to landward limit of tides), about 22 cm in vertical extent, is characterized simply by the paucity of such species, and a great abundance of *Trochammina inflata* and *Jadammina macrescens*. The transitional high-marsh zone, just below the mean high water, and about 30 cm in vertical extent, is marked by the abundance of *Tipotrocha comprimata*. The low-marsh zone, with the lowermost stands of tall *Spartina alterniflora*, extends from about 25 cm below mean sea level to about 20 cm above it. The typical foraminiferal assemblage of this zone is varied, with
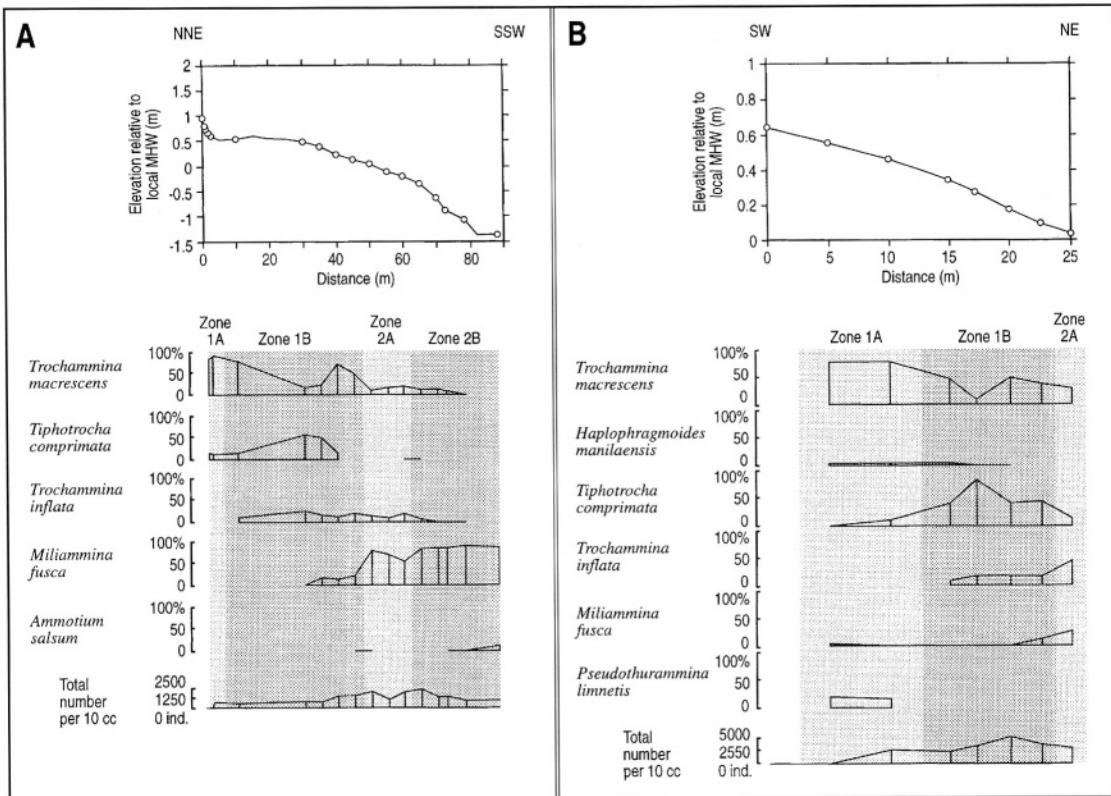
Figure 9.3 Distribution of dominant Foraminifera in Maine marshes. A, Machiasport transect, 44°41′N, 67°24′W; B, Wells Upper Marsh-Edge transect, 43°21′N, 70°33′W. Circles on profiles indicate sampling stations. Redrawn from Gehrels (1994).

abundant *Miliammina fusca, Ammotium salsum, Polysaccammina hyperhalina, Arenoparrella mexicana,* and subtidal estuarine species.

(c) Patterns of foraminiferal species abundance in Sapelo Island (Georgia) salt marshes were reported by Goldstein and Frey (1986). When considered against a simple three-zone scheme of elevation, the dominance of *Miliammina fusca* and *Ammonia parkinsoniana* (*A. tepida* in subsequent publications of Goldstein) here would indeed be typical of the low marsh. The numerical abundance data, however, show that *A. parkinsoniana* is a dominant member of all three foraminiferal associations recognized in Sapelo Island marshes (Goldstein and Frey, 1986). The marsh habitats (within a >2 m tidal range) that support the associations are as follows: (1) tidal-creek banks and streamside-levee marshes (association I); (2) ponded-water marshes (association II); and (3) marshes on major tidal inlets (association III). *Miliammina fusca* also dominates associations I and II. *Arenoparrella mexicana* and *Triloculina oblonga* are two additional dominants of association I. *Jadammina macrescens* and *Trochammina inflata* are not dominant species anywhere, but they are recognized as 'accessory species,' the former in association I, the latter in both associations I and II. *Tipotrocha comprimata* is extremely rare; *Haynesina germanica* is not reported. Overall, the epibenthic or shallow endobenthic *Miliammina fusca* is the dominant foraminifer in Georgia coastal marshes (Goldstein *et al.,* 1995), whereas in Connecticut and Massachusetts marshes, species whose microhabitats are less restricted (e.g. the epibenthic to deep endobenthic *Trochammina inflata* or *Jadammina macrescens*) are the dominant taxa (Saffert and

Thomas, 1998); apparently, this difference is related to the extensive development of low marshes in Georgia and high marshes in New England (Saffert and Thomas, 1998).

The separation between a high marsh and a low marsh fauna becomes less clear in the microtidal setting of the Gulf of Mexico, with a < 0.5 m tidal range along the Louisiana and Texas coasts (Murray, 1991b). For the marsh environment as a whole, all of the species from the Atlantic seaboard mentioned above occur widely in Gulf Coast marshes (see, e.g., Phleger, 1955, 1960b; Scott *et al.*, 1991).

A comparison of marsh Foraminifera from eastern South America (35° to > 50° S latitudes) with their counterparts from North America (35° to >50° N) shows a very close similarity, and *Jadammina macrescens* and *Trochammina inflata* are common constituents of all or most assemblages (Scott *et al.*, 1990). The same association is characteristic of high marshes in northern Europe, from microtidal to macrotidal regimes (Murray, 1991b).

Biogeography, local ecology, and the patchiness of species distributions introduce a strong element of variability in the vertical zonation of marsh Foraminifera, but a high-marsh and a low-marsh fauna are marked by the same or similar groups of species in discontinuous geographic locations. An example of such remarkable faunal similarities is provided by a summation of Pacific Rim marsh faunas (Scott *et al.,* 1996; see Table 9.1); the most noticeable features are the overwhelming dominance of *Jadammina macrescens* and *Trochammina inflata* in the high-marsh assemblages, and the consistent occurrence of *Miliammina fusca* in the low-marsh ones.

9.2.2 Marsh Foraminifera as sea-level or tide-level indicators

Locally, the vertical limits of marsh foraminiferal zones may seem to be fixed with relation to mean tide levels. On this basis, the sedimentary record of marsh assemblages has been used to identify past tide levels. For example, the foraminiferal zone boundaries and the abun-

dance peaks of *Tipotrocha comprimata* in Quaternary coastal sediments of Maine may indicate tide levels with a precision of about 15 cm, and thus may be better clues to ancient tide levels than marsh plants (Gehrels, 1994). Even on a much wider regional scale, the presence and varying abundances of typical marsh Foraminifera have convinced some researchers that such data can help determine sea level or tide level with a precision of 5–10 cm (Scott and Medioli, 1980a. 1986). In this kind of paleoecological analysis, the choice of the modern baseline for the comparison of the fossil assemblage attains a special significance. For example, a well-known model of foraminiferal habitat elevation above sea level (Scott and Medioli, 1986) does not fully apply to the marsh assemblage of coastal Georgia, because (a) species considered as typical of the high marsh (*Jadammina macrescens, Tipotrocha comprimata*), if present, range from high to low marsh, and (b) the model does not include species (*Reophax nana*, *Textularia palustris, Siphotrochammina lobata*) that are regionally common in habitats less than 1.5 above the mean low water (Goldstein and Watkins, 1999).

Environmental factors other than the ebb and flow of tides, especially unrelated salinity variations in substrate pore water may have a critical influence on the distribution of marsh Foraminifera. For example, in the Great Marshes of Barnstable, Massachusetts, the foraminiferal zonation ('marsh fringe,' 'middle marsh,' and 'marsh edge') is related to (a) the salinity gradient, which is strongly affected by precipitation and groundwater seepage, (b) the frequency of flooding, and (c) sediment characteristics, but it does not show a connection with elevation above mean sea level (de Rijk, 1995, de Rijk and Troelstra, 1997). Thus, a global scheme of deciphering minor sea-level changes based on frequency variations of salt-marsh Foraminifera would be unreliable. Furthermore, in the context of the small elevation differences reported for marsh foraminiferal zones, the depths of subsurface microhabitats may become extremely significant. Common infaunal species of Nanaimo, British Columbia, Canada, show the following depth preferences in the substrate: *Jadammina*

Table 9.1 Marsh faunas of the Pacific Rim. After Scott *et al.*, 1996 (original data sources: Scott, 1976a,b; Patterson, 1990; Jennings and Nelson, 1992; Hayward and Hollis, 1994; Jennings *et al.*, 1995; Scott *et al.*, 1996). Areas: 1, Hokkaido, Japan; 2, British Columbia, Canada; 3, Washington State, U.S.A.; 4, Oregon, U.S.A.; 5, northern California, U.S.A.; 6, central California, U.S.A.; 7, southern California, U.S.A.; 8, Chile; 9, New Zealand. L = Low-marsh assemblage; H = high-marsh assemblage. Asterisks indicate calcareous species; all others are agglutinated.

Species/Area	1	2	3	4	5	6	7	8	9
Jadammina macrescens forma *macrescens*	H, L	H	H	H					H
Jadammina macrescens forma *polystoma*			H		H	H	H		
Trchammina inflata		H	H	H	H		H	H		H
Trochamminita salsa								H	H
Haplophragmoides manilaensis	H								
Haplophragmoides wilberti			H						H
Haplophragmoides spp.				H				H	
Pseudothurammina limnetis								H	
Miliammina fusca	H, L	L	L	L	H, L	L	L	L	
Ammotium salsum			L	L					
Ammobaculites exiguus		L		L					
Reophax nana				L					
Polysccammina hyperhalina							L		
Ammonia beccarii		L							
Elphidium spp.		L							L
Hayensina depressula									L

macrescens, 2–8 cm; *Trochammina inflata*, 0–20 cm (high marsh) or 0–25 cm (low marsh); *Haplophragmoides wilberti*, 3–7 cm; and *Miliammina fusca,* 0–3 cm (Ozarko *et al.*, 1997). Similar documentation is available from other areas. A considerable part of the agglutinated assemblage is found below a sediment depth of 2.5 cm in Massachusetts and Connecticut salt marshes,

with *Trochammina inflata* commonly present at levels as deep as 20–25 cm (Saffert and Thomas, 1998). In the salt marshes of St. Catherines Island, Georgia, various agglutinated species are found within the upper 10 cm of the substrate, but in deeper levels, the common species are *Arenoparrella mexicana* and *Haplophragmoides wilberti* (Goldstein *et al.*, 1995). Clearly, a sam-

pling of the uppermost one or two centimeters of the substrate would produce a misleading model for the interpretation of small shifts in past sea level (Ozarko *et al.*, 1997). Finally, taphonomic effects must be factored in, even when calcareous species (very poorly preserved, because of the acidity of marsh sediments) are not taken into consideration. Goldstein and Watkins (1998) estimate that, in salt marshes of the southeastern U.S., as much as 90% of the foraminiferal assemblage in the upper 10cm of sediment may be removed by taphonomic processes, and that some deep endobenthic species (e.g. *Arenoparrella mexicana*) may be much better preserved than shallow endobenthic species (e.g. *Miliammina fusca*), thus introducing a significant bias in the data. Furthermore, typical high-marsh species are better preserved than low-marsh species (see chapter 16 for a discussion). Thus, although modern distributions of salt-marsh Foraminifera may permit the recognition of microhabitats separated by a few centimeters, especially in temperate latitudes, foraminiferal paleoecological analysis is unlikely to yield past elevation levels that are nearly as precise.

9.2.3   Mangrove swamps

Mangrove swamps cover about 70% of the coasts of the world, and many well-known foraminiferal species of salt marshes also occur in these swamps (Boltovskoy, 1984). In particular, two such marsh species, *Ammotium salsum* and *Arenoparrella mexicana,* also dominate mangrove assemblages in diverse areas, e.g. Trinidad, Florida, Ecuador, Brazil, and Colombia (various reports, summarized in Boltovskoy, 1984). There may be a remarkable similarity between mangrove foraminiferal assemblages from very different longitudes. For example, species of *Ammotium, Arenoparrella, Haplophragmoides, Miliammina,* and *Trochammina* are common to mangove-stand assemblages in Sumatra (Biswas, 1976) and Trinidad (Todd and Brönnimann, 1957; Saunders, 1958). An exception is seen in the mangrove Foraminifera of northern New Zealand; *Miliammina fusca* and two wide-spread calcareous species of marginal marine waters (*Ammonia beccarii* and *Elphidium excavatum*) are the dominant species (Hayward and Hollis, 1994). The transition from a characteristic mangrove-swamp foraminiferal assemblage to a lagoonal assemblage may take place rather abruptly. On the southern coast of Puerto Rico, such a change takes place within a horizontal distance of a few meters, the true mangrove fauna being entirely agglutinated (except for *Ammonia tepida*), and the lagoonal fauna being largely calcareous (Culver, 1990). Horizontal and vertical zonations of foraminiferal species within mangrove swamps are unclear, but some have been reported from the Brazilian coast (e.g. Zaninetti *et al.*, 1979; Scott *et al.*, 1990). It has been suggested that these foraminiferal zonations may not be directly associated with mangroves, but are controlled by salinity, temperature, substrate organic content, and exposure to the atmosphere (Scott *et al.*, 1990). A parallel argument may be made for many marsh assemblages.

9.3   ESTUARIES AND LAGOONS

An estuary, according to a definition commonly accepted in marine ecology, is a 'semi-enclosed coastal body of water having a free connection with the open sea and within which the seawater is measurably diluted with fresh water deriving from land drainage' (Cameron and Pritchard, 1963). Coastal lagoons, unlike typical estuaries, do not have a wide-open (i.e. free) connection to the open sea (McLusky, 1981). Within any particular latitudinal zone or biogeographic province, similar foraminiferal assemblages exist within true estuaries and coastal lagoons. The broad features of these assemblages and their distributions are summarized below. The common environmental feature is the brackish salinity, between 35‰ and 0.5‰. In addition, estuarine waters may range from well-mixed to highly stratified, and the salinity may vary more than 3‰ from surface to bottom (Officer, 1983).

Foraminiferal communities of estuaries and

lagoons may have conspicuous common elements with both the local marsh or mangrove fauna and the local, inner-shelf, normal-marine fauna; large-scale distribution patterns are generally related to a salinity gradient. Such a pattern is well-illustrated by a comprehensive distribution study of New Zealand marginal marine species (Hayward and Hollis, 1994). Several foraminiferal facies (or species associations) related to salinity and tide levels can be identified here on a regional scale; some of these are typical of intertidal vegetative habitats, but the exact nature of vegetation has little effect on the foraminiferal associations. Eight species, reported from many areas outside New Zealand, are obligate brackish in all of the studied New Zealand estuaries, harbors, inlets, and lagoons. Some are well-adapted to a considerable salinity range, and the foraminiferal facies intergrade (Fig. 9.4). Using their overall distributions, however, the species can be arranged in groups on a scale of preference for increasing salinity: (1) *Trochamminita salsa* (least saline); (2) *Haplophragmoides wilberti, Miliammina fusca*; (3) *Trochammina inflata, Jadammina macrescens, Ammotium fragile, Pseudothurammina limnetis*; (4) *Helenina anderseni* (most saline). Several facultative brackish-water species are also present in New Zealand coastal habitats (Fig. 9.4). In the absence of adjacent marsh or mangrove swamps, and the presence of very high seasonal fresh-water discharge, estuarine foraminiferal zonations may be poorly developed. For example, in the Russian River estuary, northern California, the only agglutinated species of significance is *Miliammina fusca*. In the main channel of this estuary, the assemblage is generally dominated by species that are typical of shallow marine habitats of this area, but excludes species of *Ammonia* and *Ammobaculites* that are abundant in nearby estuaries. Furthermore, the marine species invade the estuary only in summer when fresh-water discharge is low, and disappear in winter when discharge is high and the salt-water wedge is removed or reduced in size (Erskian and Lipps, 1977).

Foraminiferal differences among nearby estuaries may relate to tide levels. On the Atlantic seaboard of eastern Canada (Nova Scotia and New Brunswick), such differences are seen in the assemblages of three estuaries: Miramichi, Restigouche, and Chezzetcook, the first mainly shallow subtidal, the second mainly deep subtidal, and the third mainly intertidal (Scott *et al.*, 1980). The sharpest contrast between the intertidal and subtidal estuaries is in the absence of agglutinated species *Ammotium cassis* in the former, which may be due to the speculated preference of *A. cassis* for bottom water with copious suspended particulate matter (Olsson, 1976; Scott *et al.*, 1980), or to the large salinity and temperature fluctuations in this intertidal zone. Furthermore, calcareous species such as *Ammonia beccarii* and *Elphidium williamsoni* are characteristic of intertidal, rather than subtidal, communities. Inter-estuary faunal differences are much less pronounced in the upper estuaries (dominated by the agglutinated *Miliammina fusca*) than in the lower, where the marine influence is strong. In general, however, significant abundances of agglutinated species such as *Saccammina atlantica, Reophax arctica*, and *Cribrostomoides crassimargo* are typical of deeper-water eastern Canadian estuaries. Other agglutinated species may show very high local dominance in the deeper parts of an estuary. For example, in the western part of the Restigouche estuary, *Eggerella advena* and *Ammotium cassis* may constitute more than 90% of the assemblage in areas deeper than 10 m, whereas in shallower waters, diverse species, including the calcareous *Elphidium excavatum*, *Haynesina orbiculare*, and *Buccella frigida*, together with the agglutinated *Miliammina fusca*, may be common (Schafer and Cole, 1978).

Extreme dominance of agglutinated species has been reported also from several estuaries far from Restigouche. A striking example is the dominance of *Ammobaculites crassus* in Chesapeake Bay estuaries (Virginia) in 1–15‰ salinity (Ellison and Nichols, 1970; Ellison, 1972). A very high abundance of *A. crassus* is supported by estuarine vegetation (eelgrass) and organic-rich sediment, and this may be the only foraminiferal species in some of these areas. In surrounding habitats, the *Ammobaculites* facies is
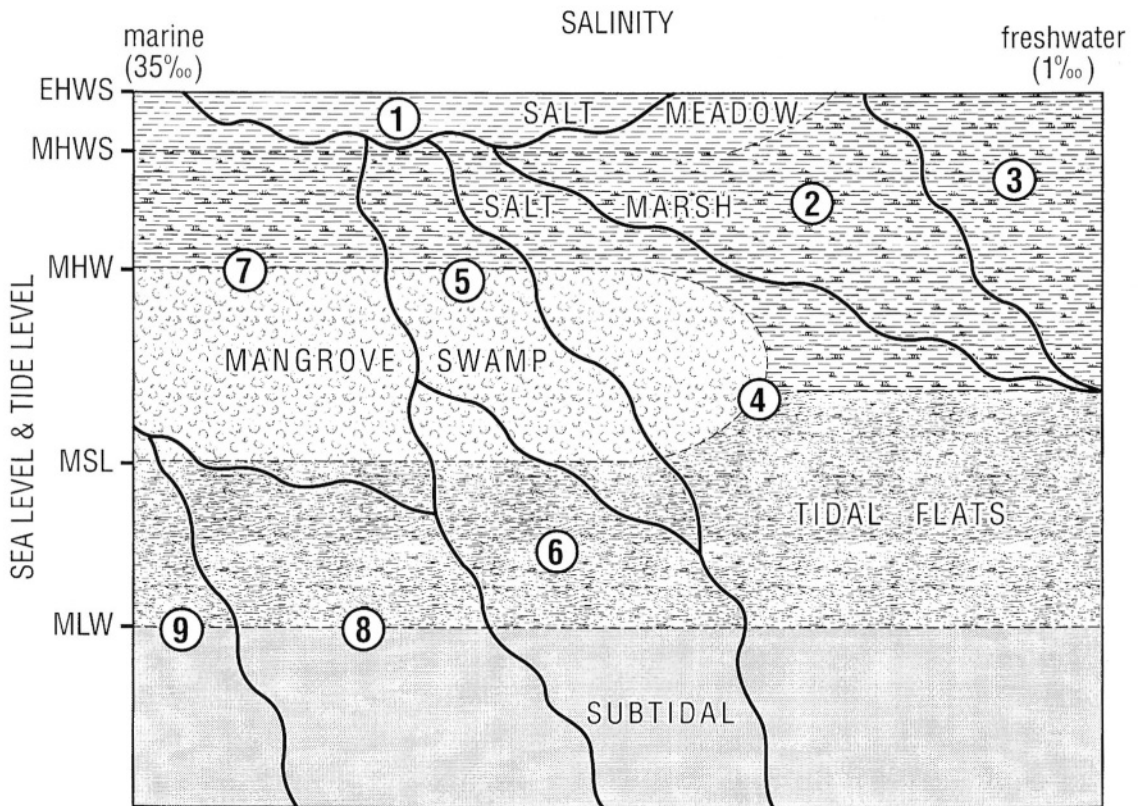
Figure 9.4 New Zealand brackish-water foraminiferal associations (circled numbers), named after dominant species: 1, *Trochammina inflata* association (subdominant *Jadammina macrescens, Miliammina fusca, Haplophragmoides wilberti*); 2, *Haplophragmoides wilberti* association (subdominant or codominant *Miliammina fusca, Trochammina inflata, Trochamminita salsa*); 3, *Trochamminita salsa* association (subdominant *Miliammina fusca, Haplophragmoides wilberti*); 4, *Miliammina fusca* association (subdominant *Haplophragmoides wilberti, Trochamminita salsa, Trochammina inflata, Ammotium fragile*); 5, *Elphidium excavatum* association (subdominant *Miliammina fusca, Ammonia beccarii*); 6, *Ammonia beccarii – Miliammina fusca* association (subdominant *Reophax moniliforme, Textularia earlandi*); 7, *Ammonia beccarii – Elphidium excavatum* association (also common: *Haynesina depressula, Buccella frigida, Helenina anderseni*); 8, *Ammonia beccarii* association (subdominant *Haynesina depressula, Elphidium advenum*). A ninth, high-diversity assemblage includes typical brackish-water species (e.g. *Ammonia beccarii, Haynesina depressula, Elphidium advenum*), as well as normal marine species (e.g. *Elphidium charlottensis, Patellinella inconspicua, Quinqueloculina* spp., *Bolivina* spp.). Abbreviations: EHWS, extreme high water, spring level; MHWS, mean high water, spring level; MHW, mean high water; MSL, mean sea level; MLW, mean low water. Modified from Hayward and Hollis (1994).

replaced by an *Elphidium* facies (seaward), a *Miliammina-Ammoastuta* facies (in marshes), and a thecamoebian facies (upstream). Comparable relative abundances of *Ammobaculites* or *Ammotium* have also been reported from the U.S. Gulf coast, e.g. in Sabine Lake of Texas and Louisiana (salinity < 10‰), where *Ammobaculites* or *Ammotium* (taxonomy uncertain) may constitute 40–80% of the assemblage (Kane, 1967). Other areas where a species of *Ammotium* (*A. cassis*) dominates a brackish-water assem-

blage include southern Brazil (Closs, 1963), Baltic Sea (Lutze, 1965; Olsson, 1976), and Sweden (Olsson, 1976). Locally, the effect of salinity change on the relative abundance of *Ammotium* is shown by the data of Phleger (1954) and Anderson (1968) from the same area of the eastern Mississippi Sound, Alabama. The foraminiferal assemblage showed a strong dominance (>90%) of *Ammotium* (reported as *Ammobaculites* sp.) when Phleger sampled the area. Following an increase in salinity (< 10‰)

between 1954 and 1967, probably due to the construction of a bridge system that diverted fresh-water drainage away from the Mississippi Sound, *Elphidium gunteri* and *Ammonia parkinsoniana* became the dominant species (Lamb, 1972).

As in the case of Foraminifera of marshes and mangrove swamps, the species thriving at very low estuarine salinities are usually agglutinated taxa. For example, *Miliammina fusca* and *Ammomarginulina fluvialis* can construct their agglutinated tests at about 5‰ salinity in the Hudson River estuary, New York, but *Ammonia tepida* can secrete only the organic lining, and not the hyaline layers (McCrone and Schafer, 1966). In this context, the survival of a few isolated populations of calcareous species in fresh water (section 9.4) demonstrates an extraordinary adaptation related to the geological history of their habitats.

Some agglutinated species can thrive in both brackish and hypersaline waters. The tolerance of such species to unusually high salinities is seen in the distribution of estuarine and lagoonal foraminiferal assemblages along the west African coast (5°–20°N). Near the mouth of the Casamance estuary, the mixohaline calcareous assemblage is dominated by species of *Ammonia* and *Elphidium,* but those of *Bolivina* and *Lagena* are also present. In the upper reaches of the estuary, as the salinity increases (because of the arid climate), the relative abundances of calcareous species progressively decrease, and those of agglutinated species progressively increase, with *Ammotium salsum* dominating. In the Casamance River, specimens of *A. salsum* have been found even in waters with 100‰ salinity. Farther south, in the nearly landlocked Ebrie Lagoon with a much higher rainfall, salinity remains below normal marine (hypohaline), but *A. salsum* is still the dominant species (Debenay, 1990).

Among calcareous taxa, *Ammonia* and some species of *Elphidium* are well-known for their tolerance to salinity fluctuations. These are present in estuarine faunas of many latitudinal zones. In the Pennar estuary, Bay of Bengal, where monsoonal river discharges cause severe seasonal reduction of salinity, living populations of *Ammonia beccarii* and *Elphidium* spp. are found in a salinity range of about 0.5 to 35‰ (Reddy and Jagadishwara Rao, 1984). On the Arabian Sea coast of the Indian peninsula, Nigam *et al.* (1995) found that the relative abundance of *Rotalidium annectens* covaries with estuarine salinity, and used the stratigraphic variation in this abundance (in an inner shelf core) as a tracer of past monsoonal intensities.

Lagoonal salinities may range from brackish to hypersaline, depending on local climate and tidal flushing. Foraminiferal assemblages of lagoons show great variability, but many are similar to the assemblages of local estuary mouths. On the other hand, different hydrographic characters of adjacent brackish-water lagoons may lead to different foraminiferal assemblages. An illustration is provided by the biotas of Alvarado and Camaronera lagoons on the southern coast of the Gulf of Mexico (Phleger and Lankford, 1978). Alvarado Lagoon is directly connected to the Gulf by an inlet; Camaronera, with no direct link with the Gulf, is connected to Alvarado by a narrow channel, but is more influenced by runoffs from surrounding mangrove swamps. The faunas of both lagoons have a strong mangrove swamp component (e.g. *Ammotium salsum* and *Miliammina fusca*). A marine component (e.g. *Ammonia parkinsoniana* and *Elphidium* spp.) is present in Alvarado, but not in Camaronera, where *Ammotium salsum* usually constitutes about 90% of both living and dead assemblages. In lagoons with significant tidal inflow, the dominance of *Ammonia beccarii* or *A. parkinsoniana* is common. For example, in the lagoon of Venice, Italy, where the degree of marine- and brackish-water mixing and the seasonal variabilty of hydrographic properties are reflected in the presence of several foraminiferal biotopes, the dominant species is invariably *Ammonia beccarii,* constituting about 50–75% of the assemblage (Albani and Serandrei Barbero, 1982; Albani *et al.*, 1998).

In brackish waters, the general trend of foraminiferal species diversity, as measured by richness (species count), is one of decrease with

decreasing salinity. This pattern is well illustrated by data from continental shelves, estuaries, and lagoons of the Black Sea, which is entirely brackish. Foraminifera are present in the oxic (and H_2S-free) upper depths of the Black Sea margin, but there is a persistent diversity gradient among the sampled areas (Yanko and Troitskaja, 1987; Yanko, 1990b, 1998), with the highest number (79) near Bosporus, where the salinity is relatively high (26‰), because of the influx of Sea of Marmara waters. The lowest numbers (< 10) are in lagoonal or deltaic areas, where the salinity is depressed to < 2‰ by freshwater discharge. A parallel decline is seen also in the number of Mediterranean immigrants that form the main component of the Black Sea foraminiferal assemblages (Fig. 9.5).

The geographic distribution of some brackish-water foraminiferal species covers spectacularly wide latitudinal and longitudinal ranges. These species have a high tolerance to the variability of marginal-marine environments, but why is their distribution not blocked by major oceans? Examining this question in the context of marsh,

mangrove-swamp, and tidal-flat Foraminifera of New Zealand, Hayward and Hollis (1994) conclude that these species travel great distances aerially, by accidental transport (and occasional survival) on the muddy feet or feathers of migratory seabirds, because 'for the majority of these birds the first and last landfalls on their journeys are intertidal mud and sand flats.' Such intercontinental sweepstakes dispersal (see Simpson, 1953) by seabirds has been suggested also for small plants, such as the common sundew (*Drosera anglica*), a tiny, carnivorous, bog plant that is widely distributed in the northern hemisphere. The dispersal of this plant to the Hawaiian islands was apparently by means of seeds transported on muddy feet of birds (Carlquist, 1980). The most likely carrier is the Pacific golden plover, which breeds in Alaska, and winters in large numbers in Hawaii, in the habitat favored by the sundew (H.D. Pratt, personal communication).

Transport by birds is also a plausible mechanism for many shorter-distance migrations of foraminiferal species, including that from a
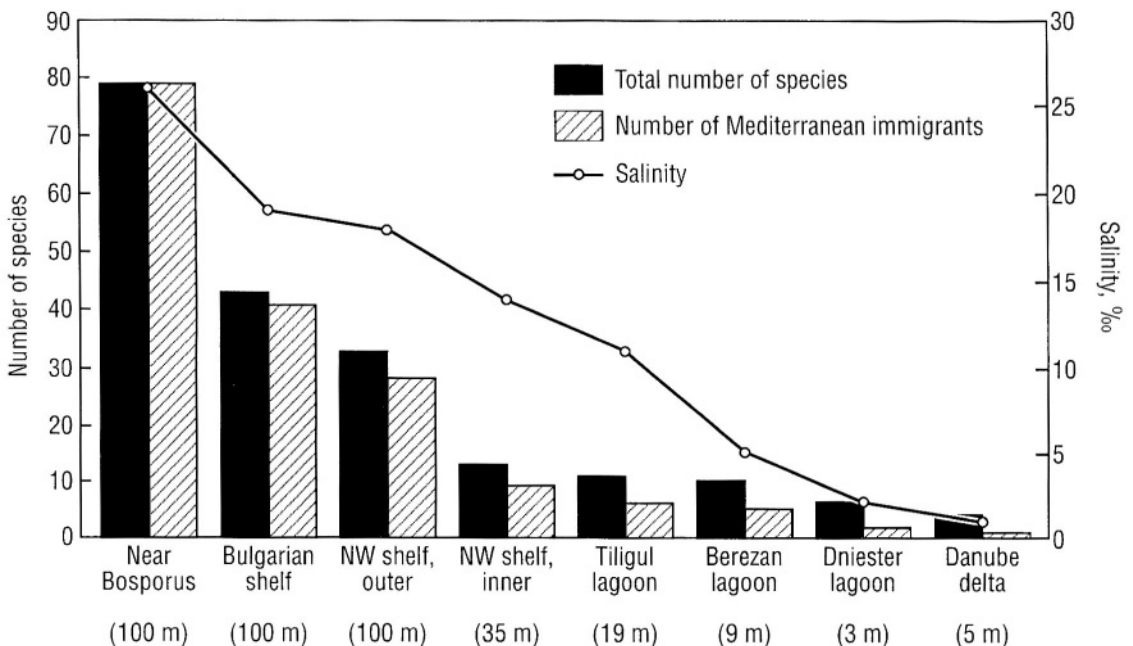
Figure 9.5 Variations in salinity and benthic foraminiferal diversity (richness) at the western margin of Black Sea; depths of sampling areas shown in parentheses. Source: V. Yanko (personal communication).

marine environment to a landlocked saline lake or well (see examples in Resig, 1974). The activity of other animals may also play a role in foraminiferal transport. The introduction of *Ammonia, Elphidium,* and miliolids in the landlocked, brackish Salton Sea of California has been ascribed to 'birds, naval seaplanes, transplantation of marine fishes, and speed-boating' (Arnal, 1954). *Trochammina hadai,* a common species of Japanese estuaries, was introduced in the 1980s into San Francisco Bay, California, where it is now abundant; the species was probably released into this habitat with ballast seawater (McGann and Sloan, 1996).

9.4   FRESH-WATER FORAMINIFERA

Typically, the crossing of the threshold from brackish to fresh-water environments is marked by the disappearance of foraminifers other than the organic-walled Allogromiida. There are, however, a few localities where both agglutinated and calcareous species are known to thrive in fresh water, and are interpreted to be the 'survivors of a prehistoric brackish fauna' (Brady *et al.*, 1870). The best documentation of such fresh-water foraminiferal taxa is from northern Argentina and southern Brazil in water depths of a few meters and salinities as low as 0.1‰ (Boltovskoy and Lena, 1971; Boltovskoy and Wright, 1976). A calcareous species, *Nonion tisburyensis,* is the most persistent member of this assemblage, but agglutinated species, belonging to *Miliammina, Psammosphaera,* and *Trochammina,* are also known; all of these species occur also in nearby brackish areas. *Miliammina fusca* is known to occur in Lake Maracaibo, Venezuela, in waters of about 1‰ salinity (Hedberg, 1934).

9.5   OPEN INNER SHELVES

9.5.1   Clastic shelves

For the purposes of this discussion, the shallowest part of a continental shelf, from the low tide to a depth of about 30 m, is regarded as the inner shelf, although the foraminiferal biotope in many areas may not be significantly different at somewhat greater depths (e.g. at 50 m). A wide range of species is present among inner-shelf foraminiferal assemblages, and there is a large body of literature on their distributions (see Botovskoy and Wright, 1976; Murray. 1991b). A few examples of assemblages from clastic substrates are given here; those from carbonate substrates are discussed in section 9.5.2. The bottom-water salinity in these habitats is within the normal marine range, i.e. about 34–35‰. Unless indicated otherwise, the data refer to total (living and dead) populations of species.

Compared to inshore brackish areas, open inner shelves, including those of large bays, generally support much higher numbers of foraminiferal species, usually with the dominance of the calcareous group. The large-scale distribution of foraminiferal taxa on inner shelves reflects a biogeographic zonation in which temperature (especially its seasonal variation) is frequently the critical factor that promotes or hinders the proliferation of certain species or assemblages. Precise latitudinal comparisons of inner-shelf foraminiferal communities are difficult to make, because of uneven area and sample coverages, patchiness of small-scale distributions, and non-uniform laboratory procedure. Judging simply by numbers of species reported from entire (inner, middle, and outer) continental shelves, it is probable that for open inner shelves, there is a general diversity increase from higher to lower latitudes, in keeping with the general diversity trend of shallow marine biotas (e.g. Briggs, 1974). Locally, a significant change in species diversity from one shallow-marine biogeographic province to the next is seen in an exceptionally well documented record of foraminiferal distribution in equal-volume samples taken from the Cape Hatteras region, North Carolina (Schnitker, 1971). Cape Hatteras (35°14´N, 75°32´W), where the Gulf Stream leaves the continental margin, is the location of the most pronounced marine faunal boundary on the eastern North American continental

shelf, between the Atlantic Northern Inner Shelf and the Atlantic Southern Shelf foraminiferal provinces (Culver and Buzas, 1981b; or the Virginian and Carolinian molluscan provinces, see chapter 6). The mean numbers of species (living and dead) found in two sample groups from 20–25 m water depths (each with 10 samples) are 13 for the northern area and 33 for the southern (and somewhat warmer) area. There is also a pronounced increase in total species richness (s) from inshore waters to those near the shelf edge (at about 80m). In Schnitker's samples, the mean value of s in the 50–80 m depth range is 35 in the northern area (5 samples), and 47 in the southern area (9 samples). In a large suite of samples taken from the Georgia continental shelf (between 30°41′N and 32°00′N latitudes), the values of s and the Shannon-Wiener function of diversity (see Gibson and Buzas, 1973) are distinctly lower in nearshore waters (where they rise steadily) than in waters deeper than 15 m (Fig. 9.6; Sen Gupta and Kilbourne, 1974).

Several regional studies on Arctic Foraminifera have been published, but the coverage of the inner shelf is poor. On the whole, agglutinated species such as *Spiroplectammina biformis, Textularia torquata,* and *Eggerella advena* are dominant or common (Arctic Canada;
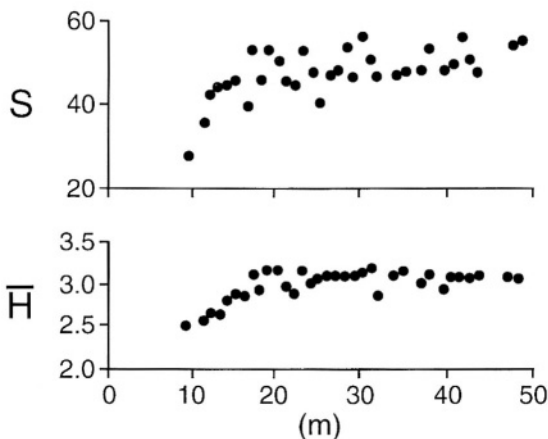
Vilks, 1989). The calcareous component of the fauna may include several species of *Elphidium* (including *E. excavatum*), *Buccella inusitata, Astrononion gallowayi, Islandiella islandica,* and various miliolids (Alaska; Loeblich and Tappan, 1953). Many of these have been reported to continue in water depths >100m (e.g. Schafer and Cole, 1986), but habitat determinations on the basis of distributions of total populations is difficult on high-energy Arctic shelves, because sediment reworking is extensive (Vilks, 1989). In the eastern Arctic, in shallow depths (< 30 m) of Freemansundet Strait (Barents Sea), *Cassidulina reniforme* (restricted to cold, northern waters), *Elphidium excavatum,* and *Cibicides lobatulus* (epibenthic on coarse sediment) dominate the assemblage (Hansen and Knudsen, 1992).

The effect of substrates and factors related to water depth on a cold-water nearshore fauna is reported for a 58-species assemblage from McMurdo Sound, Antarctica, where seven biotopes (sediment with boulders, open deeper water, sponge mat, sediment under sponge mat, seasonally anoxic basin, shallower water, and anchor ice) are recognized in waters < 27 m deep (Bernhard, 1987). Several species that are relatively rare are restricted to particular biotopes, e.g. *Notodendrodes antarctikos* and *Chilostomella* sp. to the open deeper-water biotope. The more abundant species are present in multiple biotopes, but among them, *Globocassidulina* sp. cf. *G. biora* and *Reophax dentaliniformis* are more common in sediments with boulders; *Epistominella exigua, Cribrostomoides jeffreysii,* and *Trochammina ochracea* in shallow areas; *Uvigerina bassensis* in open deeper water; and *Tolypammina vagans* and *Polymorphina* sp. in seasonally anoxic basins.

As in the case of estuaries, species of *Elphidium* and *Ammonia* frequently dominate inner shelf assemblages in many latitudinal zones. In a total assemblage of 22 species from an inner shelf of the English Channel (Lyme Bay, maximum depth about 50 m), the dominant species are *Ammonia beccarii, Elphidium excavatum, Quinqueloculina lata,* and *Brizalina pseudopunctata* in muddy sands, and *Textularia torquata* in

Figure 9.6 Benthic foraminiferal species diversity on part of Georgia shelf, mean values plotted against depth; top, species richness (number of species); bottom, Shannon-Wiener function. Modified from Sen Gupta and Kilbourne (1974).

shelly sands. The major difference between the dominance patterns of living and dead assemblages is in the proportion of *Stainforthia fusiformis,* extremely high in the former, but mostly insignificant in the latter, because of postmortem destruction of its delicate tests (Murray, 1986). In the southern North Sea, *Elphidium excaratum* is the dominant foraminifer in about 25–30 m water depth in the living assemblage (Murray, 1992). The foraminiferal community in the intertidal zone of Puerto Deseado, Patagonia (salinity about 32–34‰) consists of about 130 species (Boltovskoy and Lena, 1970), but sizeable living populations were recognized in only four species: *Buliminella elegantissima, Elphidium articulatum, Epistominella exigua,* and *Elphidium gunteri* (ranked according to relative abundance; Boltovskoy and Lena, 1969).

On the Georgia continental shelf, U.S.A., *Ammonia beccarii* dominates the assemblages in the shallowest waters, but at about 15 m water depth, where there is a shift in the diversity gradient (see above), *Elphidium excavatum* becomes dominant. An inshore thanatotope, whose outer limit is close to the 25-m isobath, has been recognized in this area on the basis of cluster analysis of relative-abundance data. Species common in this thanatotope, besides *A. beccarii* and *E. excavatum,* are *Planulina exorna, Planorbulina mediterranensis, Asterigerina carinata,* and *Quinqueloculina lamarckiana* (Sen Gupta and Kilbourne, 1976). *Ammonia beccarii, Elphidium gunteri, Nonionella atlantica,* and *Hanzawaia concentrica* (among others) are dominant on the inner continental shelf of Nigeria (0–35 m; Adegoke *et al.,* 1976). The same or sibling species are dominant on clastic inner shelves of the Caribbean Sea (e.g. Seiglie, 1966) and the northwestern Gulf of Mexico (personal observation). On the inner shelf of Senegal (depths < 25 m), the typical species are *Cribroelphidium poeyanum, Elphidium gunteri, Haynesina depressula, Nouria poltmorphinoides, Pileolina tabernacularis, Ptychomiliola separans,* and *Spiroplectinella wrighti* (Debenay and Redois, 1997).

Numerous workers, including Alcide d'Orbigny (Heron-Allen, 1917), have studied continental shelf foraminifers from the Mediterranean Sea (see Murray, 1991b). The species diversity of some inner-shelf assemblages is high, as illustrated by the data on replicate samples of living populations collected from 16 points (spaced one meter apart on a sampling grid) at one locality in the Gulf of Trieste, northern Adriatic Sea (Hohenegger *et al.,* 1993). The water depth here is about 15m; winter and summer salinities and temperatures are about 36‰ and 42‰, and 9°C and 23°C, respectively. Forty species were found living, using the Rose Bengal staining test. These included eight agglutinated species (*Reophax nana, Spiroplectinella sagittula, Cribrostomoides jeffreysii,* and *Eggerelloides scabra* dominating), 10 porcelaneous species (*Miliolinella subrotunda* and *Triloculina affinis* dominating), and 22 hyaline species (*Brizalina striatula, Nonionella turgida, Ammonia tepida, Elphidium advenum, E. granosum, Bulimina* sp., and *Epistominella vitrea* dominating).

As shown by this spotty survey, a largely calcareous assemblage dominated by *Elphidium,* with or without co-dominance of *Ammonia,* is typical of cold-temperate to tropical, inner continental shelves with clastic substrates and normal marine salinity (Sen Gupta, 1977). This nearshore *Elphidium-Ammonia* association was noticed by Natland (1933) in a pioneering study of foraminiferal depth zonation off California, and was later recognized as the characteristic element of a biota present along the eastern Pacific shoreline (in depths of 0–30 m) from Central America to northern California (Smith, 1964). Reports from many other continental shelves indicate that one species of *Elphidium, E. excavatum,* may be nearly as widespread as *Ammonia beccarii.* This question is not fully resolved, because taxonomic distinctions among some *Elphidium* species are confusing and highly controversial, due to the intraspecific variablity of retral processes. Current practice places at least four previously recognized 'species' (now labeled 'formas') within *E. excavatum* (Feyling-Hanssen, 1972). Further taxonomic investigation may result in a bigger lumping. One of the variants, *E. excavatum* forma *clavatum,* is apparently restricted to a high northern latitude belt on both sides of the Pacific and Atlantic Oceans

(Smith, 1970). This is also the common form of *E. excavatum* in marginal marine environments, including brackish water, in New Zealand (Hayward and Hollis, 1994). In contrast, *Elphidium discoidale* is known be a 'typical warm-water foraminifer' (Boltovskoy, 1970); its presence at 41°S latitude on the northern Argentine inner shelf has been taken as indicative of the influence of a Brazilian coastal water mass (Boltovskoy, 1970).

Species of *Elphidium* are generally known or assumed to be inhabitants of the continental shelf (although not necessarily the inner shelf), and their presence in bathyal or abyssal sediment is regarded as evidence of sediment reworking (e.g. Phleger, 1951b). There are exceptions, however. Populations of *E. excavatum* have been recovered from waters as deep as 2000 m off eastern Canada and northeastern U.S., and recognized as living by staining with Sudan Black B or Rose Bengal (Schafer and Cole, 1982; Corliss and Emerson, 1990). Another species, *E. batialis,* is apparently restricted to deep waters; living populations have been reported from depths of 1000 m off northeastern Japan (Matoba, 1976).

Extraordinarily high turbidity and voluminous sediment influx can prevent the establishment of foraminiferal communities on inner continental shelves. On the Amazon shelf of northern Brazil, no foraminifers were found in samples collected near the river mouth in water depths of 8–20m (Vilela, 1995).

9.5.2   Coral reefs

Modern larger foraminifers (adult lest size > 1 mm) produce the bulk of the global foraminiferal reef carbonate (Langer *et al*., 1997). In the Pacific and Indian Oceans (for which data have been compiled), their distribution and that of reef-building corals have comparable latitudinal limits, 42°N–40°S for the former, and 39°N–36°S for the latter (Belasky, 1996). The worldwide distribution of symbiont-bearing larger Foraminifera has been summarized and discussed in chapter 8. Many of these species and numerous smaller species are well adapted

to the shallow, well-lit, but nutrient-poor waters of coral reefs and reef slopes in all tropical seas.

Characteristic reef-flat foraminiferal assemblages are particularly diverse in the Pacific and Indian Oceans, and include large, free or attached, calcareous species with distinctive morphologies, e.g. *Calcarina spengleri, Amphistegina lessonii, Marginopora vertabralis, Homotrema rubra, Miniacina miniacea,* and *Carpenteria proteiformis* (Marshall Islands; Cushman *et al*., 1954). A comprehensive list of foraminiferal species constituting a typical Pacific reef-flat community would be much larger, as shown by Baccaert's census (1986) on a small part of the northern Great Barrier Reef, Australia. From three reef flats off Lizard Island, 104 species were identified; eight of these were agglutinated, 43 porcelaneous, and 53 hyaline. The dominant species were as follows: (a) porcelaneous: *Peneroplis planatus, Sorites orbiculus,* and *Marginopora vertebralis,* and (b) hyaline: *Amphistegina lobifera, Calcarina spengleri, Baculogypsina sphaerulata,* and *Elphidium crispum.* The foraminiferal community was found to live mainly on or in the spongy algal cover of the reef, which provides nourishment and protection from desiccation at low tide. Some robust hyaline foraminifers (*Amphistegina, Calcarina, Baculogypsina,* and *Marginopora*) were found attached by their pseudopodia to the thalli of the calcareous alga *Halimeda.*

The most widespread foraminifer genus of coral reefs and other shallow, tropical carbonate banks or hard ground is *Amphistegina.* Five species are known from the Indo-Pacific region, and four from the Gulf of Aqaba (Reiss and Hottinger, 1984); two of these, *A. lessonii* and *A. lobifera,* are abundant in waters < 30 m deep. A single, indigenous, shallow-water species, *A. gibbosa,* is present in reefal areas of the Caribbean Sea and Gulf of Mexico. Nummulitid genera, except for *Heterostegina,* are mostly present in deeper waters (see chapter 8). *Alveolinella* and *Borelis,* two porcelaneous genera of uncommon morphology (planispirally coiled along an elongate axis, with numerous chamberlets; reminiscent of late Paleozoic fusulinids), are frequently found in Indo-Pacific reef sediment

(Hohenegger, 1994); *Borelis* is also present in other tropical areas (see chapter 8).

In coral reef substrates off Fernando de Noronha, northern Brazil, Lévy *et al.* (1995) observed a depth separation of porcelaneous genera within a water depth of 30 m – a soritid-*Quinqueloculina-Triloculina* group dominating in depths less than 10m, and a *Pyrgo-Borelis* group in greater depths, the ubiquitous hyaline reef genus *Amphistegina* being associated with the second group. Faunal differences between reef patches and muddy sediment are strikingly visible in two adjacent bays, both shallower than 25 m, on the leeward side of St. Lucia, West Indies (Sen Gupta and Schafer, 1973). The species count is comparable, 138 in Choc Bay (with coral reefs) and 112 in Castries Bay, but the dominance pattern is very different. *Amphistegina gibbosa, Rotorbinella rosea, Sorites marginalis,* and *Textularia conica* dominate the Choc Bay assemblage, whereas *Ammonia tepida* and *Elphidium poeyanum* dominate the Castries Bay assemblage. *Quinqueloculina lamarckiana* is the only species that occurs abundantly in both bays. As shown by observations in the Gulf of Aqaba, algal covers on hard substrates may be the preferred habitat of many larger or smaller foraminifer species associated with coral reefs. Seasonal transport of 'algal clouds' lead to dispersal of these species (Reiss and Hottinger, 1984).

9.5.3 Seagrass habitats

About fifty species of marine angiosperms, commonly known as seagrasses, inhabit today's inner continental shelves (den Hartog, 1977). They stabilize the seafloor sediment, and provide shelter, including anchor, to a most diverse biota. Thus, the presence of seagrass in subtidal and intertidal habitats may lead to significant modifications of these habitats, causing pronounced changes in benthic communities, including an increase of epifauna and shallow infauna (e.g. Posey, 1988). The trophic resources of seagrass meadows are large and varied, and considerable nutrient recycling takes place in these environments (den Hartog, 1977; Zieman

and Zieman, 1989). Seagrass ecosystems are recognized to be among the richest and most productive coastal ecosystems, a considerable part of the primary production being carried out by a variety of epiphytic algae, which directly provide food and shelter to a spectrum of meiofauna and microfauna. The adaptation of benthic Foraminifera to particular species of seagrass is poorly understood, and their possible co-evolution remains an enigma. However, associations of foraminifers and seagrass meadows are widely reported in the literature. The best-known associations are those of the Soritidae, a porcelaneous foraminiferal family (whose member species have dinoflagellate or chlorophyte endosymbionts; see chapter 8), with seagrass meadows, especially those of the tropical and subtropical Thalassia (Bock, 1969; Murray, 1991b; Martin, 1986; Hallock *et al.,* 1986a; Lévy, 1991; Hallock and Peebles, 1993). In fact, several soritid species (e.g. *Archaias angulatus, Cyclorbiculina compressa, Sorites marginalis, S. orbiculus, Parasorites orbitoloides*) are regarded as tracers of ancient seagrass habitats, and hence as useful paleoenvironmental markers (Brasier, 1975; Eva, 1980; Anderson *et al.*, 1997).

Various porcelaneous and hyaline Foraminifera are known to be attached to the Mediterranean seagrass *Posidonia.* Examples of the first group are species of *Vertebralina, Sorites, Nubecularia,* and *Cornuspiramia*; those of the second are *Planorbulina, Miniacina, Cyclocibicides,* and *Webbinella* (Kikuchi and Pérès. 1977; Murray, 1991b; Langer, 1993). In addition, motile grazers and temporarily attached taxa such as species of *Peneroplis* and *Rosalina* are common. Langer (1993) estimates that over 95% of foraminiferal species living in seagrass or macroalgal substrates are permanently or temporarily motile. Furthermore, some of the attached seagrass Foraminifera may be attached to roots or stems, and not to blades of seagrasses (Langer, 1993). For example, in the Gulf of Aqaba, large populations of the hyaline species *Acervulina inhaerens* and *Miniacina* sp. are attached to the stems, and not to the blades, of *Cymodocea*; the tests of soritids (*Amphisorus hemprichii* and *Sorites orbicutlus*) attached to *Cymodocea* and *Zostera* are

modified for a good fit on the stems (Reiss and Hottinger, 1984). In the same area, the porcelaneous species *Peneroplis planatus* prefers the horizontal rhizomes and stems of *Halophila,* and the sediment underneath, over the erect blades (Faber, 1991).

The dependence of soritids on seagrass or algal turf can be inferred from the composition of the foraminiferal community of West Flower Garden Bank, the northernmost modern coral reef in the Gulf of Mexico. Because of the water depth of the reef (>20 m), extensive vegetative covers are missing, and so are the soritids, although living *Amphistegina* and *Peneroplis* are present (Poag and Tresslar, 1981). It must be emphasized, however, that the soritid-seagrass association is complex, because soritid species may be epiphytic on seagrass in one place, but not in another. *Archaias angulatus* is the dominant shallow-water larger foraminifer in the Florida-Bahamas carbonate province (Hallock *et al.*, 1986a), and is often associated with *Sorites marginalis* in seagrass habitats. However, studies in the Florida Keys show that the first soritid, being also present in reef rubble, is more eurytopic than the second, although its preference for *Thalassia* substrates is well-documented (e.g. Martin, 1986; Hallock *et al.*, 1986a; Hallock and Peebles, 1993). In this province, the euryhaline soritid *Androsina lucasi* is reported from both mangrove and seagrass habitats (Lévy, 1991).

Seagrass habitats are known to support foraminiferal communities even when the water is brackish or hypersaline. The abundance of *Ammobaculites* in Chesapeake Bay, Virginia, provides an example of the first case (see section 9.3), whereas the foraminiferal biota of Shark Bay, a semi-isolated embayment of the Australian Indian Ocean, illustrates the second case (Logan and Cebulski, 1970; Davies, 1970). In salinities ranging between 40‰ and 56‰, seagrass stands support a large foraminiferal community, including the agglutinated *Textularia,* the porcelaneous *Peneroplis, Marginopora, Quinqueloculina,* and *Triloculina,* and the hyaline *Elphidium*, *Amphistegina* and *Cibicides*. In salinities as high as 70‰, a few porcelaneous taxa survive on substrates with algal cover; the dominant species are *Miliolinella circularis, Peneroplis planatus,* and *Spirolina hamelini.* The tolerance of *Peneroplis planatus* to hypersaline conditions is also demonstrated by a study in the Abu Dhabi Lagoon, Persian Gulf. Here the species is epiphytic on seagrass in about 42‰ salinity, and on seaweed in salinities as high as 70‰ (Murray, 1970).

Foraminiferal species richness in tropical or near-tropical seagrass meadows is high; 66 species were found living in a small area of *Thalassia* in the Florida Keys, but the number was adversely affected by turbulence (Bock, 1969). The relationship between population densities of foraminiferal epiphytes and those of host seagrasses is unknown, but in one field test in Papua New Guinea, where a soritid (*Marginopora vertebralis*) is attached to blades of various seagrasses, no correlation was found between the two parameters (Severin, 1987a). As discussed earlier, large populations of the same species flourish in sediments of Pacific reefs (see also Ross, 1972). The dispersal of foraminiferal epiphytes on uprooted or torn seagrass blades has been reported (Bock, 1969; Davaud and Septfontaine, 1995). In addition, gas bubbles trapped in decaying seagrass may help transport foraminiferal tests, as in the case of *Sorites* and *Peneroplis* in Tunisian intertidal areas (Davaud and Septfontaine, 1995).

9.6 SUMMARY

Hundreds of known benthic foraminifer species live in coastal marine environments. Most of them are rare. The dominant species are widely distributed, many across major biogeographic barriers. The transoceanic distribution of some abundant marsh and estuarine species is hard to explain, except by accidental transport and high tolerance to environmental variables. The transition from a brackish to a normal-marine nearshore fauna is generally marked by increases in species diversity and the proportion of calcareous species in the community. A few calcareous genera are represented by the same or sibling species on the soft, clastic substrates

of many inner continental shelves, spanning large latitudinal and longitudinal ranges. Hard substrates and marine vegetation in the tropics support a large variety of taxa, including nearly all living species of larger Foraminifera. With a few exceptions, the biogeographic imprint on nearshore, open-marine faunas is best seen in the composition of the entire assemblage, rather than in the presence or absence of a few dominant species.

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10

Benthic foraminiferal microhabitats below the sediment-water interface

Frans J. Jorissen

10.1 INTRODUCTION

Benthic Foraminifera do not live exclusively at the sediment-water interface, and can be found alive at considerable depths in marine sediments, in many cases down to 10 cm (Fig. 10.1). Within this depth interval, large changes take place in the natural environment, especially in the case of fine-grained sediments, the surface layer and the deep sediment layers forming two very different worlds. At the sediment-water interface, the sea water may be rich (even saturated) in oxygen, high-quality organic matter is often available, and in the photic zone, there is light. Deep in the sediment, conditions are drastically different: often there is no oxygen, except in halos around metazoan burrows, but there may be toxic substances(e.g. H_2S) instead. Furthermore, the remaining organic matter may be mostly refractory, with a low nutritional value (see chapter 11) . Apparently, the deeper sediment layers, with their poverty of resources and lack of oxygen, form an inhospitable or even hostile environment for many organisms, and as a consequence, animal life is generally scarce (Fenchel and Finlay, 1995). Nevertheless,

a relatively important stock of infaunal organisms, including benthic Foraminifera, may be present.

There must be significant differences in the mode of life between the Foraminifera living at the resource-rich, oxygenated, sediment-water interface, and their counterparts living deeper in the sediment. Understanding such differences in the functioning of these two groups of Foraminifera is essential for our comprehension of the ecology of this important group of meiofauna, and its role in marine ecosystems. The facts that benthic Foraminifera fossilize well, and may constitute the only tracers of ancient benthic environments, provide an additional reason to investigate the ecology of both epifaunal and infaunal components of the assemblage.

10.2 ECOLOGICAL CONSTRAINTS AT AND BELOW THE SEDIMENT-WATER INTERFACE

In most oceanic environments, only the top centimeters or millimeters of the sediment contain
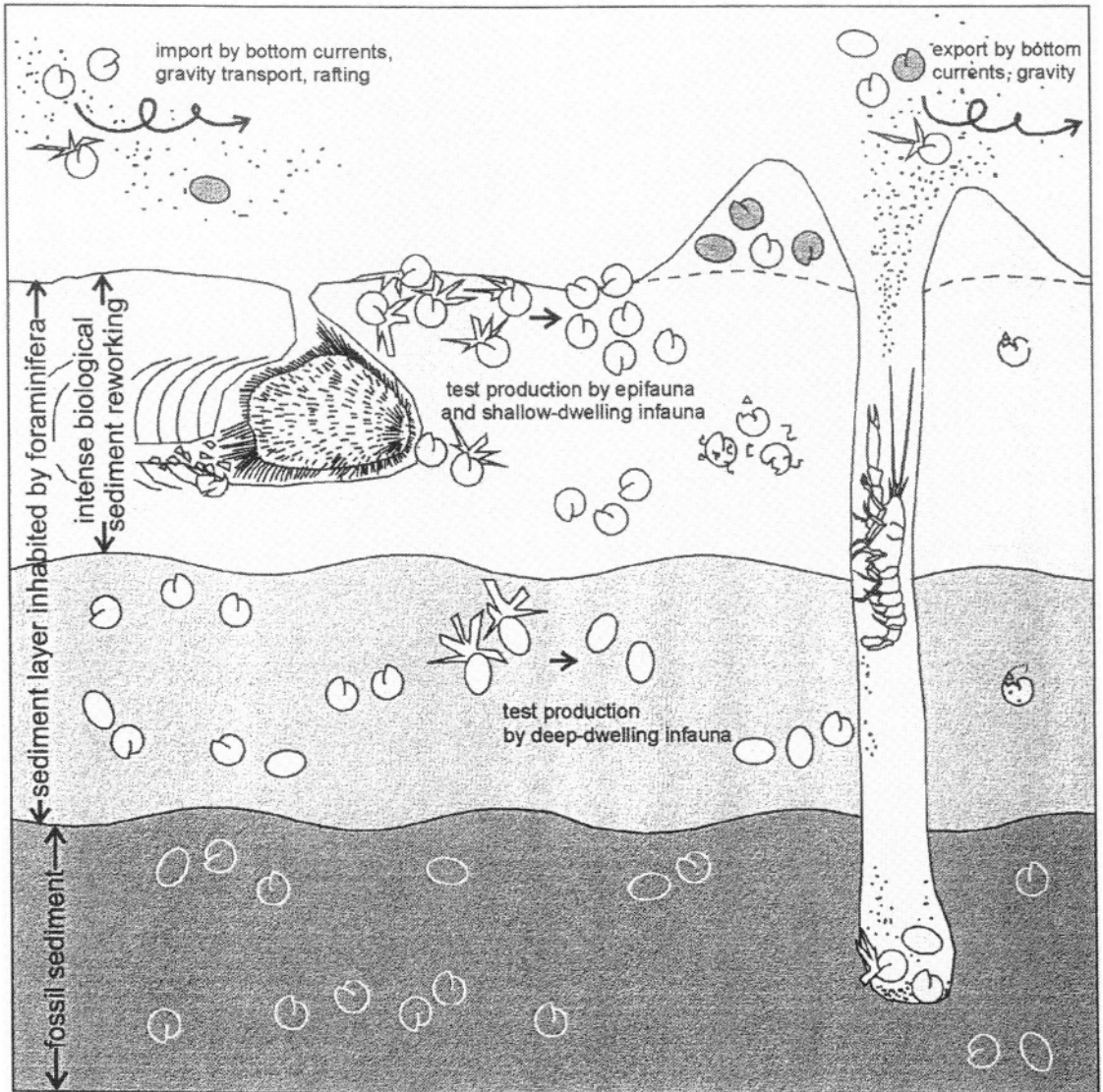
Figure 10.1 Sketch showing the various microhabitats occupied by live foraminifera (in white) in a marine benthic environment. Figure reproduced by courtesy of Henko De Stigter.

oxygen (e.g. Jørgensen and Revsbech, 1989). The oxygen content, which usually shows an exponential downward decrease, is the result of the equilibrium between downward diffusion and the depletion caused by the aerobic degradation of organic matter in the sediment. Macrofaunal burrows, however, may locally create oxic environments deeper in the sediment (Aller and Aller, 1986; Meyers *et al.,* 1987, 1988). A much deeper than usual oxygen penetration may be found in coarse-grained, high-energy, shallow-water environments, or in very oligotrophic deep-sea areas (e.g. Rutgers van der Loeff, 1990).

Below the oxic zone, other oxidants are used as electron acceptors by bacteria responsible for the anaerobic degradation of organic matter. In

the microxic zone (see chapter 12), where oxygen drops to minimal values, nitrate, Fe^{4+} and Mn^{3+} are reduced. Below this zone, in completely anoxic sediments, sulfate reduction and methanogenesis take place (Froelich *et al.,* 1979). The precise depth at which each of the oxidants of this succession is used depends again on the downward diffusion of oxygen, and on the amount of reactive organic matter introduced into the sediment. In case of an increasing flux of organic matter, a larger part tends to be mineralized under anaerobic conditions (Fenchel and Finlay, 1995). In such situations, the lower part of the oxic zone may overlap with the upper part of the zone of sulfate reduction (Fenchel, 1969).

The majority of all marine macro- and meiofauna are aerobes, and occur only in the oxic surface layer of the sediment. Some species, however, seem to be present exclusively in the microxic zone, where nitrate reduction takes place, and only a few taxa occur in the zone of sulfate reduction. All three groups are present among protozoans (Fenchel and Finlay, 1995), but most infaunal organisms living in apparent anoxia may actually be microaerophiles that depend on oxygen concentrations below the actual detection limits, or may survive periods of anoxia.

The flux of organic particles from surface waters to the seafloor is the main food source for most deep-oceanic ecosystems. Only a small fraction of the organic matter arriving at the seafloor is directly consumable by the macro- and meiofauna. Most of these labile particles are immediately consumed at the sediment-water interface and in the first millimeters of the sediment (Reimers *et al.,* 1986; Carney, 1989). As a consequence, the organic matter rapidly becomes more refractory with increasing sediment depth. Deeper in the sediment, the remaining (refractory) organic matter has first to be converted into bacterial biomass (Hargrave, 1970; Carney, 1989), or at least be partially degraded by anaerobic microbial activity, before it can be consumed by meio- or macrofauna. The anaerobic bacterial biomass is highest in the sediment layer immediately below the oxic

zone (Fenchel and Finlay, 1995). Because of the scarcity of predators and competitors there, this zone will be very favorable for organisms tolerant to the low oxygen levels.

In response to this vertical trend in food availability, two main types of deposit feeders can be distinguished in oceanic ecosystems: one living at the sediment surface, and feeding on labile paniculate organic matter, the other living in the sediment, and feeding on bacterially mediated labile organic matter (Levinton, 1989). In general, the often intermittent flux of labile organic matter to the ocean floor favors consumers with an opportunistic life strategy, whereas the deeper sediment layers, with a food source that is much more stable in time, will be inhabited especially by K-strategists (Levinton, 1972, 1989; Rice and Rhoads, 1989).

10.3   BACKGROUND: BENTHIC FORAMINIFERAL MICROHABITAT RESEARCH

A 'microhabitat' is a microenvironment characterized by a combination of physical, chemical and biological conditions (oxygen, food, toxic-substances, biological interactions, etc.). These characteristics separate adjacent (and often closely spaced) microhabitats, and make a particular microhabitat attractive or at least tolerable for some taxa, but uninhabitable for others. In any given seafloor habitat, specific microhabitats are present at the sediment-water interface, in the lower part of the water column, and in the top layer of the sediment. In this chapter I will focus on the microhabitats below the sediment-water interface.

The notion of benthic foraminiferal life deep in the sediment is relatively recent. Until the 1960s, the general opinion was that benthic Foraminifera live at the sediment-water interface (e.g. Myers and Cole, 1957), and as a consequence, it was common practice to sample only the top one or two centimeters of the sediment for foraminiferal studies. Early papers that describe Foraminifera deeper in the sediment (e.g. Myers, 1943b; Richter, 1961, 1964; Buzas,

1965, 1974, 1977; Boltovskoy, 1966a; Brooks, 1967; Lee *et al.*, 1969; Schafer, 1971b; Ellison, 1972; Frankel, 1972, 1975a,b; Matera and Lee, 1972) all concern shallow water environments, where living Foraminifera are found in considerable sediment depths, but without noticeable compositional changes with depth. Since the publications of Thiel (1975), Coull *et al.* (1977), and Basov and Khusid (1983), we know that in deepsea environments too, Foraminifera can live deep in the sediment. Corliss (1985) was the first to show a vertical succession of deep-sea taxa in the sediment, with some species ('epifaunal') living in the upper centimeters, and other species ('infaunal') having clear subsurface maxima in their populations. A number of later papers (e.g. Gooday, 1986; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Corliss, 1991; Rathburn and Corliss, 1994; Jorissen *et al.*, 1995; Rathburn *et al.*, 1996; McCorkle *et al.,* 1997; De Stigter *et al.,* 1998; Jorissen *et al.*, 1998) have confirmed the presence of such a vertical distribution in deep-sea environments. On the basis of the presence of living Foraminifera in sediments without measurable oxygen, Bernhard (1989, 1992, 1993, 1996), Bernhard and Reimers (1991), Moodley and Hess (1992), and Bernhard and Alve (1996) have suggested that some benthic Foraminifera may be facultative anaerobes.

Several authors (e.g. Corliss and Chen, 1988; Murray, 1991b; Barmawidjaja *et al.*, 1992; Rathburn *et al.*, 1996) have tried to highlight differences in vertical distribution by defining various microhabitat adaptations, such as 'epifaunal,' 'epibenthic,' 'elevated epibenthic,' 'shallow,' 'intermediate,' 'deep,' and 'predominantly' or 'preferentially infaunal' taxa. On the other hand, several arguments have been raised to indicate that such separations constitute an oversimplification (e.g. Linke and Lutze, 1993).

First, the two equally important parameters that define foraminiferal distribution, i.e. sediment penetration depth and vertical abundance pattern of species, do not necessarily covary. The maximum depth at which a species occurs is defined by the tolerance of the species (modified by accidental transport) to a variable limiting factor (see Jorissen *et al.*, 1995). The

abundance pattern, on the contrary, is related mainly to microhabitat preferences of the species. In the literature, however, species are often attributed to microhabitat categories on the basis of both parameters.

Second, there is significant variability in the exact sediment depth at which a particular species can be found; it may live deep in the sediment at one site, but much closer to the sediment-water interface at a different site (Fig. 10.2). Several papers (e.g. Mackensen and Douglas, 1989; Corliss, 1991; Kitazato, 1994) show this phenomenon for the genus *Globobulimina* (Fig. 10.3). Furthermore, even at a single site, the vertical distribution may vary through time (Barmawidjaja *et al.,* 1992; Linke and Lutze, 1993; Kitazato and Ohga, 1995). The succession of foraminiferal taxa may be compressed or expanded, and taxa co-occurring somewhere in the upper part of the sediment may occupy different microhabitats at another place or time (Fig. 10.4). In view of this large spatial and temporal variability, Linke and Lutze (1993) conclude that the species' microhabitat should be considered as the reflection of a dynamic adaptation to optimize food acquisition.

Finally, it is evident that the concept of a strictly vertical stratification of taxa does not altogether correspond to the reality. On the one hand, burrowing macrofauna, which create deep oxic environments and introduce nutritious material into the sediment may cause a large spatial (vertical as well as horizontal) heterogeneity (e.g. Aller and Aller, 1986; Meyers *et al.,* 1987, 1988). On the other hand, in the oxic zone, anoxic micro-environments may be present in the center of organic aggregates or fecal pellets (Fenchel and Finlay, 1995).

A simplified concept with several microhabitat categories, however, may be very useful in paleoceanography, provided that the penetration depth, or the abundance patterns of the various taxa and/or microhabitat categories can be linked to some of the environmental parameters. Adequate knowledge of the microhabitat characteristics of extant taxa is also important for stable isotope studies, in which the $\delta^{13}C$ of
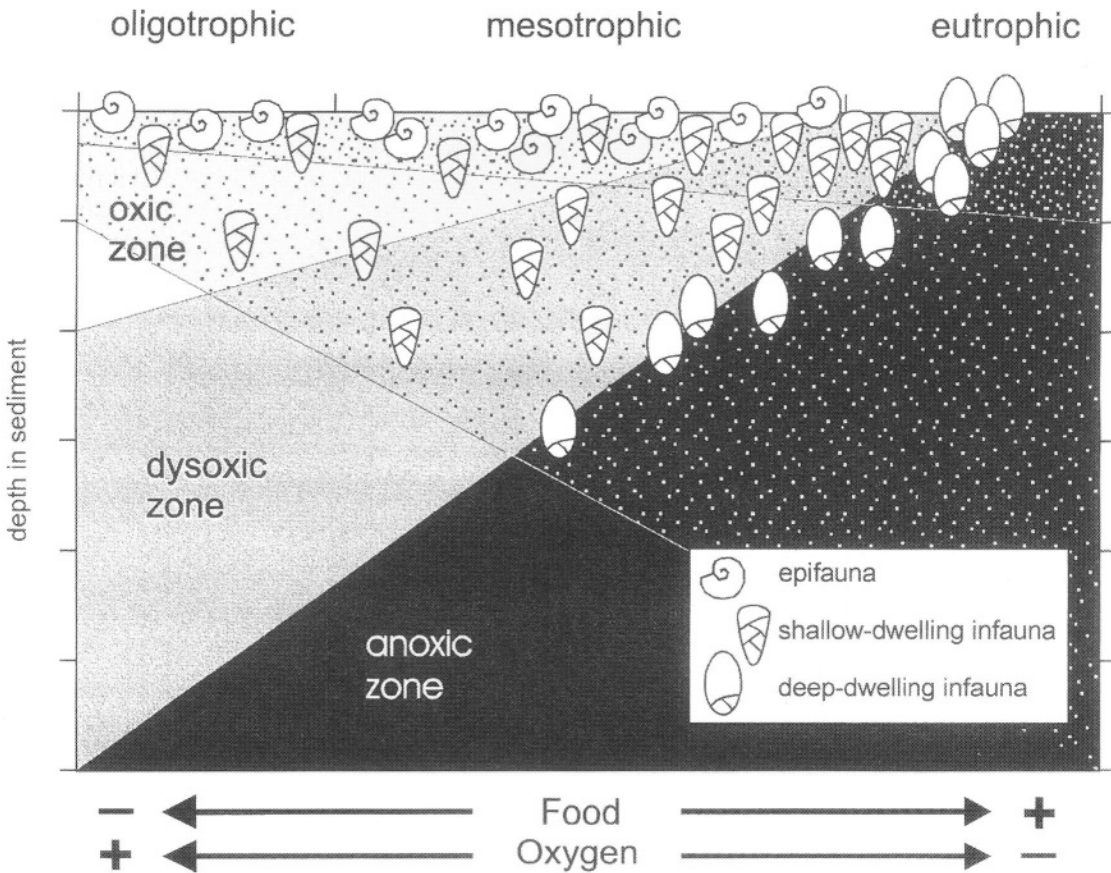
Figure 10.2 Hypothetical scheme showing variation of microhabitat depth of infaunal taxa as a function of the depth of a critical oxygen level in the sediment. Figure reproduced by courtesy of Henko De Stigter.

the benthic foraminiferal shell is used as a proxy of bottom water ventilation and export productivity. Since a significant $\delta^{13}C$ gradient exists in the top centimeters of the sediment, it is of prime importance to know whether the benthic foraminiferal species selected for analysis secrete their tests in isotopic equilibrium, and if so, where in the sediment column this secretion takes place.

The aim of this chapter is to describe benthic foraminiferal microhabitats within the sediment, and to summarize the ideas which have been proposed to explain differences in vertical distribution in the sediment among taxa, among sites, and in time. In addition, it looks into the application of foraminiferal microhabitat information

in paleoceanographic studies. It does not include a list of microhabitat preferences of species. Existing lists of such preferences (e.g. Corliss and Chen, 1988; Murray, 1991b; Van der Zwaan and Jorissen, 1991; Barmawidjaja *et al.*, 1992; Rathburn *et al.*, 1996) may be useful as ready references, but their reliability suffers from the fact that they are often based on a mix of real observations and assumptions about relationships between microhabitat and species morphology. Furthermore, these lists generally do not take into account the dynamic nature of the foraminiferal microhabitat; a particular genus or species is not necessarily 'fixed' in a particular microhabitat. These problems are more fully discussed in a later section.
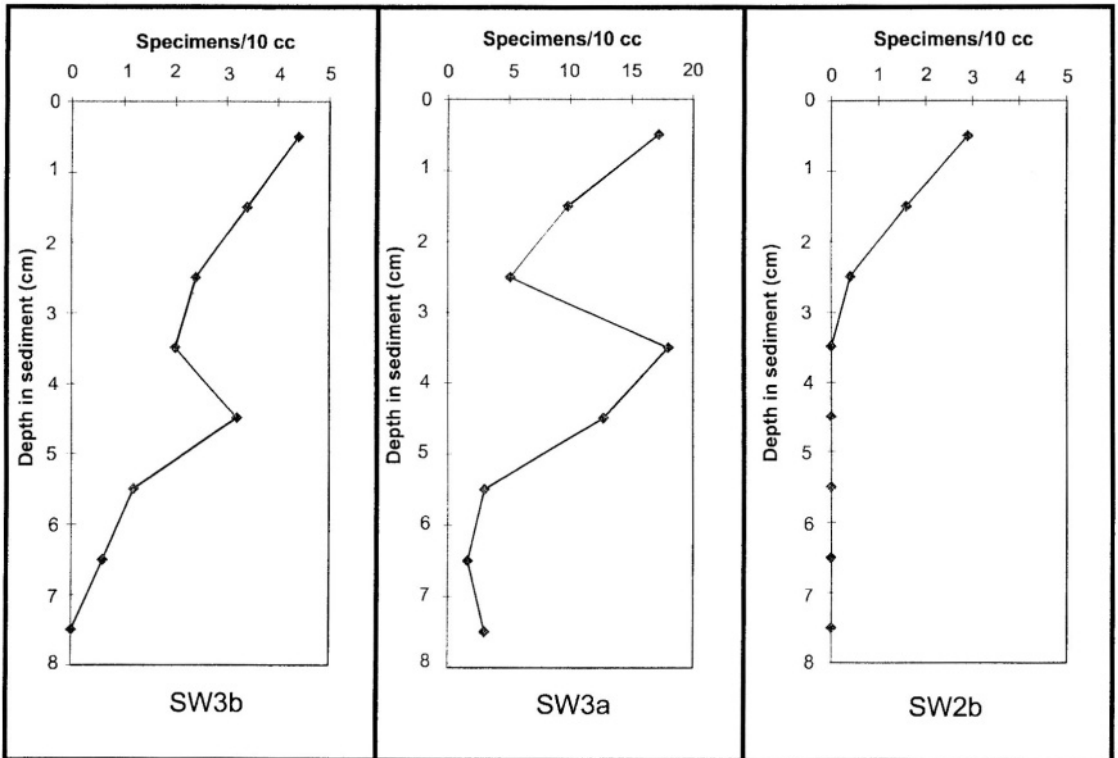
Figure 10.3 Vertical distribution profiles showing variation in the microhabitat depth of *Globobulimina* (fraction > 125 μm) at three sites in the California borderland (after Mackensen and Douglas, 1989). Stations W3a and W3b: central part of the Santa Catalina Basin, water depth 893 m and 897 m, respectively. Station SW2b: western rim of the Santa Monica Basin, water depth 529 m. According to Mackensen and Douglas (1989), bottom waters in Santa Monica Basin below 300–400 m are almost microxic ($O_2 < 0.2$ ml/l), whereas those in Santa Catalina Basin are better oxygenated (0.2–0.5 ml/l). The microhabitat of *Globobulimina* is considerably deeper in Santa Catalina than in Santa Monica Basin.

10.4 EVALUATION OF EXISTING MICROHABITAT DATA

Most published data on foraminiferal microhabitats are based on tests stained by Rose Bengal (Lutze and Altenbach, 1991). It is generally agreed that this procedure is the only one that allows a rapid gathering of numerical data from a large number of samples, but several authors (e.g. Douglas *et al.,* 1978, 1980; Bernhard 1988, 1989; Corliss and Emerson, 1990; Jorissen *et al.,* 1995; McCorkle *et al.,* 1997) have warned that foraminiferal tests may stain for a considerable time after the death of the individuals, especially under low temperatures, or in anaerobic ecosystems deep in the sediment. Generally, however, the time needed for protoplasm degradation appears to be very short in oxic environments. In many cases, the surficial sediment layers contain specimens that are either brightly stained or completely unstained. In the deeper, anoxic sediment layers, on the contrary, I have often observed a wide spectrum of staining, from complete to minimal, and from bright to very dull. Thus, recognizing a foraminiferal test as Rose-Bengal stained is based on subjective criteria. If less perfectly stained tests correspond to individuals that have been dead for some time, then loosely applied staining criteria will lead to an overestimation of the infaunal standing stock.

If we consider the vertical distribution of the entire benthic foraminiferal assemblage, several types of distribution can be distinguished. A
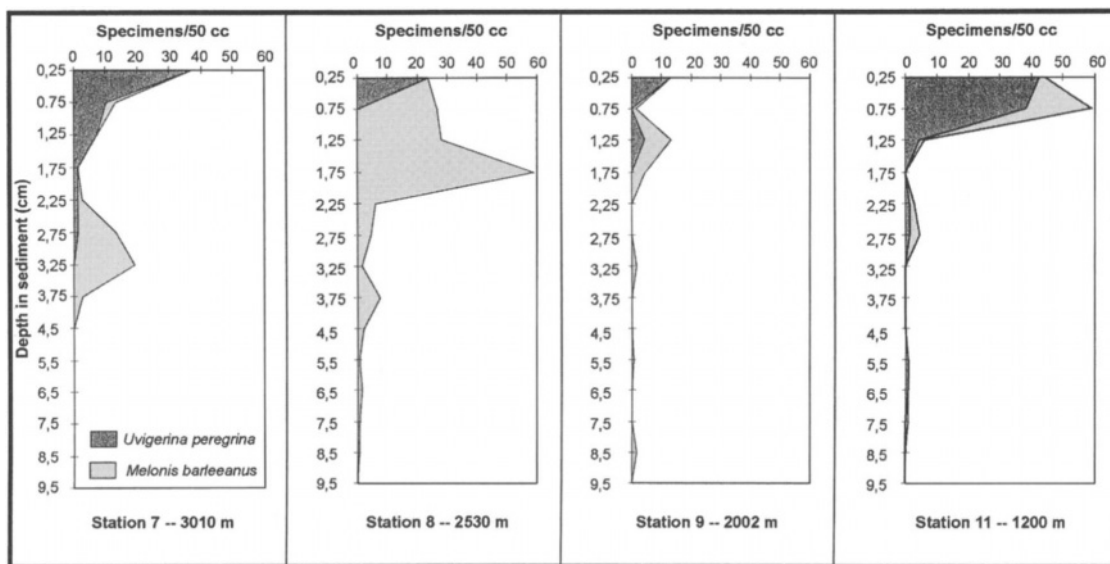
Figure 10.4 Vertical distribution of *Uvigerina peregrina* and *Melonis barleeanus* in a four-station bathymetrical transect from the Cape Blanc upwelling area (fraction > 150 μm; after Jorissen *et al.*, 1998). *U. peregrina* and *M. barleeanus* have very different microhabitat depths at 3010 m water depth (bottom-water O_2 content 4.88 ml/l). With decrease in water depth, *M. barleeanus* is found at progressively shallower depths in the sediment. At 1200 m (bottom-water O_2 3.67 ml/l), the two species are found together in the 0.5–1 cm sediment-depth interval.

number of studies report only minor variations in the number of living Foraminifera from one depth interval to another for a considerable depth in the sediment (e.g. Buzas, 1974, 1977; Collison, 1980; Hohenegger *et al.,* 1993; Murosky and Snyder, 1994; Lueck and Snyder, 1997). This situation is typical for the majority of shallow-water (0–50 m) and/or coarse-grained environments. Sites at greater depths, usually with fine-grained sediments, tend to show a clear maximum in the topmost interval, with an exponential downward decrease. At some sites however, secondary downcore maxima have been described (e.g. Corliss, 1985; Hunt and Corliss, 1993; Rathburn and Corliss, 1994; McCorkle *et al.,* 1997).

Many terms have been proposed to describe the vertical distribution of species. Those introduced by Corliss (1991) are the following: (a) epifauna (taxa found living only in the uppermost centimeter of the substrate), (b) shallow infauna (taxa confined to the 0–2 cm interval), (c) intermediate infauna (1–4 cm), and (d) deep infauna (a subsurface population maximum

below 4 cm, usually in the anoxic zone). These terms, widely used in the literature, offer the advantage of a rapid characterization of the vertical distribution patterns. Unfortunately, the separation of these four categories is based on a combination of distributional data and test morphology. The terms epifaunal and shallow infaunal may suggest a fundamentally different life strategy (living on top of the sediment versus within the sediment), but the distinction between the two groups is completely arbitrary, since it is based on an assumed connection between microhabitat and test morphology, and not on observed patterns of vertical distribution (Corliss, 1991). Another drawback of such a rigid classification is the fact that infaunal taxa may show significant variations in their precise living depth (e.g. Corliss, 1985; Corliss and Emerson, 1990). Several authors (e.g. Barmawidjaja *et al.,* 1992; Linke and Lutze, 1993; Alve and Bernhard, 1995; Kitazato and Ohga, 1995) have suggested that even at a single site, there may be short-time variations in this living depth (Fig. 10.5). Although the succession of shallow
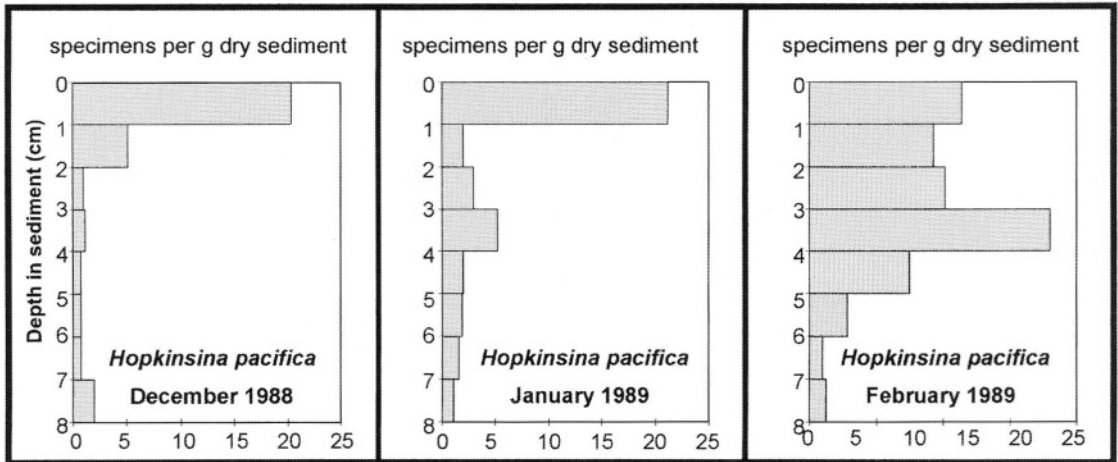
Figure 10.5 Vertical distribution of *Hopkinsina pacifica* at the same station (water depth 32 m) in three different sampling periods (after Barmawidjaja *et al.*, 1992). The succession of samples shows a significant temporal variability in microhabitat. The species lived close to the sediment surface in December 1988. In January 1989, slightly increased numbers were found deeper in the sediment, whereas in February 1989, about equal numbers were found in the five uppermost 1-cm intervals.

infaunal, intermediate infaunal, and deep infaunal taxa remains intact, the precise depth at which each of these groups is found may fluctuate considerably. For example, the genus *Globobulimina* is generally considered as a deep infaunal taxon, because its preferred microhabitat is deep in the sediment where there is a well developed vertical stratification of foraminiferal taxa. With a very thin top layer of oxygenated sediment, however, *Globobulimina* may very well be found much closer to the surface (Figs. 10.2, 10.3). Although microhabitat labels may provide a very useful characterization of species behavior, the attribution of these labels should be based exclusively on distributional data, and not on pre-conceived ideas about the functional morphology of their test. Furthermore, it should not be based on the (highly variable) exact depth in the sediment at which a species lives, but rather on the relative position of the species compared to that of other species, and on the shape of its vertical distribution profile.

10.5   VERTICAL DISTRIBUTION PATTERNS

The existing data on vertical distributions of individual taxa reveal four main patterns (Fig. 10.6). I will illustrate these patterns by typical examples, but the reader should keep in mind that they are highly variable in space and time, and that even for a single species, different patterns exist. It is important, however, to define these different distribution patterns, because they are a reflection of the response of the organisms to a set of controlling parameters.

The first type of profile (Fig. 10.6, type A) shows a very clear population maximum in the topmost interval, which in most studies is 1 or 0.5 cm thick. Few individuals are found deeper in the sediment. Taxa usually showing this vertical distribution pattern are common in deep oceanic environments. They have been termed epifaunal (e.g. *Hoeglundina elegans* described by Corliss and Emerson, 1990, and Corliss, 1991; see Fig. 10.7a) or shallow infaunal (e.g. *Uvigerina peregrina,* described by the same authors; see Fig. 10.7b). In reality, abundant species are never completely limited to the topmost interval, and are always found in small numbers at the levels below. Buzas (1974) and Buzas *et al.* (1993) argue that in soft bottomed environments, even taxa living exclusively at the topmost level are most probably infauna. They suggest that the term epifaunal be used only for species living on hard substrates, such as rocks, molluscs, or corals, or perhaps on bacterial films
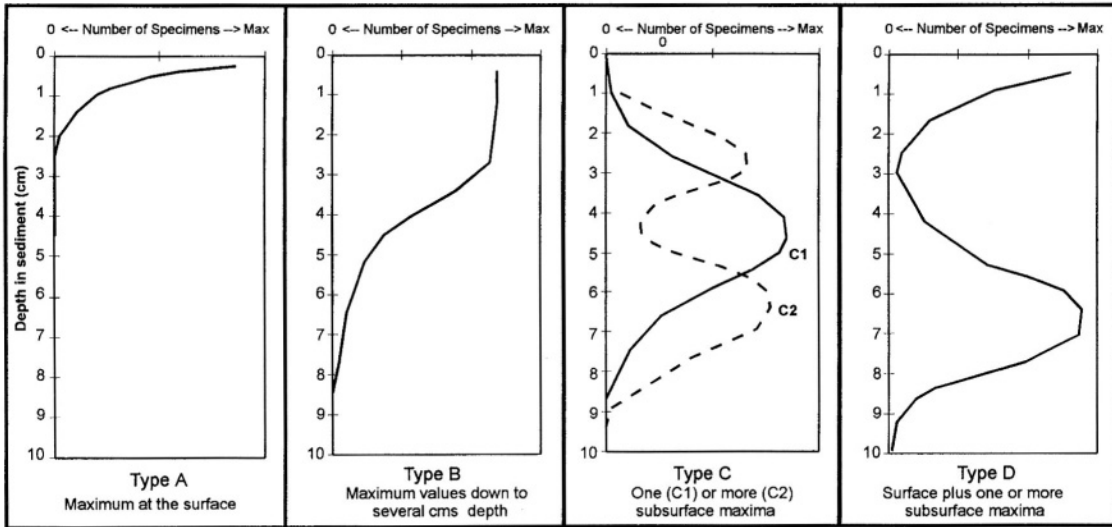
Figure 10.6 Main types of quantitative vertical distribution patterns of benthic Foraminifera; see text for further explanation.

at the sediment-water interface. For such life positions, Lutze and Thiel (1989) proposed the term 'elevated epifauna.' For all taxa that usually show type-A distribution patterns, it may be concluded that they have a marked preference for the conditions found in the top part of the sediment, or do not tolerate the conditions in deeper sediment layers.

The second type of profile (Fig. 10.6, type B) shows similar densities in several successive intervals, without a clear maximum at the topmost level, or deeper in the sediment. *Hopkinsina pacifica* (Fig. 10.7c) in the February sample of Barmawidjaja *et al.* (1992) is a typical example. Species that repeatedly show such a pattern have been considered as shallow infaunal (if the maximum values occur in the top 2 cm), or, in cases where the high densities continue to much deeper levels, as 'transitional' (Rathburn *et al.,* 1996). This type of distribution is relatively common in coarse grained, shallow-water environments, perhaps because the sediment is intensely burrowed to a considerable depth. The profile is very rare in deep-sea environments, where pore-water characteristics change rapidly within a short depth interval. This type-B distribution profile should be typical for taxa which do not have a clear preference for the topmost

sediment layer (or which do not successfully compete there with other taxa), and which tolerate the conditions found deeper in the sediment.

The third type of profile (Fig. 10.6, types C_1 and C_2) shows relatively low values in the first interval(s), and one (C_1) or more (C_2) downcore maxima. *Melonis barleeanus* (Fig. 10.7d; Corliss and Emerson, 1990; Corliss, 1991) and *Globobulimina affinis* (Fig. 10.7e; same authors) provide typical examples. Judging by the precise depth at which the downcore maxima are found, species with such distribution patterns have been termed intermediate (*M. barleeanus*) or deep infaunal (*G. affinis*). Taxa with type-C distribution have provoked a spirited discussion in the literature. The essential questions are how and why these taxa flourish in the poorly oxygenated environment of the deeper levels of the substrate.

The fourth type of profile (Fig. 10.6, type D) shows a combination of a surface maximum with one or several maxima deeper in the sediment. *Bulimina marginata* (Fig. 10.7f; Jorissen *et al.,* in press) or *B. aculeata* of Kitazato (1989) are typical examples. Taxa with such a distribution profile apparently find suitable environments at the sediment surface as well as deeper in the sediment.
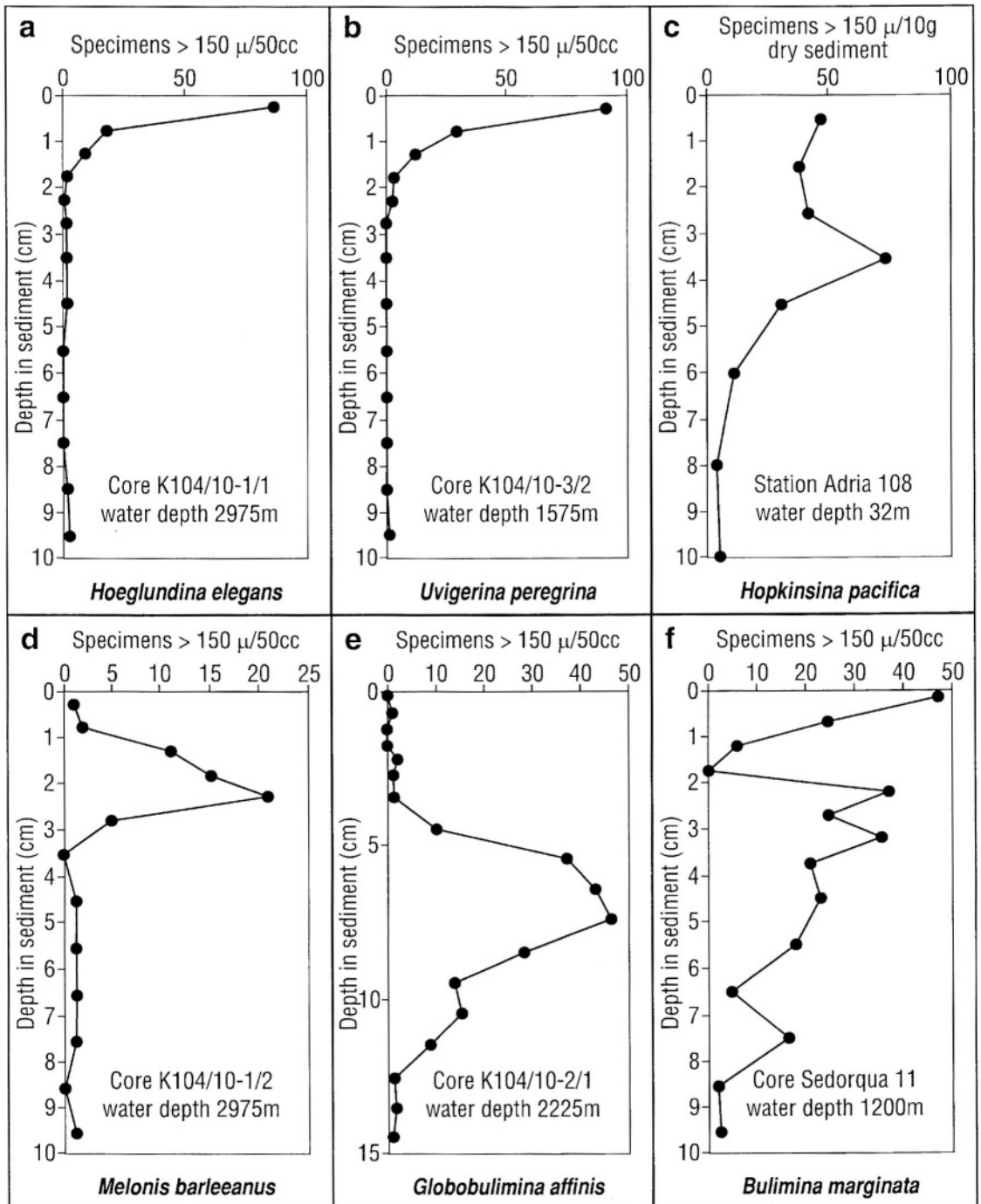
Figure 10.7 Typical examples of vertical distribution patterns of benthic foraminiferal species; a, *Hoeglundina elegans*, core K104/10-1/1, after Corliss (1991); b, *Uvigerina peregrina*, core K104/10-3/2, after Corliss (1991); c, *Hopkinsina pacifica*, station 108, February 1989, after Barmawidjaja *et al.* (1992); d, *Melonis barleeanus*, core K104/10-1/2, after Corliss (1991); e, *Globobulimina affinis*, core K104/10-2/1, after Corliss (1991); f, *Bulimina marginata*, station 11, after Jorissen *et al.* (1998).

10.6   FACTORS CONTROLLING VERTICAL DISTRIBUTION PATTERNS

It is evident that these four types of vertical distribution are reflections of the tolerance and/ or preference levels of taxa with respect to one or more controlling parameters. Until now, a rather limited array of parameters has been evoked to explain differences in the vertical distribution of benthic Foraminifera. Early papers, dealing with foraminiferal occupation of deeper sediment layers without a conspicuous vertical succession, mainly suggest sediment mixing by wave action, porosity, and bioturbation as the cause of microhabitat depth differences among sites. Following the discovery of a rather invariant vertical succession of species in deep-water sediments, four other factors have been proposed to explain the differences among taxa and among sites.

(1) **Bottom-water oxygenation** may play a role in determining the lower vertical limit of taxa with type-A or type-B distribution. A number of recent field and laboratory studies, however, show significant foraminiferal standing stocks (of taxa with type-C or type-D distribution) in apparently anoxic sediments, suggesting that oxygen concentration is not a critical factor for all taxa (e.g. Bernhard, 1989, 1992, 1993; Corliss and Emerson, 1990; Bernhard and Reimers, 1991; Alve, 1994; Rathburn and Corliss, 1994; Moodley *et al.*, 1997; Jorissen *et al.,* 1998; see also chapter 12). However, even if several taxa can survive prolonged anoxia in laboratory studies (e.g. Alve and Bernhard, 1995; Moodley *et al.,* 1997), oxygen concentration can not be dismissed as an important ecological factor for benthic Foraminifera. It is very well possible that anoxic conditions may inhibit reproduction in many taxa, and thus ultimately cause their disappearance. The total absence of benthic Foraminifera after prolonged anoxia (Bernhard and Reimers, 1991), and in Mediterranean deep-sea sapropels strongly suggests a controlling role for oxygen concentration. Furthermore, the upward movement of several taxa in response to decreasing oxygen in bottom water, and probably also pore water (Alve and Bernhard, 1995),

and the very clear succession of species along a bottom-water dissolved oxygen gradient (0.02–0.5 ml/l) described by Bernhard *et al.* (1997) in Santa Barbara Basin, suggest the existence of a lower tolerance limit for many species in the microxic/dysoxic range (see chapter 12). However, several other parameters of the sedimentary environment, such as porosity, water content, alkalinity, or sulfide content covary with pore-water oxygen concentration, and it is possible that it is not oxygen concentration itself, but one of the critical covarying factors, such as the concentration of toxic substances (sulfides), that restricts the foraminiferal living depth. Furthermore, oxygen concentration (or a related parameter) may limit the maximum penetration depth, but it can hardly explain species abundance profiles.

(2) **Food availability** is the other parameter that may control the foraminiferal microhabitat depth. In oligotrophic parts of the ocean, where oxygen penetration can be very deep (Rutgers van der Loeff, 1990), but where the small quantity of labile organic matter is rapidly consumed at the sediment-water interface (Reimers *et al.,* 1986; Carney, 1989), benthic Foraminifera are (like all macro- and meiofauna) limited to the topmost centimeters of the sediment. Here, food limitation best explains the absence of fauna deeper in the sediment (e.g. Shirayama, 1984; Corliss and Emerson, 1990; Jorissen *et al.,* 1995). Foraminifera feed on a wide range of food particles, but an increasing body of evidence indicates food selectivity in various species (e.g. Caralp, 1989b; Goldstein and Corliss, 1994; Kitazato, 1994; Rathburn and Corliss, 1994; Hemleben and Kitazato, 1995; Kitazato and Ohga, 1995). For instance, Goldstein and Corliss (1994) report that planktonic diatom frustules are common in sediment parcels ingested by *Uvigerina peregrina,* but are never found in *Globobulimina.* Kitazato (1994) even suggested that the latter genus has a preference to feed on older organic detritus.

For taxa with type-A distribution, their surface maximum could very well be caused by the presence of labile, easily metabolizable, organic matter at the sediment surface. Although part

of the fresh organic matter arriving in the benthic ecosystem is mixed into the sediment by bioturbation, the bulk is consumed at the sediment-water interface (Reimers *et al.*, 1986; Carney, 1989). A specific case of taxa with a type-A distribution, for which the density seems to be controlled by food availability, is found in species that feed on bulk deposits of fresh phytodetritus (so-called 'phytodetritus feeders;' see Gooday and Lambshead, 1989; Gooday, 1993).

Taxa with type-B distribution do not live exclusively at the sediment surface, and must therefore tolerate the paucity of high-quality food items, or a lower food quality. This is even more true for taxa with subsurface maxima (types C and D), which must feed on material with a low nutritional value (Caralp, 1989b), or on labile particles made available by nitrate-, iron-, or sulfate-reducing bacteria that cause anaerobic degradation of organic matter (Alve, 1990; Bernhard, 1992). Jorissen *et al.* (1998) suggest that intermediate infaunal taxa have their largest populations in the zone of nitrate reduction, whereas deep infaunal species are the only remaining taxa in the zone of sulfate reduction (Fig. 10.8). They suggest that these successive taxa feed either on the decay products of low quality sedimentary organic matter, made available by bacterial anaerobic degradation, or on the bacterial stocks themselves. The exact depth in the sediment of the various oxidants and their accompanying microbial stocks depends on the interplay between the organic flux, bottom-water oxygen concentration, bio-irrigation, and sediment porosity.

(3) **Competition and predation** have rarely been evoked to explain foraminiferal microhabitat depths. Obviously, the reduced predational pressure in the infaunal microhabitat is an advantage for benthic Foraminifera. Theoretically, density peaks of infaunal Foraminifera may be created by a much lower macrofaunal grazing pressure. At present, we do not know whether Foraminifera actively choose infaunal

microhabitats to avoid predation. At the sediment surface, habitat space is limited, and competition for space may occur. In food-rich environments, however, competition for resources is minimal, and the environment will be inhabited by opportunistic taxa with large reproductive potentials. Because of their high turnover rate, these taxa will rapidly dominate the assemblages. Many epifaunal and shallow infaunal taxa with type-A distributions (with clear maxima in the resource-rich surface sediments and an exponential decrease below) most probably have such an opportunistic life strategy. Such taxa can rapidly adjust to intermittent food supply, and will often dominate the fossil assemblage, even if they attain high densities only during the most eutrophic periods (Jorissen and Wittling, 1999). In this context, species feeding on phytodetritus deposits probably represent an extreme.

Since the anaerobic bacterial conversion of refractory organic matter into labile components is a slow process (Fenchel and Finlay, 1995), taxa living deep in the sediment are adapted to an environment with a relatively constant supply of low-quality food. Logically, such taxa will have a life strategy aimed at very efficient food utilization, in combination with a maximum resistance to ecological stress. Under normal conditions, their densities will be relatively low, but constant in time. However, such normally deep infaunal taxa are known to have amazingly high densities in some cases where bottom-water oxygen concentrations are very low (e.g. Phleger and Soutar, 1973; Sen Gupta and Machain-Castillo, 1993). Under such circumstances, the opportunistic epifaunal or shallow infaunal taxa will probably no longer tolerate the low oxygen concentration, and will disappear. The result of this partial extinction or disappearance is that the normally deep infaunal taxa may find the sediment-surface microhabitat open, and may be able to colonize

Figure 10.8 Comparison of the vertical distributions of *Melonis barleeanus*, *Globobulimina affinis*, and *Bulimina marginata* with profiles of oxygen and nitrate in a five-station bathymetrical transect from the Cape Blanc upwelling area (northwestern Africa). The profiles show that *M. barleeanus* tends to have a maximum in the zone of nitrate reduction, whereas the other two species have significant standing stocks in completely anoxic sediments (after Jorissen *et al.*, 1998).
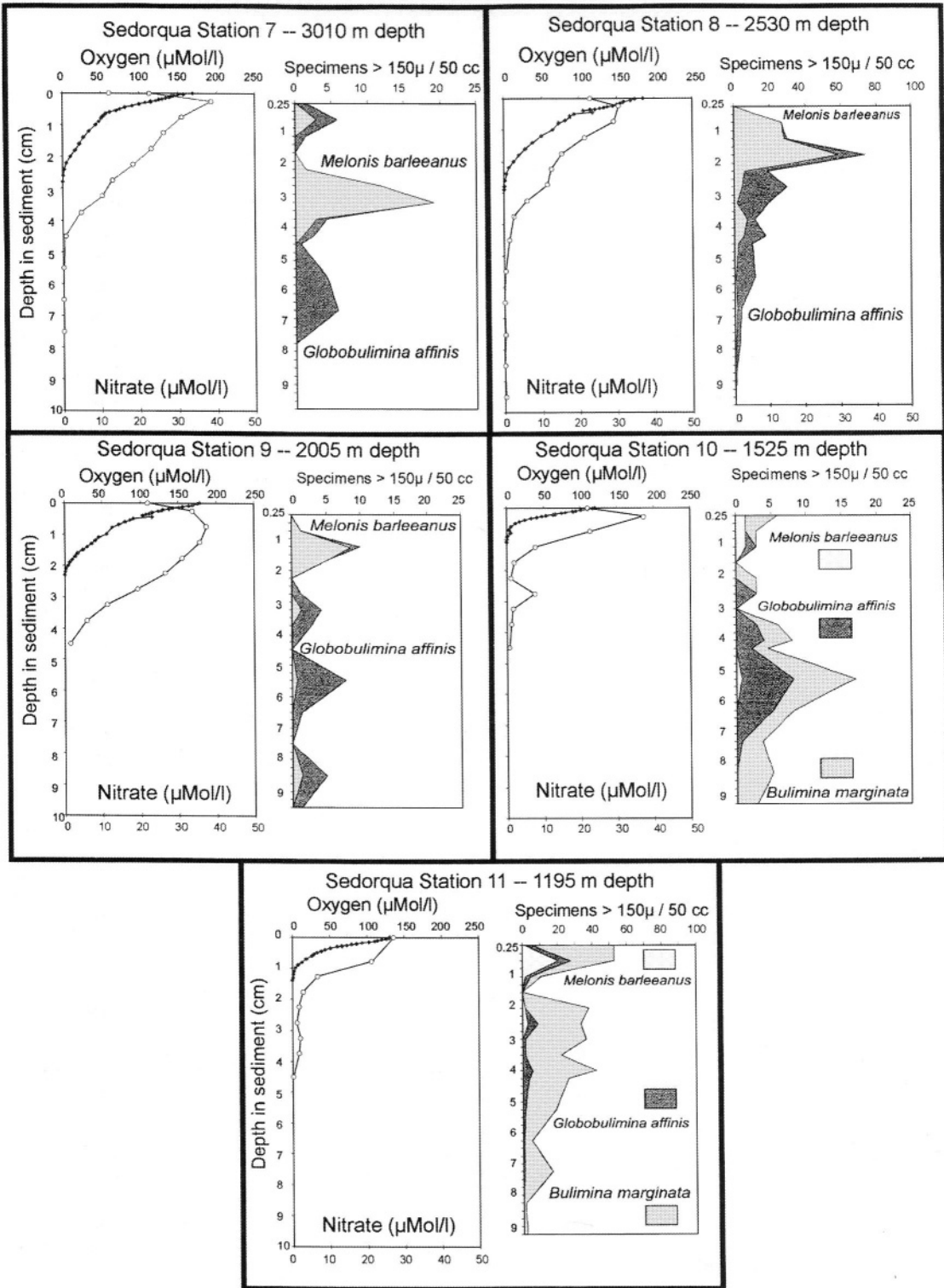
this extremely food-rich environment, where they can reach very high standing stocks.

(4) **Bioturbation** may influence benthic foraminiferal microhabitats in several ways: by creating oxic microenvironments at depth in the sediment (Aller and Aller, 1986; Meyers *et al.,* 1987, 1988), or by trapping food-rich particles, and partially introducing them into the sediment. Thomsen and Altenbach (1993) show a significant increase in bacterial biomass and foraminiferal densities in haloed sediments around artificial burrows. Bioturbation can also actively transport Foraminifera to deeper sediment layers, and cause accidental infaunal occurrence of taxa that are usually found at the sediment surface.

The four factors explained in this section will each have their individual influence on the foraminiferal microhabitat, but they will also interact strongly. Jorissen *et al.* (1995), following the suggestions of Shirayama (1984) and Corliss and Emerson (1990), developed a conceptual model that shows the interplay between oxygen concentration and food availability (Fig. 10.9). They argue that in oligotrophic settings, a critical food level determines the penetration depth of most species, whereas in eutrophic settings, a critical oxygen level would determine this depth. The tolerance limits to these two factors will strongly vary among species, explaining the differences in the lower depth limits described in the literature.

10.7   RELATIONS BETWEEN TEST MORPHOLOGY AND MICROHABITATS

Several workers have suggested a close relationship between test morphology and microhabitat (e.g. Corliss, 1985; Jones and Charnock, 1985; Corliss and Chen; 1988; Corliss, 1991; Corliss and Fois, 1990). The existence of such a relationship would be very significant, since it would enable us to infer the microhabitats of extinct taxa, and thus extract essential information about ancient ecosystems. According to Corliss and Chen (1988) and Corliss (1991), epifaunal taxa are (a) plano-convex, biconvex or rounded

trochospiral, with large pores absent or only found on one side, or (b) milioline. In contrast, infaunal taxa can be rounded planispiral. flattened ovoid, tapered and cylindrical triserial, spherical, or flattened tapered biserial, and tend to have pores all over the test. The main shortcoming of this classification is that the primary separation between epifaunal and infaunal taxa is linked to an arbitrary boundary drawn on the basis of pore patterns (Corliss, 1991), and is only to a minor degree based on actual observations. The plano-convex, rounded, or biconvex trochospiral taxa, listed as epifaunal (Corliss and Chen, 1988; Corliss, 1991; Murray, 1991b; Rathburn *et al.,* 1996), are indeed morphologically distinct from the planispiral, biserial, or triserial taxa listed as shallow infauna. but in the majority of field observations, their vertical distribution patterns do not segregate along such morphological lines.

Furthermore, it appears that even in cases where test form, coiling type, and pore pattern are very similar, important differences in microhabitat may exist. Loubere *et al.* (1995) show that shallow and deep infaunal populations of *Uvigerina peregrina* have a slightly different morphology, but belong to the same species. Differences in microhabitat selection between morphologically close species of the same genus have been reported for *Bolivina* (Barmawidjaja *et al.,* 1992), *Bulimina* (Jorissen *et al.,* 1998), *Cibicidoides (* Rathburn *et al.,* 1996), and *Melonis* (Jorissen *et al.,* 1998). Barmawidjaja *et al.* (1992) showed that within a group of closely related *Bolivina,* the ornamented *striatula*-types are always limited to the sediment surface, whereas unornamented, but otherwise morphologically similar, *B. dilatata* and *B. spathulata* have a clear infaunal tendency. This corroborates an earlier observation by Corliss (1991) that only shallow infaunal taxa (in his data set) possess a surface ornamentation. In the genus *Bulimina, B. inflata* is limited to the sediment surface, and in view of its overall coarse perforation, should be considered as shallow infaunal, according to the criteria defined by Corliss (1991). In contrast, *B. marginata,* which has a similar test, but a spinose, instead of a costate, ornamentation,
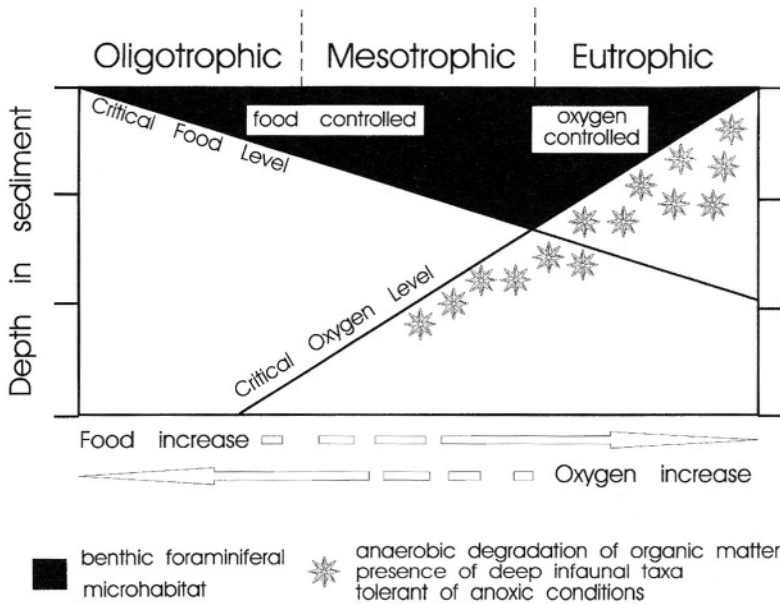
Figure 10.9 Hypothetical model showing the depth of the benthic foraminiferal microhabitat as a function of food availability in the sediment (oligotrophic and mesotrophic ecosytems) and/or oxygen concentration (eutrophic ecosystems). Note that many deep infaunal taxa may be found in completely anoxic conditions (represented by the star symbols). After Jorissen *et al.*, 1995.

often has a type D-distribution (Fig. 10.6), and sometimes shows prominent maxima deep in the sediment (Jorissen *et al.,* 1998).

An examination of the published data on foraminiferal microhabitats shows that the observed microhabitat patterns for most species are very consistent. Although the exact depth at which a specific taxon is found is variable, its position with respect to those of other taxa is very stable in most cases (Fig. 10.4). The genus *Nonionella* provides a striking exception to this rule. *N. turgida* is found with deep infaunal maxima in the western Atlantic Ocean (Corliss and Emerson, 1990) and in the Santa Monica Basin (species identified as *N. stella,* Mackensen and Douglas, 1989), but is the taxon with the most evident epifaunal tendency at shallow sites in the Adriatic Sea (Barmawidjaja *et al.*, 1992).

In view of the large spatial and temporal variability of foraminiferal microhabitats, and the large depth intervals over which living individ-

uals of some taxa are found, a statement about the microhabitat of a species or genus may just be a generalization. For instance, from observations on hard substrates (Lutze and Thiel, 1989), *Cibicides wuellerstorfi* is generally considered as an epifaunal (elevated) taxon. However, nonnegligible populations of the species have been described also within soft sediments (e.g. Corliss, 1991; McCorkle *et al.*, 1997; Jorissen *et al.*, 1998), which suggests that not all *C. wuellerstorfi* secrete their tests at the sediment-water interface.

In summary, the relationship between test morphology and microhabitat is complex, and all generalizations have significant exceptions. On the basis of a statistical analysis, Buzas *et al.* (1993) concluded that for the taxa they considered, microhabitat assignments on the basis of morphology were about 75% accurate. Although it can not be denied that there is a correspondence between test morphology and

microhabitat, the afore-mentioned examples show that some taxonomically close species (with only subtle morphological differences) may have significant differences in their microhabitats. It is possible that a thorough study of minor morphological characteristics (ornamentation, pore density, pore diameter, length/width ratio, presence of a basal spine, etc.) may lead to a considerable improvement in our comprehension of the various links between test morphology and microhabitat.

10.8   MICROHABITATS AND CARBON ISOTOPIC COMPOSITIONS

The stable isotopic composition of foraminiferal shells is extensively used in paleoceanography (see chapter 14). In particular, the $\delta^{13}C$ of benthic Foraminifera has been used as a proxy of export productivity and deep water circulation. The $\delta^{13}C$ of the oceanic bottom water depends on two main factors: the downward organic flux, which introduces ^{13}C-depleted organic matter produced in the surface waters, and the ventilation by bottom currents, which tends to supply waters with a high $\delta^{13}C$ Within the sediment, the organic matter is remineralized, releasing ^{13}C-depleted CO_2 to the pore waters. The result is a strong $\delta^{13}C$ gradient in the first few centimeters of the sediment. After the discovery of significant interspecific differences in the $\delta^{13}C$ of benthic Foraminifera, it was suggested that most species form their test in isotopic equilibrium with the composition of the surrounding water, and that the interspecific differences could be the result of microhabitat differences (e.g. Woodruff *et al.,* 1980; Belanger *et al.,* 1981; Grossman, 1984a,b). Several studies have confirmed this hypothesis, showing that generally, epifaunal taxa have a high $\delta^{13}C$ value, whereas infaunal taxa have a lower $\delta^{13}C$ (e.g. Grossman, 1987; McCorkle *et al.,* 1990; Rathburn *et al.,* 1996). The isotopic composition of infaunal taxa appears to be strongly influenced by that of the pore water.

   An excellent overview of the relations between foraminiferal microhabitats and stable isotopic compositions is given by McCorkle *et al.* (1997). Although the interspecific differences are clear, and apparently consistent, the almost total absence of a difference among specimens of deep infaunal taxa sampled at various sediment depths is striking (McCorkle *et al.,* 1990, 1997). According to McCorkle *et al.* (1997), this may imply that calcification takes place in a relative narrow subzone of the foraminiferal microhabitat range. Loubere *et al.* (1995), on the contrary, present data suggesting that the calcification of infaunal *Uvigerina* takes place in a microenvironment associated with macrofaunal activity, with a geochemistry very different from that of the average pore water. The comparison between the $\delta^{13}C$ profiles in pore waters and those of deep infaunal taxa (*e.g., Globobulimina* in McCorkle *et al.,* 1990, 1997) shows that the offset between the two profiles in a pair increases towards greater depth in the sediment. This suggests that calcification takes place preferentially close to the redox front, an idea which is matched by the suggestion of Bernhard (1992) that *Globobulimina* lowers its metabolism under completely anoxic conditions. An alternative explanation could be that an individual foraminifer forms its test over a prolonged time interval in a relatively wide depth zone in the sediment, and that the ultimate isotopic composition of its test is a reflection of the mean level within this depth interval.

   The species *Cibicides wuellerstorfi* (also placed under *Fontbotia, Planulina* or *Cibicidoides;* see Sen Gupta, 1989), which has been observed on elevated substrates, is supposed to secrete its test in equilibrium with the ambient bottom water, without being influenced by the substrate pore-water chemistry. This species has been used widely as an indicator of bottom-water characteristics (e.g. Duplessy *et al.,* 1984; Sarnthein *et al.,* 1988). However, as slated previously, observations of live *C. wuellerstorfi* within the sediment suggest that not all individuals of this species secrete their test in isotopic equilibrium with the bottom water. Furthermore, Sarnthein *et al.* (1988) speculate that regional organic-flux maxima could modify the isotopic composition of the water immediately above the sediment-

water interface. In areas with significant phyto-detritus deposits, a strong $\delta^{13}C$ gradient, resulting from the liberation of $\delta^{13}C$-depleted CO_2, may develop even above the sediment-water interface. Mackensen *et al.* (1993c) indicate that such a phenomenon can influence the isotopic composition of epifaunal Foraminifera; the larger food availability could trigger reproduction and/or chamber formation, and calcification could thus take place during times of strong $\delta^{13}C$ gradients close to the sediment-water interface. This 'Mackensen effect' is supported by the suggestion of Jorissen and Wittling (1999) that test production of *C. wuellerstorfi* is limited to a very short period of the year in the distal zones of the Cape Blanc upwelling area, when the organic flux is locally maximal. As a consequence, the isotopic composition of the tests of epifaunal taxa such as *C. wuellerstorfi* may represent conditions present during relatively short periods of time, and will not always reflect the average, long-term, isotopic composition of the bottom water mass.

A comparison of isotopic compositions of epifaunal and infaunal taxa could give important clues about the $\delta^{13}C$ gradient within the sediment, and thus, about the amount of organic matter remineralized in the benthic ecosystem (e.g. McCorkle and Emerson, 1988). Zahn *et al.* (1986) show an increasing difference in $\delta^{13}C$ between *Cibicides wuellerstorfi* and *Uvigerina peregrina* with an increase in organic flux. McCorkle *et al.* (1997), however, argue that if Foraminifera position themselves according to a geochemical cue (such as an oxygen gradient, or an organic-rich patch) or a food-related cue (such as bacterial decomposition), then species from a wide range of sediment depths may inhabit geochemically similar microenvironments. As an extreme example, in case of strongly dysoxic or microxic bottom waters, deep infaunal taxa may occupy the sediment surface, and may reflect the isotopic composition of the bottom water, but not of the pore water (Fig. 10.2). Proxies such as the $\Delta\delta^{13}C$ (epifaunal-infaunal difference) should, therefore, be used only after a clear understanding of the benthic environment in which the analyzed foraminiferal species actually lived.

10.9 PALEOCEANOGRAPHIC IMPLICATIONS OF BENTHIC FORAMINIFERAL MICROHABITATS

The knowledge of microhabitats is essential for a proper utilization of benthic foraminiferal species as paleoceanographic tools. Several authors have noted that the relative proportion of infaunal taxa becomes more significant as the organic flux increases (e.g. Corliss and Chen, 1988; Corliss and Fois, 1990; Rosoff and Corliss, 1992; Jorissen *et al.,* 1995). This suggests the possibility of developing a microhabitat based proxy for the organic flux. Furthermore, several taxa with a morphology indicative of an infaunal microhabitat show a systematic population increase under strongly dysoxic or microxic conditions (e.g. Bernhard, 1986; Kaiho, 1991; Sen Gupta and Machain-Castillo, 1993: Bernhard et *al.,* 1997). The proxy for bottom-water oxygenation developed by Kaiho (1991, 1994) is based on this principle. Kaiho (1994) shows a good correlation between the percentage of a number of 'oxic' indicators (in an assemblage of 'oxic' and 'dysoxic' species) and bottom-water oxygen concentration in the range of 1.5–3.0 ml 1 O_2. The 'oxic' taxa, which are considered epifaunal, appear to have a tolerance threshold at about 1.0 m 1 1 O_2. For the range of 0–1.5 ml/l O_2, Kaiho (1994) proposes a bottom-water oxygenation proxy that utilizes the relative dominance of a category of 'dysoxic' Foraminifera; this group contains taxa that have been described as shallow, intermediate, or deep infaunal. Rathburn and Corliss (1994), however, show that 'low oxygen taxa,' such as *Bolivina, Bulimina, Globobulimina, Uvigerina* and *Chilostomella,* are rare at a number of sites in the Sulu Sea, where bottom-water oxygen concentration is 1.76 ml/1 or less. They conclude that the dominance of these taxa is typical of environments with a high organic flux, rather than of environments with low oxygen concentrations.

The parameters of bottom-water oxygenation and organic flux (food availability) are closely interrelated, and it is often extremely difficult to distinguish their separate influences. Further-

more, bottom-water oxygenation does not necessarily covary with the penetration depth of oxygen in the sediment, and thus, with the extent of the oxygenated infaunal microhabitat. The sediment depth at which the oxygen concentration becomes zero may be very different at sites with very similar bottom-water oxygen concentrations (e.g. Rathburn and Corliss, 1994; Relexans *et al.,* 1996; Jorissen *et al.,* 1998). Within the sediment, the slope of the pore-water oxygen profile is determined by the balance between oxygen diffusion from the sediment surface and oxygen consumption by degrading organic matter. In areas with high organic flux, oxygen values in the substrate will rapidly drop to zero, and the depth of the oxygenated sediment layer will be minimal. Of course, bottom-water oxygen content is not necessarily low in such cases, because bottom currents may cause rapid oxygen renewal. As a consequence, even a strong dominance of infaunal taxa in the sediment is not always indicative of a dysoxic or microxic sediment-water interface.

Our best hope to find foraminiferal markers of benthic ecosystem oxygen content (species that are not primarily dependent on the organic flux) lies in the deep infaunal taxa, because they combine a high tolerance for low oxygen concentrations with that for low-quality food. Logically, the percentage of deep infaunal taxa in a benthic foraminiferal community should covary with the importance of anaerobic degradation of organic matter. As explained below, three different processes are relevant.

(1) Oligotrophic-mesotrophic ecosystems: an increase of the organic flux or export productivity. When the organic flux is very low, the bulk of organic matter is consumed at the oxic sediment-water interface. Thus, very small amounts of organic matter are mixed into the sediment by bioturbation and will be degraded in the anoxic zone. Much of the scarce organic matter brought into the sediment will be completely refractory, and will ultimately be fossilized. As a consequence, deep in the sediment, there is a near absence of anaerobic bacterial degradation, and thus also of deep infaunal taxa. A higher export productivity will increase both the amount of organic matter introduced into the sediment, and the importance of anaerobic degradation processes.

(2) More eutrophic ecosystems: a decrease in the quality of the introduced organic matter. The decrease in labile components may be the result of downslope transport or advection of old, terrestrial, refractory, organic matter from shelf environments, a more efficient recycling of organic matter in the surface waters, or the changing composition of the phytoplankton/zooplankton community. If the labile component of the organic matter, which is directly usable by the epifauna and shallow infauna. decreases, the densities of these two groups will diminish. Also, if the organic matter input remains the same, more organic matter will be degraded under anaerobic conditions deep in the sediment. As a consequence of the reduction of the epifauna and shallow infauna, and the increase in organic matter degradation within the sediment, the proportion of deep infaunal taxa will go up.

(3) Lowered oxygen concentration in bottom water. If bottom-water oxygenation falls below the critical value for a particular species, the species will disappear, probably as a result of failure to reproduce. As a consequence, other taxa that are more tolerant will show an increase in their proportions in the community. If a significant number of epifaunal and/or shallow infaunal taxa disappear, much more trophic-resources will become available to deep infaunal taxa; these may eventually move to the sediment surface, and replace taxa less tolerant to dysoxic or microxic conditions (Fig. 10.2). Under such circumstances, deep infaunal taxa can completely dominate benthic foraminiferal faunas; this phenomenon is known to precede sapropel formation in the Mediterranean Sea (e.g. Rohling *et al.,* 1997; Jorissen, 1999).

It appears that in most cases the percentage of deep infaunal taxa can be used as a proxy for the depth of the zero-oxygen sediment layer. Only under extreme conditions, however, when bottom-water oxygenation falls below a critical threshold for most surface-dwelling taxa, can the percentage of deep infaunal taxa be used

as a proxy of bottom-water oxygen values. Although Kaiho (1994) remarks that many 'oxic' indicators are systematically absent when oxygen values are below 1 ml/l, this putative multi-species low tolerance limit needs confirmation, and the exact values have to be determined for important species.

A second foraminiferal group which is of promise in paleoceanography consists of the so-called 'phytodetritus feeders' (Gooday, 1988; Gooday and Lambshead, 1989; Lambshead and Gooday, 1990; Gooday *et al.*, 1992a; Gooday, 1993). Smart *et al.* (1994) and Thomas and Gooday (1996) suggest that the relative abundance of *Epistominella exigua, Alabaminella weddellensis,* and other phytodetritus exploiting species may be used as a proxy of pulsed organic matter inputs. An opportunistic lifestyle, shared by all phytodetritus species, enables them to profit from short periods of abundant food availability. However, these periods of feast are not necessarily connected with seasonal influx of phytodetritus; they may be related to other processes that cause an intermittent organic flux. Gooday and Turley (1990) give the example of upwelling areas, in which most of the organic-matter is delivered to the sea bottom as phytodetritus. Although upwelling in many areas is labeled as 'permanent,' in reality the upwelling process is periodically interrupted (from a few days to several weeks) when the flow of deeper, nutrient-rich waters ceases (e.g. Jones and Halpern, 1981). A different context in which opportunistic 'phytodetritus' species may be successful is that of a very eutrophic ecosystem with very low seasonal bottom-water oxygen content. In such an environment, opportunistic, surface dwelling species will profit from short periods of bottom-water re-oxygenation that would make abundant trophic resources accessible to the benthic fauna.

The so-called 'elevated epifaunal' taxa (Lutze and Thiel, 1989; Altenbach and Sarnthein, 1989; Linke and Lutze, 1993), such as *Cibicides wuellerstorfi* and *Planulina ariminensis,* have tentatively been proposed as indicators of bottom current activity. Putatively, these taxa feed on particles transported by bottom currents, and would therefore be independent of any vertical flux of organic matter. However, observations of live *C. wuellerstorfi* at some depth in the sediment suggest that these taxa are not necessarily confined to elevated positions, and that their use as a proxy for bottom-water current activity may not be realistic.

Of necessity, the foregoing discussion is qualitative. Although our understanding of foraminiferal microhabitats has advanced significantly in the last decade, quantification of the foraminifer-microhabitat relationships is still rudimentary. This quantification remains one of the main challenges of foraminiferal ecology.

10.10 ACKNOWLEDGMENTS

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11

Benthic Foraminifera and the flux of organic carbon to the seabed

Paul Loubere and Mohammad Fariduddin

11.1 INTRODUCTION

Organic carbon supply is a fundamental aspect of all biological communities, and the organic carbon flux is generally limited for marine benthic organisms. Benthic organisms shrouded in darkness, at water depths greater than a few tens of meters, are entirely dependent on imported organic carbon for their energy requirements. As we will show in this review, areal variations in the flux of organic carbon to the seafloor have a pervasive effect on the benthic community, including the Foraminifera.

Because the processes and ecology are so different, we will examine separately the marine environments within and below the euphotic zone. Our review will be presented in four sections. The first will examine the production of organic matter in the marine realm and its delivery to the ocean floor. The second will summarize observations concerning Foraminifera and food supply. The third will review our basic understanding of the benthic response to organic carbon flux, and present ideas on and models of the response of benthic Foraminifera

to that flux. These models will be examined using data concerning foraminiferal microecology, spatial distributions, morphology and abundances. The last section will survey the state of our knowledge and raise important questions which limit our understanding of benthic Foraminifera and their geologic record.

11.2 ORGANIC CARBON SUPPLY

11.2.1

Organic carbon compounds are initially supplied to the marine biologic community from three dominant sources. These are: nearshore production of benthic plants, production of the open ocean phytoplankton and fluvial supply of particulate organic matter (Newman *et al.,* 1973; Hedges and Parker, 1976; Westerhausen *et al.,* 1993; Rice and Rhoads, 1989). Each of these sources also supplies dissolved organic matter which will feed bacteria and thus enter the particulate food chain. The organic matter from the three sources can be roughly divided into three

categories based on its energy content and appeal to the biota. These are: labile, resistant and refractory (Middleburg *et al.,* 1993). The labile material is of the greatest importance to biological productivity in the ocean, and is used up most rapidly. The resistant material is used by a specialized population of organisms and can survive in the marine environment for longer periods of time. Refractory organic carbon is nearly biologically inert. It is important to draw these distinctions of type because benthic organisms, including Foraminifera, will respond mostly to the flux of labile material. These carbon compounds are not generally preserved in marine sediments, which by and large accumulate only the refractory material that is no longer, and perhaps never was, of interest to the biota. In the past it has been the practice to examine the relationship of benthic Foraminifera to organic carbon by comparing taxon abundances to sediment organic carbon content. However, the sediment organic material is a residue from a variety of processes not always directly linked to biological productivity. Recent work on sediment organic carbon has shown that a good deal of the preserved material is adhered to clays, and that sediment organic carbon content is mostly a function of clay content and surface area (Keil *et al.,* 1994; Mayer, 1994; Hedges and Keil, 1995). Also, research on the northwestern and northeastern Atlantic continental margins indicates that much carbon transported from the shelf onto the slope (mid-slope carbon high) and deeper water is degraded, refractory material (Rowe *et al.,* 1986; Duineveld *et al.,* 1997).

A global view of biological productivity and the supply of labile organic matter to the seabed is difficult to create. This view must incorporate three factors: euphotic zone production, the fraction of that production that sinks into the deep-sea, and the local flux of material transported along the seafloor (e.g. Reimers *et al.,* 1992; Smith, 1987). Surface-ocean production is seasonally variable and can be episodic or subject to longer term trends. Transport processes along the seafloor are, by their nature, localized and quite variable in time. Nevertheless, a general picture of organic matter generation is available from syntheses of measured euphotic zone productivity (e.g. Berger *et al.,* 1987; Berger, 1989), satellite images of phytopigment concentrations in oceanic surface waters (Feldman, 1994), model estimates of productivity based on the pigment concentrations (Longhurst *et al.,* 1995; Antoine *et al.,* 1996; Behrenfeld and Falkowski, 1997), and the extrapolation and mapping of benthic respiration (Jahnke, 1996).

11.2.2 Flux to the seabed

The supply of organic matter generated in the upper layers of the open ocean can be generally divided into two fractions: the recycled and the new production. New production is traditionally the part of total production which is sustained by new nitrate introduced into the euphotic zone (Eppley and Peterson, 1979; Jumars, 1993). The ratio of new production to total production is referred to as the *f*-ratio. In any steady state consideration of phytoplankton production, the new production is that part of the total which will escape to the deeper ocean and be oxidized there by the benthos. Therefore, variations in the *f*-ratio are of considerable significance to the benthic organic carbon supply. The range of values for the ratio is from about 0.4 to 0.05. with some of the lowest values observed in the central equatorial Pacific (McCarthy *et al.,* 1996: Head *et al.,* 1996). Lampitt and Antia (1997) show that for the open ocean there is, nevertheless, a systematic relationship between surface-ocean biological productivity and organic carbon flux to the seafloor.

Besides depending on the *f*-ratio. the flux of phytoplankton production reaching the seafloor depends on water depth. This relationship is most acute in the upper 1000 m of the water column (Martin *et al.,* 1987; Berger *et al.,* 1987). The relationship between the nature of the flux and the water depth has been examined empirically using sediment trap data, and several different equations have been fitted to the curve. In all cases, the flux of material reaching the seabed at depths greater than 1000 m is only a few percent of the euphotic zone production,

indicating that efficient recycling of production occurs in the upper few hundred meters of the water column. The result of this is a slim diet for the deep-sea fauna in most areas of the world ocean.

In certain regions, most notably the northwest Indian Ocean and the northeast Atlantic, surface-ocean biological productivity is highly seasonal and organic matter reaches the seabed in pulses, sometimes of fresh phytodetritus (e.g. Smith *et al.,* 1996). Biological response to these pulses is reviewed below. In other areas of the world ocean, such as the eastern equatorial Pacific, seasonality is muted and longer term cycles (El Niño) influence the flux of organic matter to the seafloor. Where the flux is relatively low, it appears that labile organic matter is oxidized at the sediment-water interface. Labile matter has a life span of less than a year (Cole *et al.*, 1987).

11.3 BENTHIC FORAMINIFERAL RESPONSES

11.3.1

Since the earliest regional surveys (e.g. Phleger, 1951a; Pujos-Lamy, 1972; Ingle *et al.*, 1980), it has been evident that benthic foraminiferal taxa show water depth zonation. Modern statistical analysis (e.g. Culver, 1988) uses this zonation to determine water depths to within 50–250 meters for selected continental margins. The reason for the zonation of the Foraminifera has not been clearly established since many environmental variables covary with water depth. One school of thought, developed first in the 1970s, holds that characteristics of oceanic water masses control foraminiferal distributions (see chapter 1). To a degree this must be true, since waters in the upper mixed layer of the ocean, except at higher latitudes, are much warmer than those below the thermocline. Also, these upper waters are subject to strong variations in their properties in response to seasonal changes and the weather. The sunlit portion of the oceans above the seasonal thermocline is in many ways a very

different environment from that found at depth. Because of this difference, we will treat the shallow ocean separately from the deep sea (water depth greater than about 200 meters).

11.3.2 The shallow ocean

Although it is recognized that organic carbon availability is important to benthic Foraminifera in the shallow ocean, it has been difficult to assess its exact effect. This is because organic carbon flux is not usually directly measured in foraminiferal studies (organic carbon content of sediments is only an indirect proxy for labile organic carbon flux), and because availability of food is often covariant with many other ecologic factors that are important to the Foraminifera. Further, it is probably also true that in many nearshore settings food availability is not a primary limiting factor for the benthos. Other variables such as substrate, current and wave regime, temperature, salinity, pore-water oxygen content, and biotic interactions could often be more significant.

In the nearshore region, the effect of labile organic carbon availability has been best documented in areas affected by sewage effluent and eutrophication in estuaries or fjords. For the latter settings, the overconsumption of oxygen and the development of anoxia probably constitute the most important factors impacting the Foraminifera. This subject is examined in chapter 12, and a review of pollution effects on estuarine Foraminifera will be found in chapter 13 and Alve (1995a). Case studies of sewage outfall areas over several decades show definite foraminiferal response to these. Early studies such as those of Watkins (1961) and Bandy *et al.* (1964b) recorded changes in nearshore, colder-water foraminiferal communities and assemblages that related to closeness of a sewage outfall. Most marked were areas devoid of living Foraminifera and the concentration of a limited number of taxa near outfalls. For example, Bandy *et al. (*1964b) found that *Buliminella elegantissima* and *Bulimina marginata denudata* were overwhelmingly dominant in the living population of the outfall region for the Los

Angeles County sewage system in Southern California. Further, in the nearshore, *Discorbis columbiensis* showed a positive distributional response to sewage outfall while *Nonionella* could not tolerate the polluted environment. These observations were corroborated and extended in the follow-up study of Stott *et al.* (1996) who examined this setting after controls had brought significant environmental improvement. In this case, foraminiferal responses are driven by a very large input of organic matter which will alter not only the availability of food but also the character of the sediments and, perhaps most importantly, the distribution of oxygen in the environment. Strongly anaerobic sediments were not uncommon in the area examined by Bandy and colleagues. Also, studies of sewage outfalls include chemical and metal pollution as potential factors, so the extent to which they can be used to interpret natural settings is open to question. Finally, taphonomic processes may be enhanced in sediments with high organic content so that assemblages preserved in the sediments may be quite different from those found in the living community. Bandy *et al.* (1964b) found the abundance of agglutinated Foraminifera much increased in their assemblages for this reason. Nevertheless, similarities between foraminiferal communities of polluted environments and those found in the stratigraphic record of sediments with high organic content were noticed early on (e.g. Seiglie, 1968). Furthermore. Schafer *et al.* (1995) found a general inverse relationship of species diversity to organic carbon loading in the vicinity of aquaculture operations in eastern Canada, and an increase in non-calcareous Foraminifera as organic content of the sediments increased. At very high organic content (>20%,) no Foraminifera were observed. The mechanisms responsible for these changes probably are not linked directly to increased food supply, and are likely the product of changing sediment properties, sedimentation rate, and oxygen concentrations. One case where increased food supply may be important is that found along the southern coast of Israel where sewage outfall enhances the productivity of the adjacent continental shelf

(Yanko *et al.,* 1994c). This agrees with the results of Watkins (1961), Setty (1976), and Clark (1971). In the Yanko *et al.* study the foraminiferal abundances were elevated above background and assemblages contained many large, robust specimens. The composition of assemblages was not much different from that on the adjacent unpolluted shelf. There was no documentation of the organic carbon flux to the seabed in this study, and presumably, it was less dramatic than described in the reports mentioned above. So. it may be that in the shallow-water environment, there is a gradient in foraminiferal response to increasing organic carbon flux. At the low end this response may simply be an increase in the standing stock. At higher fluxes, taxa may be progressively excluded or encouraged by environmental changes driven by organic carbon accumulation and oxidation within the sediments (sediment properties, oxygen availability). At the extreme, Foraminifera are excluded from the environment and a 'dead zone' is produced. Quantification of these steps is not possible with the data at hand.

In shallow marine settings free of anthropogenic influence, the role of labile organic carbon availability is ambiguous. Nevertheless, a number of studies show that biomass of Foraminifera responds to seasonal and regional variability in marine plant production. For example, Murray (1985) has shown a relationship between fertility and foraminiferal abundance in the North Sea. Alve and Murray (1994) have traced the impact of the spring phytoplankton bloom on foraminiferal abundance in a mesotidal inlet in England, Schroder-Adams *et al.* (1990) document a likely control of foraminiferal abundances in the high Arctic by sea-ice limited biological productivity, and Bernhard (1987) shows a similar productivity control on abundances in the Antarctic. Lueck and Snyder (1997) compared two regions on the continental shelf of North Carolina (U.S.A.), and found differences in foraminiferal abundances linked to benthic community productivity, in this case possibly driven by nutrient enriched groundwater fluxing through the sediments. Earlier, Lee *et al.* (1966) suggested that many littoral Foraminifera are bloom feeders.

The exact impact of the availability of labile organic carbon on shallow-water foraminiferal communities and assemblages is difficult to assess, because of the correlations that organic carbon flux has to other important environmental variables. For example, Hayward *et al.* (1996) collected data for both Foraminifera and environmental variables for an ecological analysis of a tidal inlet in New Zealand. They found assemblage changes that could possibly be related to food supply. However, the effects of the environmental factors are obscured by correlations among organic carbon, mud content of the sediments, salt marsh index, total oxidized nitrogen, and dissolved reactive phosphate. Defining taxon ecologic responses to the different environmental variables under these conditions is not possible.

Finally, it is important that labile organic carbon in the shallow-water setting comes in many different forms, from pretreated sewage and bacteria (e.g. Goldstein and Corliss, 1994) to algal mats, algal coatings on sediment grains, and stands of macroalgae. Additionally, shallow-water Foraminifera may bear endosymbionts (see chapter 8), and perhaps even farm bacteria (Langer and Gehring, 1993). This means that foraminiferal taxa will vary not only in response to the quantity of organic matter but also its form. The taxa present and their abundance for a given setting will depend on feeding type adaptations (e.g. Lipps, 1983).

11.3.3 The deep sea

The supply of labile organic carbon is much reduced in the deeper ocean (depth > about 200 m) and is much more likely to be a primary limiting factor in benthic ecology. Altenbach and Sarnthein (1989) and Gooday *et al.* (1992a) provide a summary of the abundance and possible importance of benthic Foraminifera to deep ocean communities. In many instances, benthic Foraminifera may be a dominant component of the fauna. For example, off Cape Hatteras on the U.S. east coast, *Bathysiphon filiformis* occurs in great abundance and its tubes are a prominent feature of the ocean floor (Gooday *et al.*,

1992b). It is interesting to note that much of the information on foraminiferal biomass and community importance in the deep sea centers on non-calcareous taxa, while the abundance, productivity, and community relations of the calcareous taxa remain obscure. In contrast, the calcareous taxa are usually better preserved in marine sediments, and receive most of the attention in geological and paleoceanographic studies. Gooday *et al.* (1997) provide an interesting examination of non-calcareous deep-sea Foraminifera and their relationship to organic carbon flux. A review of both agglutinated and calcareous deep-sea Foraminifera with an emphasis on organic carbon flux may be found in Gooday (1994). The review below will concentrate on the calcareous taxa.

Causes for the depth zonation of benthic foraminiferal communities below the thermocline have been the subject of debate for decades. In many ways the foraminiferal zonation parallels that seen for other benthic organisms (reviewed in Loubere, 1996), and is thus a part of the general biotic response to the deep-sea environment. The depth zonation of species and species groups, however, is not consistent from one continental margin to another (Pujos-Lamy, 1972; Miller and Lohmann, 1982; Lutze and Coulbourn, 1983/84). Early attempts to analyze this variation focused on relating foraminiferal taxa to deep-ocean water masses whose physical and chemical properties were supposed to control species distributions (e.g. Schnitker, 1980). More recent water mass based studies show statistical relationships on a regional level (e.g. Denne and Sen Gupta, 1991), but these have not been consistent for inter-regional comparisons (Miller and Lohmann, 1982; Lutze and Coulbourn, 1983/84; Corliss *et al.*, 1986; Mackensen *et al.*, 1993). This is particularly true for the taxon *Uvigerina peregrina*, which at different times was associated with warmer bottom waters and deep waters with low oxygen content. A major shortcoming of the water mass control hypothesis has been the lack of a model based on ecological principles or theory that would explain why relatively small physical and chemical differences in ambient water would control species distributions.

Regional surveys of benthic foraminiferal distributions show that there are horizontal as well as vertical gradients in taxon abundances. This is clearly seen in Poag's (1981) atlas of Foraminifera in the Gulf of Mexico, which illustrates strong distributional changes in the vicinity of the Mississippi River Delta. Similarly, Lutze and Coulbourn (1983/84) recognized lateral changes in benthic foraminiferal communities on the continental margin of northwestern Africa. Some of their findings are shown in Fig. 11.1 which presents regional patterns of abundance for the living taxa. These community or assemblage distribution patterns were associated with changing sedimentary regime, and with organic-carbon content of the sediment. A similar interpretation of faunal distributions was made for the northeastern U.S. continental margin by Miller and Lohmann (1982). In the case of the Gulf of Mexico, Loubere et al. (1993a) demonstrated that the flux of organic matter to the seabed was higher on the Mississippi River delta slope than elsewhere in the northwestern Gulf, so that lateral changes in foraminiferal communities could be associated with this flux. Osterman and Kellogg (1979) recognized the impact of surface-ocean productivity on benthic foraminiferal assemblages in a study of surface sediments from the Ross Sea, Antarctica. Sen Gupta et al. (1981) observed unusual foraminiferal assemblages on the Florida continental slope associated with upwelling. Van der Zwaan (1982) argued on the basis of geologic interpretation of Miocene sections in the Mediterranean region that food supply must be a dominant controlling factor of benthic foraminiferal taxon distributions. Boersma (1985) and Woodruff (1985), in their geological investigations, also concluded that food supply was important. Mackensen et al. (1985) examined foraminiferal assemblages on the continental margin of southwestern Norway, and found that some taxon distributions correlated to organic carbon content of the sediments. A larger scale analysis of Rose-Bengal stained (presumed living) benthic Foraminifera from the top centimeter of the sediments and dead assemblages for the South Atlantic by Mackensen et al.

(1993a) also found distributions that varied laterally. Part of their data is shown in Fig. 11.2, which presents assemblage distributions the authors associate with increased carbon flux to the seafloor in the vicinity of the Polar Front. Two higher productivity assemblages/communities are vertically separated under what Mackensen et al. (1993a) interpret as a water mass effect (perhaps chiefly a temperature/effect). However, the region examined is strongly affected by carbonate dissolution and a shoaling CCD (calcite compensation depth, their Fig. 4). So, changing preservation cannot be discounted as a factor contributing to vertical assemblage gradients in the South Atlantic. In this case, preservation will correlate with changing water masses (Antarctic Bottom Water vs. North Atlantic Deep Water). Schmiedl et al. (1997) conducted a study on the Southwest African margin similar to that of Mackensen et al. (1993a). They found that stained and dead foraminiferal taxon distributions were most strongly associated with interpreted food supply and pore-water oxygen content (neither directly measured). They examined taxon principal component correlations with water depth, porosity, carbonate content, total organic carbon, temperature, salinity, bottom-water oxygen content, phosphate content, and calculated TOC flux. Complete analysis of faunal responses is complicated by the correlations among the environmental variables (not given) which make distinguishing their separate effects difficult.

The benthic foraminiferal assemblage relationship to surface-ocean biological productivity and its related organic carbon flux to the seabed were first unambiguously tested by Loubere (1991) in a study where productivity was statistically uncorrelated with any other significant environmental variable. This work showed a quantitative relationship between productivity and the benthic foraminiferal assemblages, and recognized assemblages with particular ranges of surface-ocean biological productivity. The Loubere (1991) analysis was later expanded to cover the eastern Pacific (Loubere, 1994), the Atlantic Ocean (Fariduddin and Loubere, 1997), the Indian Ocean (Loubere, 1998), and finally
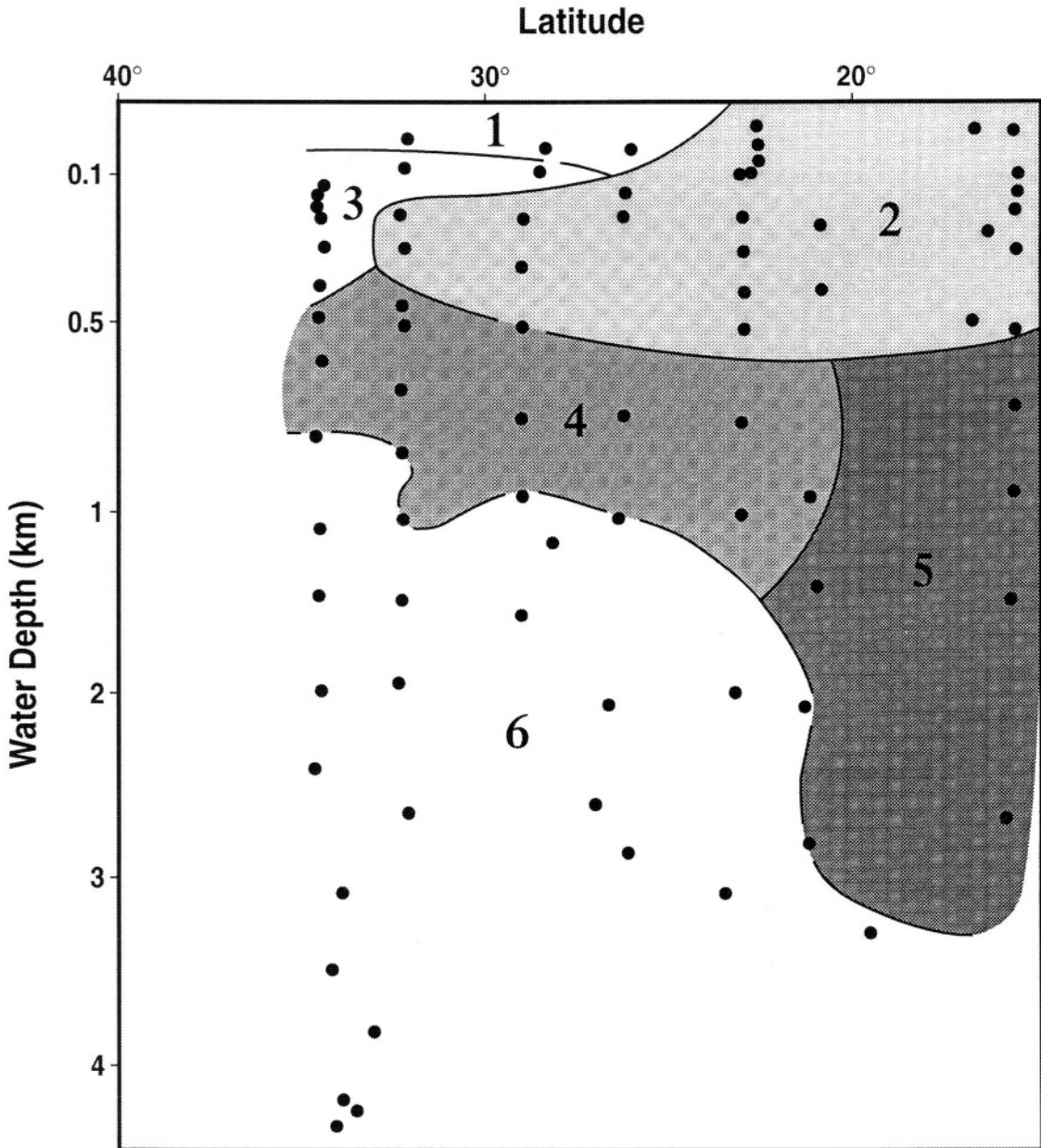
Figure 11.1 Living benthic foraminiferal community groupings on the continental margin of N.W. Africa after Lutze and Coulbourn (1983/84). View as from the ocean looking towards Africa. Groupings are based on correlations among surface sediment benthic foraminiferal abundances and show both depth and latitude related boundaries. 1 = *Cibicides lobatulus* biofacies, 2 = *Cancris auriculus* biofacies, 3 = *Globobulimina* biofacies, 4 = *Uvigerina peregrina finisterrensis* biofacies, 5 = *Uvigerina peregrina/Globobulimina* biofacies, 6 = *Cibicides wuellerstorfi* biofacies.
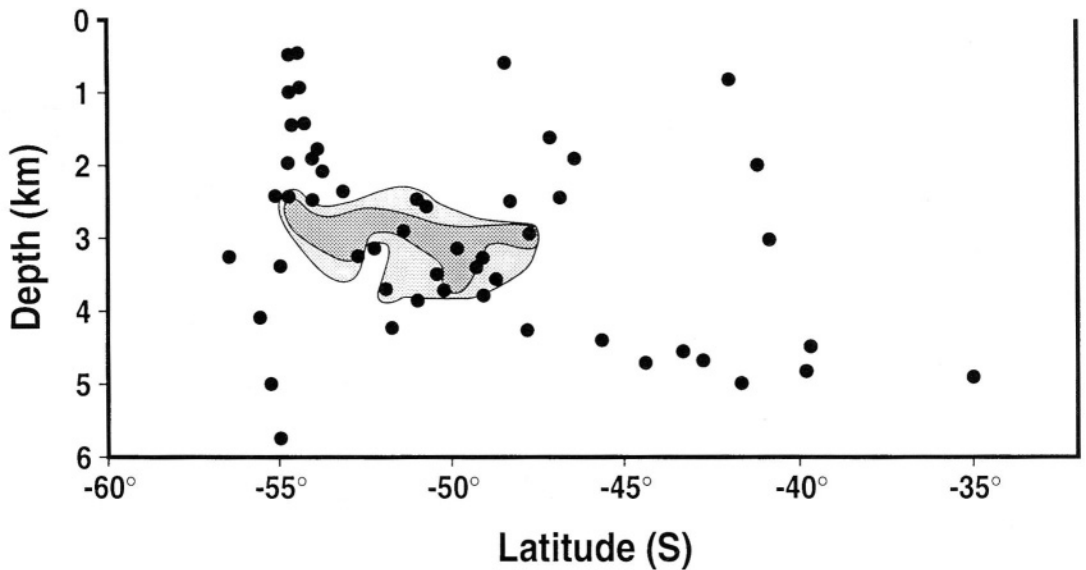
Figure 11.2 Distribution of deep sea benthic foraminiferal communities/assemblages projected onto a latitudinal transect in the South Atlantic, after Mackensen *et al.* (1993a). Dead assemblage distribution for the Southern High-Productivity Fauna (*Pullenia bulloides* assemblage).

the global ocean (Loubere and Fariduddin, 1999).

These works used geographically selected samples taken within a limited range of water depths so that the biological productivity signal would be uncorrelated to other factors that could influence benthic foraminiferal assemblage composition; this approach avoids misinterpretation of environmental effects through spurious correlations among controlling ecologic factors (e.g. Loubere and Qian, 1997). Figure 11.3 shows the regional patterns of benthic foraminiferal assemblages (factor patterns) found in the above studies for the eastern Pacific and the Atlantic. The higher-productivity upwelling areas of the two oceans are clearly mapped out on the ocean floor by the Foraminifera.

There is a global uniformity in the taxa found associated with different ranges of productivity. Higher- and lower-productivity taxon groupings of Loubere and co-workers (see Figs. 11.4, 11.5) are consistent with the results of other regional surveys in the higher latitude South Atlantic (Mackensen *et al.*, 1993a) and the South African Atlantic continental margin (Schmiedl *et al.*,

1997). The global data base of taxon abundances for the deep open ocean has also been used to quantify the foraminiferal assemblage to surface-ocean productivity relationship via multiple regression. Assemblages have been used to estimate productivity with an $r^2 = 0.97$ (eastern Pacific, Loubere, 1994) and 0.89 (global ocean, Loubere and Fariduddin, 1999).

In addition to the influence on assemblages, surface-ocean productivity also seems to affect planktonic to benthic (P/B) foraminiferal ratios (Berger and Diester-Haas, 1988) and benthic foraminiferal accumulation rates (Herguera and Berger, 1991). Both of these relationships would result from a correlation between benthic foraminiferal production and flux of organic carbon to the deep-sea floor. Little information is available about benthic foraminiferal productivity (shells generated per unit time), but standing stocks are related to food supply, as seen in the surveys of Lutze and Coulbourn (1983/84) and Schmiedl *et al.* (1997). Also, examination of P/B ratios and foraminiferal shell accumulation rates must take into account taphonomic processing within the sediments. This is not constant across all oceanic environments, and is still
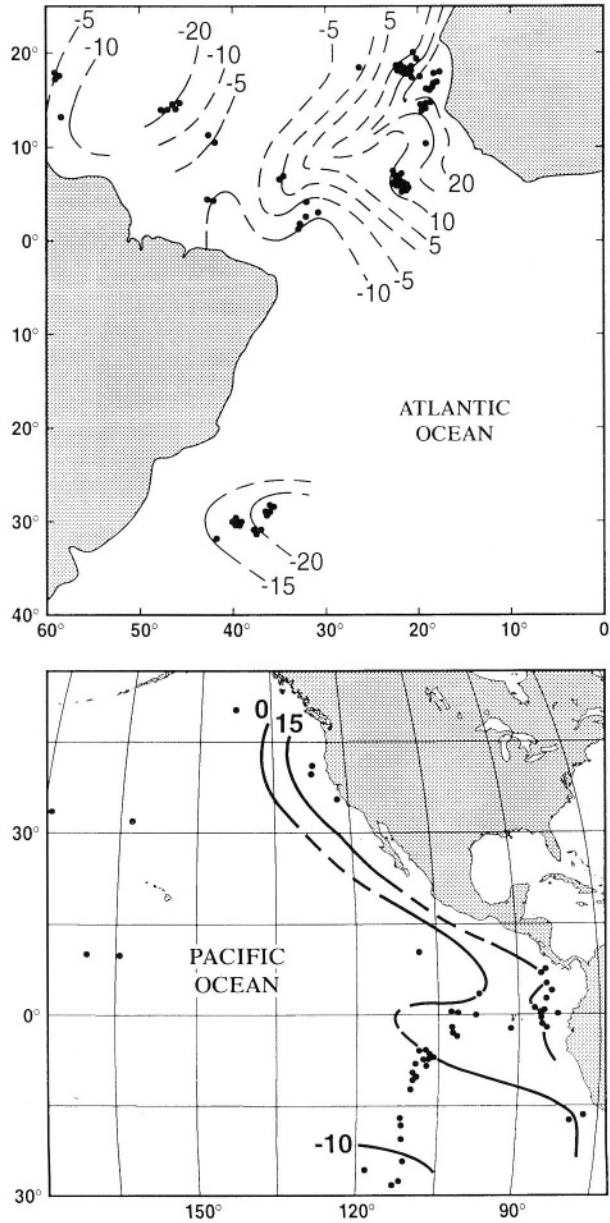
Figure 11.3 Maps of first Principal Component scores for surface sediment assemblages in the Atlantic and Pacific Oceans. In each case the scores account for a large part of the assemblage variance, and their patterns follow average surface ocean productivity gradients. Data from Loubere (1996) and Fariduddin and Loubere (1997). Higher productivity areas have positive scores.

poorly defined. The P/B ratio has been traditionally used to estimate water depth on continental margins, but also includes a productivity signal. Analysis by van der Zwaan *et al.* (1990) suggests that this signal is largely incorporated in taxa deemed to be infaunal. The relationship between accumulation rate and productivity has been quantitatively calibrated at a relatively lim-
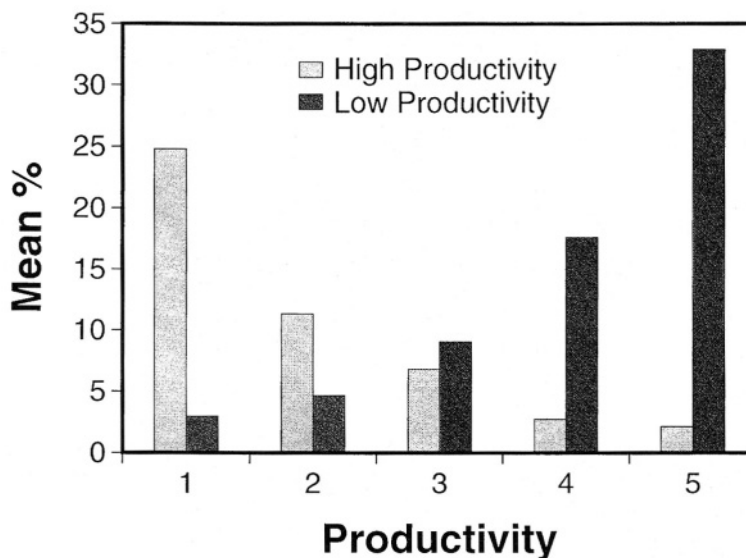
Figure 11.4 Mean abundance of the 'high productivity' and 'low productivity' benthic foraminiferal groups along the global productivity gradient for 207 samples in the Atlantic, Pacific and Indian Oceans (Loubere and Fariduddin, 1999). On the productivity axis: $1 = > 200$ gC/m²/yr, $2 = 200$–150 gC/m²/yr, $3 = 150$–90 gC/m²/yr, $4 = 90$–50 gC/m²/yr and $5 = < 50$ gC/m²/yr. The high productivity group includes: *Uvigerina sp.*, *M. barleeanus*, *M. pompilioides*, *B. alazanensis*, *B. mexicana*, *Globobulimina* sp. and *S. bulloides*. The low productivity group includes: *G. subglobosa*, *N. umbonifera* and *F. seminuda.*

ited number of locations in the Pacific Ocean. The use of the accumulation rate as a productivity signal depends on the assumption that each foraminiferal test, regardless of species, is equivalent to a set quantity of organic carbon reaching the seafloor. It must also be assumed that taphonomic processes are linked to organic-carbon flux to the seafloor so that a consistent productivity signal can be maintained through the transition from living community to fossil assemblage. Naidu and Malmgren (1995) tested both the P/B and benthic foraminiferal accumulation rate tracers for paleoproductivity at a site in the oxygen minimum zone of the Oman margin in the Arabian Sea. They found that neither appeared to properly reflect changes in surface-ocean productivity (hence organic-carbon flux to the seabed) through the past 18,000 years. The favored explanation for this was that the low oxygen content of bottom water placed constraints on the benthic foraminiferal community, and that their abundances mainly reflected changes in oxygen supply. The link between organic carbon flux and the P/B ratio and benthic foraminiferal accumulation

rates needs further exploration over a broader range of environments. In particular, justification is needed for accepting the assumption that all foraminiferal shells, regardless of species, represent the same quantity of labile organic-carbon reaching the seafloor.

Finally, associations have been found between organic carbon flux to the seabed and individual taxon abundances and taxon morphology. Corliss (1985, 1991), Corliss and Chen (1988), and Corliss and Fois (1990) have observed variations in benthic foraminiferal morphotypes which they ascribe to changing organic carbon flux to the seabed and associated microenvironments. Corliss put morphologies into three habitat-groups: epifaunal, shallow infaunal (just below the sediment-water interface), and deeper infaunal. Corliss and Chen divided their morphotypes into nine groups: rounded trochospiral, plano-convex trochospiral, miliraline, biconvex trochospiral, rounded planispiral, flattened ovoid, tapered and cylindrical, spherical, and flattened tapered. They found regular changes in the abundances of the morphotype groups in transects down continental margins. Deeper-
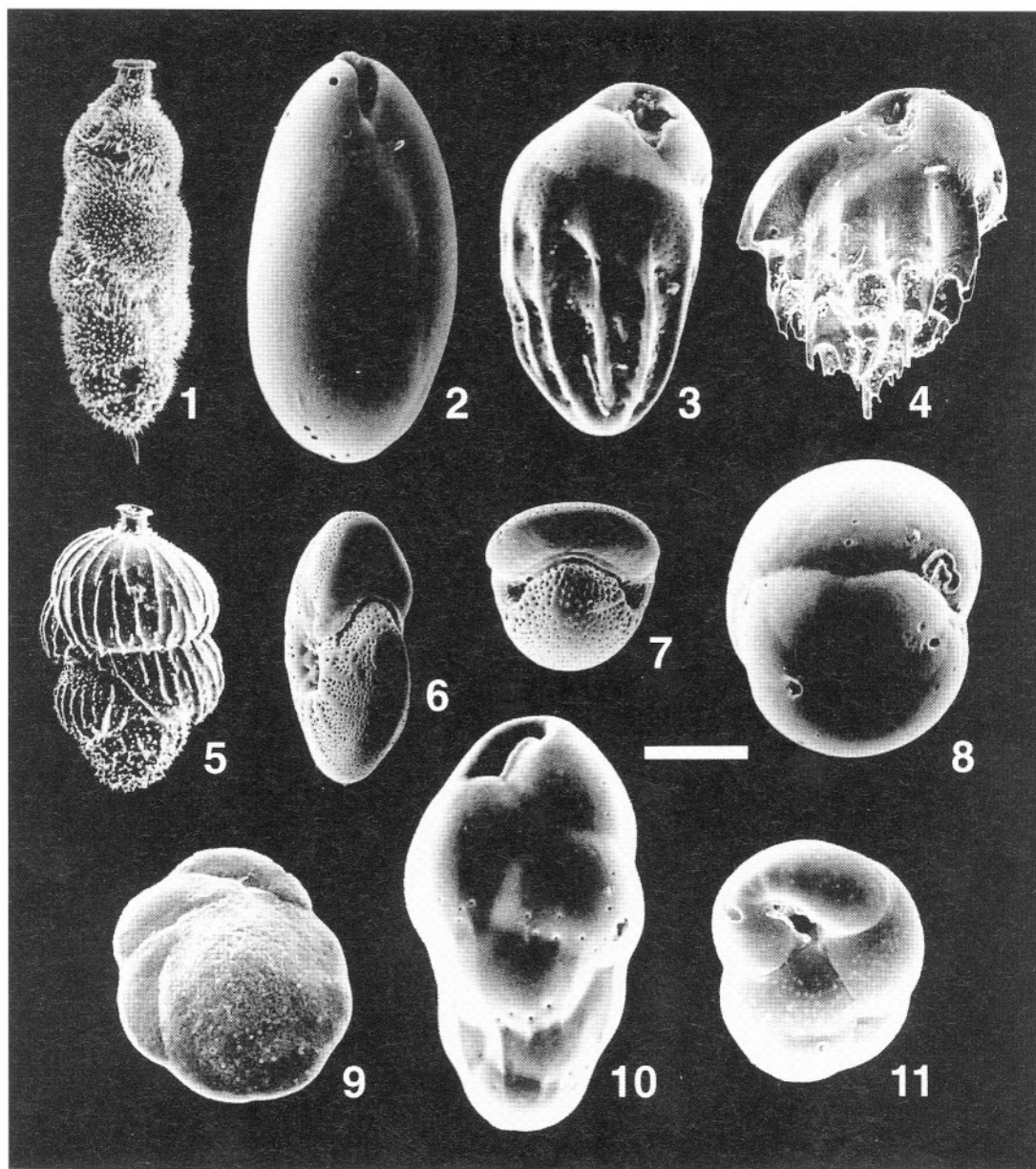
Figure 11.5 High (figures 1–8) and low (figures 9–11) productivity taxa commonly observed in the deep sea. Size of specimen on the longest dimension shown in parentheses in microns, followed by scale bar length for that specimen. **1**. hispid *Uvigerina* sp. (652:167). **2**. *Globobulimina* sp. (835:209). **3**. *Bulimina alazanensis* (371:108). **4**. *Bulimina mexicana* (742:228). **5**. *Uvigerina peregrina* s.l. (719:262). **6**. *Melonis barleeanus* (464:175). **7**. *Melonis pompilioides* (441:268). **8**. *Sphaeroidina bulloides* (255:88). **9**. *Nuttallides umbonifera* (394:158) **10**. *Bulimina transluscens* (267:66) **11**. *Globocassidulina subglobosa* (186:79).

infaunal habitat types (e.g. rounded planispiral, tapered cylindrical) decrease in abundance with increasing water depth.

At the species level, Collins (1989) examined mophometric variation in *Bulimina aculeata* and *B. marginata,* and found shape variations that could be linked to the abundance of organic carbon and mud along the margin of the Gulf of Maine. Boltovskoy *et al.* (1991) summarized studies showing the effects of food availability on the size of foraminiferal taxa. These appear to be environmentally dependent. Corliss (1979) inferred that in the deep sea, smaller size in *Globocassidulina subglobosa* was associated with limited food supply. Caralp (1989a) associated larger size and higher percentage of abnormal tests in *Melonis barleeanus* at a location on the slope of west Africa with increased supply of little altered organic matter.

11.3.4 Seasonality of the organic carbon flux to the seabed

The discussion so far has treated organic carbon flux to the deeper seabed as a homogeneous ecological factor. However, it is well documented that the flux is often highly variable in time. In many oceanic areas, there are seasonal peaks in surface-ocean biological productivity, and these may produce relatively short bursts of organic carbon rain on the seafloor. For example, Hecker (1990) and Smith *et al.* (1996) showed that blooms of phytoplankton can be accompanied by accumulation of fresh organic-detritus on the seafloor. Pfannkuche (1993) saw a marked increase in the relative abundance of benthic Foraminifera at a North Atlantic sampling station (47° N, 20° W) in response to a benthic flux event. Altenbach (1992) reviewed benthic foraminiferal response to short term events in the deep sea. Linke *et al.* (1995) presented experimental evidence of a rapid response of benthic Foraminifera to an influx of organic matter. Corliss and Silva (1993) and Silva *et al.* (1996) showed a rapid seasonal growth response in benthic Foraminifera along the California borderlands, probably in response to increased organic matter flux to the seafloor. Caralp

(1984) observed that certain species of deeper-water benthic Foraminifera appear to be more abundant when supplied with fresh organic carbon. Finally, Gooday (1988, 1993. 1996) and Gooday and Lambshead (1989) found that foraminiferal species such as *Alabaminella weddellensis. Epistominella exigua, E. pusilla. Fursenkoina* sp. and *Globocassidulina subglobosa* preferentially use freshly fallen phytoplankton detritus as a microhabitat. The organic carbon flux seasonality signal in benthic foraminiferal assemblages from deep-sea surface sediments was examined by Loubere and Fariduddin (1999). They analyzed a global assemblage data base in relation to average surface-ocean biological productivity and a seasonality index interpreted from Coastal Zone Color Scanner images of oceanic phytoplankton pigment concentrations. Loubere and Fariduddin divided the assemblage data base into groups based on productivity and seasonality, and used Discriminant Function Analysis to test for separation among these groups. Figure 11.6 shows their results. They found a simple patterning of the foraminiferal data with Discriminant Function 1 summarizing the average annual productivity response and Function 2 incorporating the seasonality response. The location of group centroids in Fig. 11.6 shows that the seasonality signal in benthic assemblages is largest at higher average annual productivity (Groups 1 and 2), and decreases as productivity drops (Groups 7, 8, and 9). At low productivities, it is difficult to identify a seasonality driven response in the taxa. This is intuitively satisfying, as one would expect an important ecologic difference between communities experiencing a substantial and continuous flux of organic matter and communities receiving that flux as a large pulse of limited duration, with low food supply in intervening months. For Discriminant Function 2, the seasonality axis, most of the discrimination is based on *E. exigua, C. hooperi,* and *C. laevigata* which are more abundant at higher seasonality. and on the hispid *Uvigerina* and *B. alazanensis* which are more abundant at low seasonality. Additionally, comparing mean assemblages shows that *M. barleeanus, A. weddellensis, C. wuellerstorfi,*
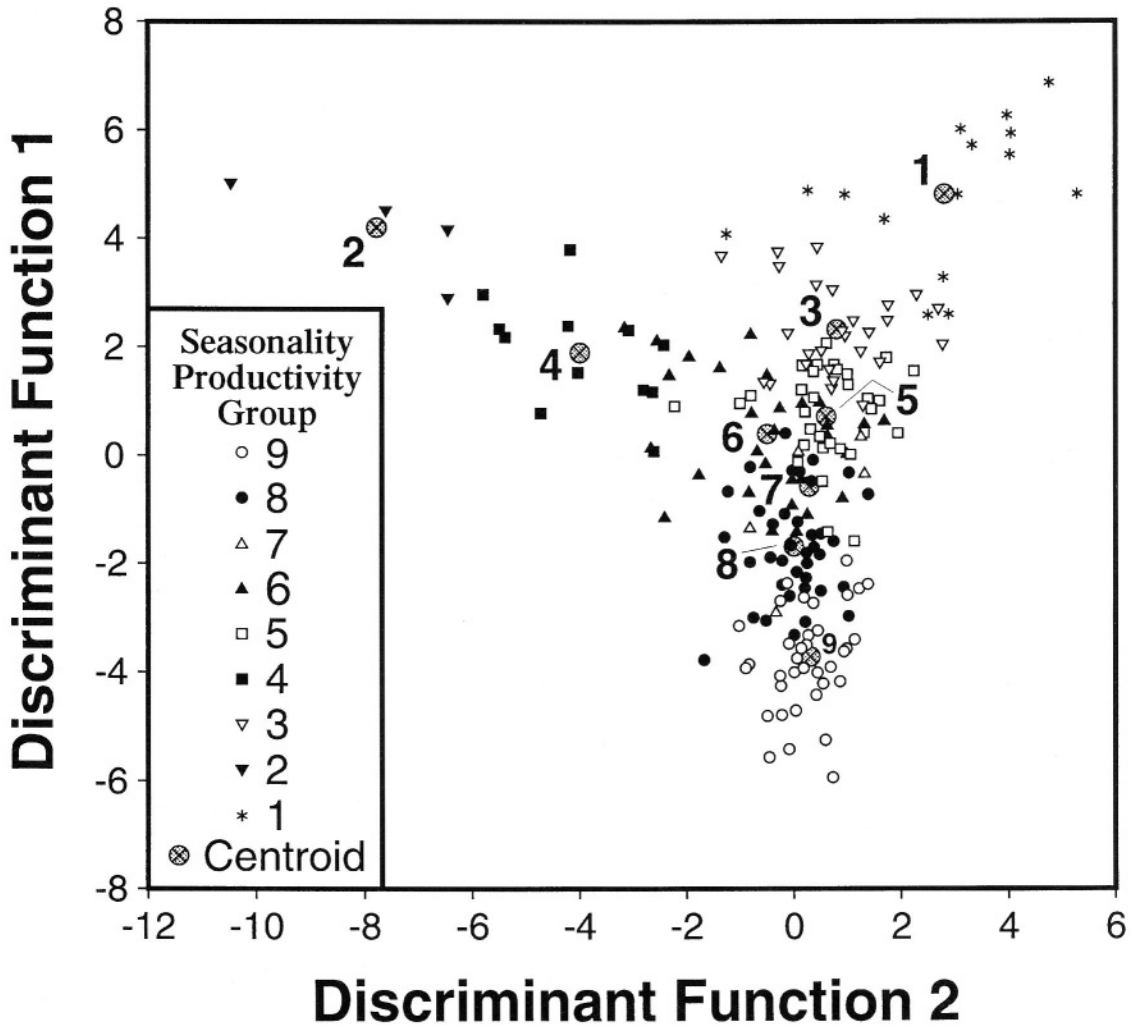
Figure 11.6 Benthic foraminiferal assemblages from the 207 surface sediment samples used in Figures 11.3 and 11.4 plotted in Discriminant Function Axis 1 and 2 space using 9 sample groups based on both productivity and seasonality. Discriminant Function 1 spreads the samples on the basis of mean annual productivity and Discriminant Function 2 on the basis of seasonality. The Groups are (productivity in units of $gC/m^2/yr$): (1) >200, high seasonality, (2) >200, low seasonality, (3) 150–200, high seasonality, (4) 150–200, low seasonality, (5) 90–150, high seasonality, (6) 90–150, low seasonality, (7) 50–90, high seasonality, (8) 50–90, low seasonality, (9) <50, low seasonality. Group centroids are labeled by numbers 1 to 9.

and *M. pompilioides* are more abundant where seasonality is high, whereas *S. bulloides* and *B. mexicana* are more abundant under lower seasonality. Finally, Loubere and Fariduddin (1999) found that distinction could also be made between settings with a single annual pulse of surface-ocean productivity and those with several or intermittent pulses.

11.4 WHY BENTHIC FORAMINIFERA REFLECT FOOD SUPPLY

11.4.1

Any examination of benthic foraminiferal response to organic carbon flux should include a view of the response of benthic organisms as a whole. This is relevant to developing theories

concerning foraminiferal ecology and to formulating questions for further research (section 11.5). Our review of the benthos here will be limited to deeper-water environments where availability of food is most clearly a limiting factor.

A broad review of benthic community response to food supply is presented in Pearson and Rosenberg (1987). The environment being considered is muddy, and often seen as relatively unchanging. The dominant organisms are polychaetes, bivalves, peracarid crustaceans (especially tanaids), nematodes, and foraminifers (Pearson and Rosenberg, 1987; Jumars *et al.,* 1990) and the deposit feeders are the dominant feeding guild. An early observation concerning deep-sea organisms was their high diversity (e.g. Sanders, 1968) which seemingly conflicts with the homogeneity of their environment. This diversity is an important, but not yet completely understood, clue about deep-sea ecology.

The broad scale distribution of deep-sea organisms shows several global patterns. The density of deep-sea dwellers decreases with distance from the coastline (Thiel, 1983), with some variation on continental slopes where organic matter depocenters occur (Duineveld *et al.,* 1997; Lampitt *et al.,* 1986). A global map of benthic organism abundance (Belyayev *et al.,* 1973) shows clearly that numbers are highest along continental margins and beneath upwelling areas, and lowest beneath the subtropical gyres.

On a regional scale, a number of studies now show that the flux of organic matter to the seafloor influences the distribution and abundance of benthic organisms. A comprehensive example of this is provided on the continental slope off Cape Hatteras (Diaz *et al.,* 1994). A strong lateral gradient in sediment accumulation rates is accompanied by a large increase in organic carbon deposition in the Cape Hatteras area (DeMaster *et al.,* 1994). This gradient is accompanied by marked changes in benthic community composition and community structure (Hecker, 1994; Blake and Grassle, 1994, Hilbig, 1994). Additionally, the abundance of benthic organisms greatly increases in response to an increasing organic carbon flux (Blake and Hilbig, 1994). As the flux goes up, the communities show a decrease in diversity, increased abundance of normally scarce taxa, and the presence of taxa normally limited to shallow (continental shelf) water environments. Analogous variations in benthic abundance and community structure are observed off western Sweden (Rosenberg, 1995), and off Southwest Ireland (Duinveld *et al.,* 1997). In all these settings there are complex mixes of organic matter derived from the continent, which may be degraded, and pulses of labile material from the sea surface. Exactly how the taxa use these different sources of organic matter is unclear. Also important to these environments is benthic disturbance and the action of currents, which may transport considerable sediment and make suspension feeding a viable feeding strategy. Carney (1989) speculates that feeding strategies in the benthos may change depending on the flux of labile material to the seafloor. When rapidly sinking high nutrient pulses of organic matter arrive, detritus feeding metazoans may consume this material directly and rapidly. It is important here that in regions of high seasonality, a substantial portion of the phytoplankton bloom may reach the benthos (Pearson and Rosenberg, 1987; Lampitt, 1985). Between the pulses, bacterial biomass derived from more refractory detritus would be a more important part of the diet.

The average size of organisms diminishes with depth and distance from the continents. Most deep-sea animals are small. Intensive natural selection for particle selection ability is seen as one reason for this (Jumars *et al.,* 1990). Carney (1989) points out that in response to decreased carbon input with depth, we should expect to find in the fauna both a decreased overall abundance and species replacement determined by the efficiency of foraging. Carney also reviews data indicating that the nutritional value of organic matter decreases with depth, further intensifying the pressure on the benthos to search efficiently, hoard resources, and maximize external resources in the processing of food.

Duineveld *et al.* (1997) review organic carbon accumulation and quality on several continental margins and find in the northeastern Atlantic that much of the material on the slope is degraded and refractory. Wheatcroft and Jumars (1987) show that labile detritus will be rapidly consumed once in the sediments which are subject to selective mixing, so the labile material will not be distributed in the sediment mixed layer much beyond its point of entry (detritus settling on the seafloor) or generation (bacterially produced labile material).

In concert with these observations, it has been found that abundance and taxon composition in the larger benthos and the meiofauna change progressively down continental margins (Coull, 1972; Coull *et al.,* 1977; Haedrich *et al.,* 1975; Rowe and Menzies, 1969; Rowe *et al.,* 1974, 1982), and that the habitation zone within the sediments thins with distance from the shore line (Shirayama, 1984).

The food resources available to the benthos are subject to the dynamics of the bottom boundary layer (BBL) and the sediment mixed layer (SML), and it is the properties of these to which the benthic organisms will respond. It appears that benthic organisms may follow three feeding strategies (Carney, 1989; Jumars and Gallagher, 1982). They may be opportunistic and rapidly consume newly arrived labile material at the seafloor. They may collect and hoard material for use at their leisure. Collection may be accomplished by hydrodynamic trapping of less dense organic material in structures and pits, and by collection into burrows (Jumars *et al.,* 1990; Bett and Rice, 1993). Finally, benthos can also harvest the bacteria which use less desirable, or inaccessible, organic matter. Aller and Aller (1986) showed that burrows and benthic structures could serve as collection points of organic matter, and also as centers of bacterial activity on the deep-sea floor. Thus, structures would offer enhanced feeding opportunities to the benthos. The bacteria would provide not only organic carbon, but also serve to extract nitrogen from surrounding waters and provide it in a usable organic form to the other benthos (Jumars, 1993, p. 41).

Deep-sea diversity remains difficult to understand, but it may be partly explained by a combination of taxon feeding strategy and environmental heterogeneity. Although one might expect most deep-sea benthos to be opportunists feeding on whatever might be present, it appears, counterintuitively, that resource partitioning may be common in abyssal environments. Jumars *et al.* (1990) consider an optimal foraging theory and conclude that there are advantages in being selective. Evidence for selectivity can be found in holothuroids (Hammond, 1983) and worms (reviews in Fauchald and Jumars, 1979; Lopez and Levinton, 1987).

The idea of environmental heterogeneity also seems initially counterintuitive as the deep sea appears homogeneous on the larger scale. However, Grassle and Morse-Porteous (1987) and Tyler (1995) argue that heterogeneity exists on the deep-sea floor as a result of small scale physical processes, episodic larger events (one might consider benthic storms here, e.g. Hollister and McCave, 1984), and biogenic heterogeneity. Concepts here are reviewed in Smith (1994). Heterogeneity would lead to a succession process with a mosaic of stages developed over the ocean floor. Jumars and Gallagher (1982) suggest a theory for this, using Markovian succession models. Different taxa would flourish in sequence after a disturbance (which might be a phytodetritus pulse) as their ecological specializations match the temporary conditions created by the succession process and the probabilities governing community membership. A key element in this idea would be that disturbances are rare enough to allow succession to develop often, but common enough to prevent climax and competitive exclusion. The influence of disturbance on benthic communities is examined in Thiery (1982), Probert (1984), and Thistle (1981). Thistle and Eckman (1990) present some evidence that benthic organisms associate preferentially with each other, indicating that heterogeneity, in response to biotic factors, does exist on the deep-sea floor.

To summarize, the response of the benthos to organic carbon flux will be mediated by a number of ecologic behaviors. These include:

particle size selection, efficiency in foraging, feeding strategies, flexibility in resource use, resource partitioning and community succession, benthic organism associations, and changing distribution within and upon the sediments.

11.4.2 Theoretical considerations

It is clear that patterns in benthic foraminiferal assemblages and abundances are related to the flux of organic carbon to the seafloor. So far, theoretical ideas about this have been mostly limited to considering adaptations to microenvironments in the sediments and, to a lesser degree, resource selection. The other factors listed in the previous section have not received much attention. Hence, a complete theoretical explanation of foraminiferal response to organic carbon flux has yet to be developed, although Sjoerdsma and van der Zwaan (1992) have presented a general empirical model. Corliss (1985) observed that deep-sea benthic Foraminifera could be classed into broad morphologic groups and that these groups could be associated with particular microenvironments within the sediments. Support for this is presented for material off the northeastern U.S.A. in Corliss and Emerson (1990). An examination of shifting morphotype abundances on the margins of Norway (Corliss and Chen, 1988) and the northern Gulf of Mexico (Corliss and Fois, 1990) show patterns that can be tied to flux of organic carbon to the seafloor, with epifaunal morphotypes becoming most abundant at greater depth where the flux is lowest. Loubere et al. (1993b) examined assemblage changes with water depth in the northern Gulf of Mexico in light of pore-water chemical measurements which could be used to constrain biogeochemical zonation in the surficial sediments (upper 15 cm) and the flux of organic matter to the seafloor. Ideas similar to those above are also presented in chapter 10 and Jorissen et al. (1995). The results of these various studies, when combined with observations on meiofaunal sediment concentration profiles, suggest that foraminiferal species are adapted to different microhabitats that are vertically stratified in the sediments.

This stratification increases and deepens in the sediment column as flux of organic carbon to the seabed increases. Thus, certain taxa are adapted to epifaunal or surface-sediment habitats, others inhabit suboxic settings, while still others exist near the pore-water anoxic boundary within the sediments. Demands of the microenvironment influence test architecture, and this produces the morphotype gradients observed above. Since the existence of the microenvironments is tied to flux of labile organic carbon to the seabed, we see changes in benthic assemblage composition as the importance of different morphotype groups changes with changing microhabitat development. Note, for example, that most of the high-productivity group taxa shown in Fig. 11.5 are 'infaunal' morphotypes by Corliss' classification, and would inhabit suboxic microhabitats. These ideas are developed in a quantitative framework in Loubere (1997). In this book, chapters 10 and 12 contain more information on microhabitats.

The review so far has emphasized a static, two-dimensional view of foraminiferal taxa that are vertically stratified in the sediments. However, areal and time dimensions must also be added to the picture. Linke and Lutze (1993) examined the concept of habitats in dynamic terms, suggesting that simple vertical stratification within the sediment column in response to general pore-water chemical gradients is an oversimplified view of benthic foraminiferal ecology. These authors find that taxa are distributed in a variety of microenvironments within and on the sediments, which can include such unusual settings as the appendages of benthic invertebrates. Staining and seasonal sampling by Gooday (1986, 1996) and Barmawidjaja et al. (1992) show that many benthic foraminiferal species do not have fixed vertical zonation within deep-sea sediments, and that such zonation as they have can change from month to month. In the subtidal environment, Hohenegger et al. (1993) and Thomsen and Altenbach (1993) observed patchy distributions of Foraminifera, and noted their association with the sediment structures of larger organisms. A number of taxa appeared to live in the oxic halo

of burrows. Similar observations for the deep sea (Gulf of Mexico) were made by Loubere *et al.* (1995), who noted that foraminiferal distributions were patchy and apparently concentrated near burrow structures.

In the context of foraminiferal response to productivity and organic carbon flux to the seabed, the critical factors controlling distribution should be the availability of labile organic matter in different microenvironments within the sediments, the distribution of those microenvironments in time and space, the availability of oxidants for respiration (oxygen being the most chemically efficient one), and competition from other organisms for the resources. Foraminiferal taxa will have adapted to these factors, and taxa present within the sediments will change as the factors change, in response to varying flux of organic matter to the seafloor.

Finally, moving away from the living population and considering assemblages preserved in the sediments, taphonomy (chemical and biotic processes that destroy foraminiferal tests during their incorporation into the sedimentary deposits) is also an important factor. This topic is examined in chapter 16. Also, Loubere *et al.* (1993b) and Loubere (1997) review taphonomic processes for the deep ocean as these relate to organic carbon flux. Taphonomy apparently enhances the organic carbon flux signal preserved in fossil assemblages.

11.5 CONCLUSIONS AND QUESTIONS

The mechanisms that control the benthic foraminiferal response to organic flux are not well understood, and the roles of the Foraminifera in the benthic community have not been clearly determined. While attention to a few large agglutinated foraminiferal taxa under special circumstances has shown their importance to the benthos (e.g. *Bathysiphon,* Gooday *et al.,* 1992b), little is known about the community position of the many small calcareous Foraminifera that make up the bulk of the geologic record of the benthos in deep-sea sediments. It has been claimed that benthic Foraminifera can be a dominant component of life on the seabed (Altenbach and Sarnthein, 1989; Gooday *et al.,* 1992a), but it remains unclear how they relate to the biological theories of community ecology developed for the metazoa.

Key issues from the biological perspective are those raised for other benthos: (a) how are populations maintained in the deep-sea settings where food supply is severely limited? and (b) how is diversity maintained in the deep-sea environment? For other organisms, as reviewed above, the answers to these questions rest with resource partitioning and environmental heterogeneity, most of which is seasonal (arrival and use of food falls), physical (benthic storms), or biologically generated (seabed environmental alteration by the activities of organisms, e.g. pits and burrows). For many deeper ocean settings, one can imagine each foraminiferal species as a bit player in a show that is running continuously but at ever changing locations, so the taxa do their brief routines at the appropriate time at each spot, flourish for a moment, and then vanish only to pop up at the next venue to repeat their act. A Markovian process was pictured by Jumars and Gallagher (1982) in which environmental change at the seabed is progressive in between disruptions (perhaps a pulse of phytodetritus from the euphotic zone), and taxa replace one another as their fitness allows them to exploit the conditions of the moment in their local setting. The authors imagined a stochastic succession (deterministic only if allowed to run to termination), perhaps with smaller organisms at the beginning and larger ones towards the end. We have some hint of this from Gooday's records of taxa which respond quickly to phytodetritus falls (early stage opportunists in the succession series), and in the evidence for a rapid physiological response of deep-sea Foraminifera to newly available organic matter (Linke *et al.,* 1995). Mostly, however, we have no idea what exactly the different benthic foraminiferal taxa do for a living on and in the seafloor. We do not know what microenvironments they most exploit, and we are ignorant of what stages they occupy in the succession series that develop within their deep-sea environments.

It is worth noting here that these series will no doubt vary, depending on both the average quantity and the variability (seasonality) of the flux of labile organic matter from the sea surface. Thus, environmental heterogeneity and disruption in the eastern equatorial Pacific, for instance, will be different from those observed in the highly seasonal northwestern Indian Ocean.

As for food acquisition, it is apparent that benthic metazoa are size selective in the material they ingest and that they have strategies for concentrating organic matter (density sorting). Additionally, they have search strategies to maximize their chances of finding new material. Finally, it also appears that larger benthic organisms can enhance local bacterial production for their own benefit. The resources the different foraminiferal taxa use, however, are presently unknown.

As noted by Carney (1989), there are fundamental ecologic differences among organisms that use freshly arrived detritus, those that feed on the bacteria and other small organisms that rapidly colonize the detritus, and those that feed on bacteria which slowly and steadily degrade the more refractory organic matter within the sediment-mixed zone. These organisms range from those that must use an often highly intermittent food supply as quickly as possible, to those that use a much less productive food source which is nevertheless fairly homogenous and continuously available. In between would be those taxa that take advantage of enhanced bacterial production, perhaps within a burrow structure or lining. The question is, what do the various taxa of the benthic Foraminifera do? There is evidence that living individuals of *Uvigerina peregrina* are unevenly distributed in the sediments and associated with the structures of other benthic organisms (Loubere *et al.,* 1995). For *Cibicides wuellerstorfi,* there is evidence for raised habitat selection (Lutze and Thiel, 1987) and attachment to larger metazoa (Linke and Lutze, 1993), which might be an adaptation for feeding strategy (suspension feeding) or for location in the environment created by the larger host. For most benthic foraminiferal taxa, however, we have no information about living distribution in relation to other benthos or food resources. These resources also include oxidizing agents (e.g. oxygen) in settings where the anoxic boundary occurs within the habitation zone of the sediments. For example, Corliss (1985) and Corliss and Emerson (1990) show that *Globobulimina affinis* lives along the anoxic boundary within the sediments, indicating survival in low oxygen conditions other taxa may not tolerate. However Loubere *et al. (*1995) present evidence that *U. peregrina,* while living within the sediments, may select burrows as a habitat, perhaps because these are better ventilated.

This review shows that a number of broad trends have been described, relating benthic Foraminifera to surface-ocean biological productivity and the flux of organic carbon to the seafloor. Taxon abundances within benthic foraminiferal assemblages change in predictable ways with shifting organic carbon flux. Benthic foraminiferal accumulation rates too may change predictably. Patterns of taxon abundance can also be associated with seasonality and variability in the organic carbon flux. The assemblage response to increasing surface-ocean biological productivity and organic carbon flux includes the appearance in the deep sea of taxa normally limited to middle and upper portions of the continental margin. The habitation zone of Foraminifera within the sediments thickens as organic carbon flux increases (within the limits normally observed in the deeper ocean). Some taxa have shown selection for depth related microhabitats under higher organic carbon flux conditions. Finally, some taxa appear to be rapid-response opportunists in colonizing newly arrived phytodetritus at the seafloor.

The conclusion of this review must therefore be that we have now reached a stage in our understanding in which we have identified patterns in benthic foraminiferal data that can be consistently linked with organic carbon flux to the seabed. The link has been quantified statistically so that reconstruction of past surface-ocean biological productivity using fossil ben-

thic foraminiferal data is possible. However, our ability to explain benthic foraminiferal taxon occurrence, production, or pattern needs improvement. Confident assessments of paleo-productivity will require a better understanding of which portion of the organic carbon signal different benthic foraminiferal taxa respond to.

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12

Foraminifera of oxygen-depleted environments

Joan M. Bernhard and Barun K. Sen Gupta

12.1 INTRODUCTION

The study of foraminiferal tests from oxygen-depleted environments is of interest in a variety of disciplines, most notably economic geology, environmental geology, ecology, and cell biology. Fossilized Foraminifera from ancient oxygen-poor environments may help identify petroleum source rocks. From an ecological and environmental-impact perspective, foraminiferal tests can be used to deduce historical, baseline conditions prior to environmental changes, including eutrophication connected to anthropogenic activities. Lastly, the physiology of Foraminifera capable of surviving anoxia is of interest to cell biologists because these protists are traditionally considered to be obligate aerobes.

Before discussing aspects of foraminiferal distribution and adaptation in oxygen-depleted environments, it is necessary to define the various terms used to describe oxygen depletion (Table 12.1). The majority of these terms originated from the seemingly disparate disciplines of geology and physiology. In general, the adjectives 'anoxic' and 'anaerobic' both indicate an absence of oxygen. Whereas either term can be used to

Table 12.1. Oxygen range limits for some environmental terms used in this chapter.

Term	O_2 range limits (ml/l)	Comments
oxic	> 1.0	
dysoxic	0.1–1.0	
microxic	present to 0.1	with or without reducing conditions
anoxic	0	with or without reducing conditions
postoxic	0	subclass of anoxic, without reducing conditions

describe an environment, an organism, or a chemical reaction, 'anoxic' is typically used for environmental descriptions while 'anaerobic' is generally used as a biological descriptor. In some instances, the use of either term is somewhat problematic because analytical detection limits prohibit confident measurement of trace concentrations of oxygen. Some authors have used the term 'anoxic' to refer to conditions where $O_2 = 0$–0.1 ml/l, but associating a term that means 'no oxygen' with values above zero, however small, is confusing. Thus, we use 'microxic' for environments in which oxygen is measurable but less than 0.1 ml O_2/l,

and restrict 'anoxic' to environments without detectable O_2. The term is a variant of 'microoxic,' coined by Jørgensen and Revsbech (1983), for 'environments of very low oxygen concentrations.' We employ 'postoxic' (Berner, 1981) as a subclass of 'anoxic' for situations where there is a lack of both oxygen and reducing conditions ('suboxic' of Fenchel and Finlay, 1995, but not of Tyson and Pearson, 1991). For environments with 0.1–1.0 ml O_2/l (~ 5–$45\,\mu M$), we employ 'dysoxic,' which is equivalent to the 'dysaerobic' regime of Rhoads and Morse (1971). This definition of dysoxic (Fenchel and Finlay, 1995; Bernhard, 1996) does not agree with that of Tyson and Pearson (1991), who use the 0.2–2.0 ml O_2/l range. Environments with more than 1 ml O_2/l are placed under the single term 'oxic.' Generally, 'hypoxic' is used as a physiological term that refers to any depletion in oxygen that inhibits the normal respiration rate of a particular organism. The term 'microaerophile' is used for an aerobe that requires very little oxygen, but is adversely affected by higher oxygen concentration ($[O_2]$).

Oxygen-depleted environments are extensive in the marine realm. Over 1 % of the water samples from the world ocean recorded in the U.S. National Oceanographic Data Center database (for the 1905 1982 period) were severely dysoxic or microxic (i.e. <0.2 ml/l; Fig. 12.1; see also Kamykowski and Zentara, 1990). Because oxygen concentrations in sediments are generally lower than $[O_2]$ of the overlying seawater, we expect oxygen depletion in most of the benthic environments corresponding to the shaded regions of Fig. 12.1.

The most widespread dysoxic and microxic marine environment is the subsurface sediment. Since most aerobic, benthic organisms live near the sediment-water interface, oxygen consumption is high in this habitat. At a particular sedimentary depth, depending primarily on respiration rates and abundances of organisms, oxygen demand will exceed supply and sediments will become anoxic. The top of the anoxic zone is typically within the top few decimeters of sediment, even where overlying waters are well-aerated.

The second most laterally extensive oxygen-depleted marine environment is termed the Oxygen Minimum Zone (OMZ). The formation
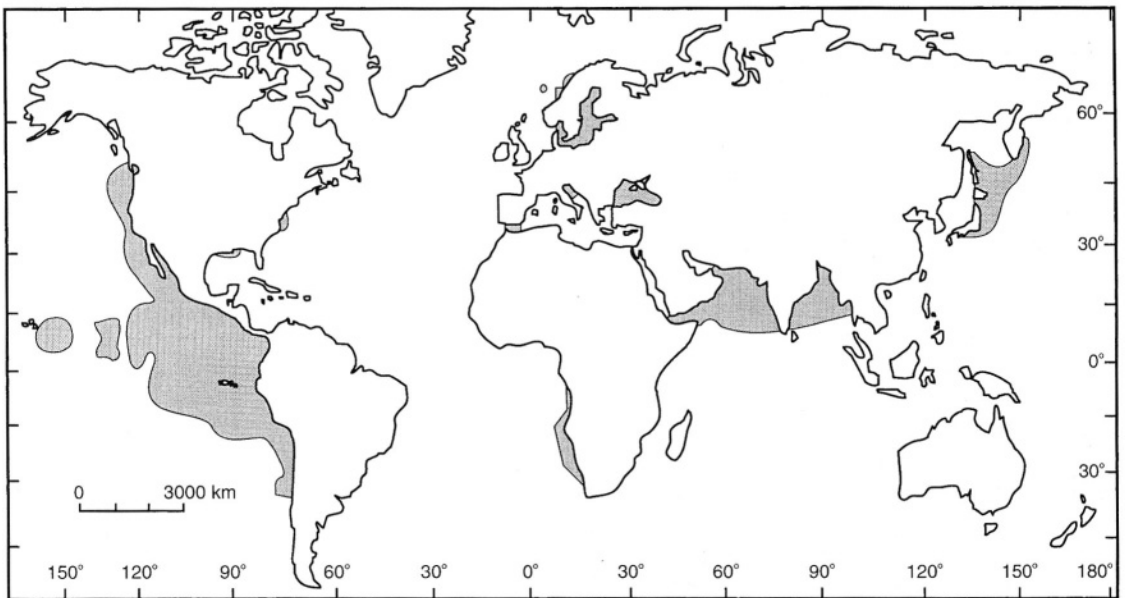
Figure 12.1 Global map (excluding high latitudes) showing areas of water with <0.2 ml O_2/l (redrawn from Kamykowski and Zentara, 1990); data from U.S. National Oceanographic Data Center.
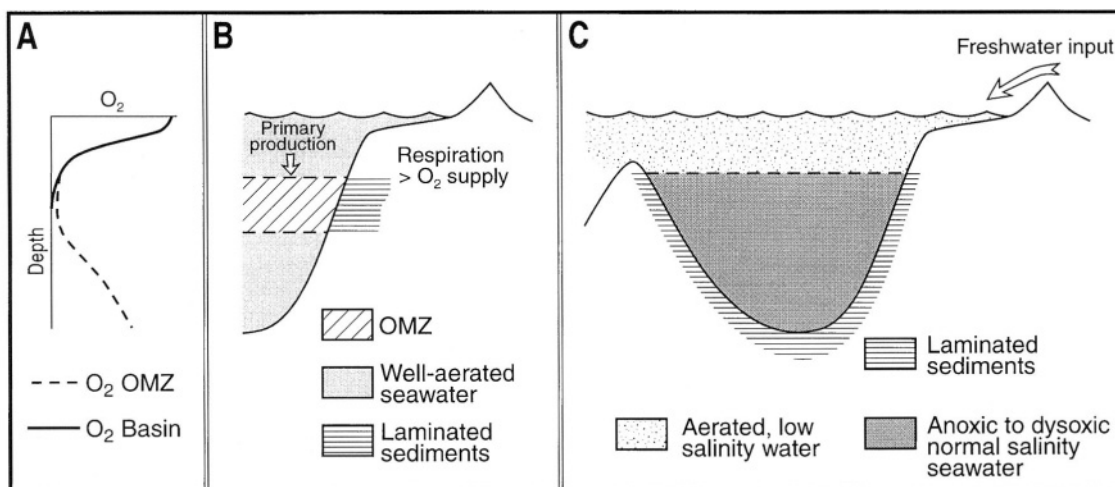
Figure 12.2 Schematic profile of dissolved oxygen (A) in two types of oxygen-depleted water column: Oxygen Minimum Zone (B) and silled basin or fjord (C). See text for explanations (see also Demaison and Moore, 1980, for more detailed descriptions).

of an OMZ depends mainly upon large-scale oceanic circulation, geography, and primary productivity (Figs. 12.2A, B). The intermediate-depth water masses of eastern oceanic margins typically consist of 'aged' water that has not been recently aerated at the sea surface. Thus, the $[O_2]$ in these water masses is depressed compared to surface concentrations. The inter-mediate-water $[O_2]$ will become even more depleted if the water is situated under a region of high primary productivity, due to the oxida-tion of the large amounts of organic debris settling through the water column. Because the water column of an OMZ is depleted in oxygen, the $[O_2]$ in surface sediments where the OMZ impinges upon the seafloor will also be depau-perate in oxygen.

Some silled basins and fjords also constitute laterally extensive, dysoxic marine environments that may have anoxic surface sediments. In these types of basins, stagnation leading to oxygen depletion can be caused via two major path-ways: (1) from the presence of a sill that inhibits recharge of aerated waters, and (2) from fresh-water input that will produce a strong halocline, inhibit mixing, and lead to stratification in the bottom waters (Figs. 12.2A, C). If enough carbon loading occurs in either of these situa-

tions, bottom waters will become dysoxic, microxic, or anoxic.

Spatially restricted oxygen-depleted environ-ments occur at marine hydrocarbon seeps. Such seeps have fluxes of H_2S emanating from the sediments and commonly support populations of *Beggiatoa,* a large, motile, filamentous, chemolithotrophic, sulfide-oxidizing bacterium. Growth of *Beggiatoa* requires the presence of O_2 in the overlying water and H_2S in the under-lying sediment (Jørgensen, 1977; Spies and Davis, 1979; Larkin and Strohl, 1983; but see also Fossing *et al.,* 1995; McHatton *et al.,* 1996). Thus, an oxic-anoxic interface exists within these mats, even if they are very thin (Fig. 12.3). The longevity of *Beggiatoa* mats at hydrocarbon seeps is unknown, but they are necessarily ephemeral, 'being controlled by the shifting point sources of sea-floor hydrocarbon emission' (Sen Gupta *et al.,* 1997). *Beggiatoa* mats are also known from many environments other than hydrocarbon seeps (e.g. silled basins, sewage outfalls).

Another example of spatially and temporally restricted marine dysoxic environments is an area of large food falls. Such areas are organi-cally enriched due to settling of dead organisms such as whales or other vertebrates. The lateral
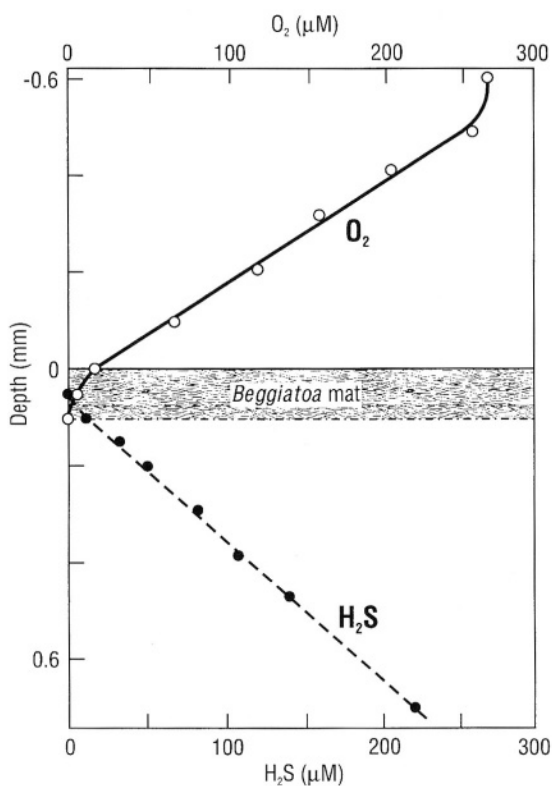
Figure 12.3 Schematic cross section through a *Beggiatoa* mat, showing oxygen (O_2) and hydrogen sulfide (H_2S) profiles which were measured with microelectrodes. Modified from Jørgensen (1982).

extent of these enriched environments obviously depends on the original size of the carcass. The temporal persistence of such patches is on the order of years to decades (Smith and Baco, 1997; Deming *et al.,* 1997).

Seasonal or periodic anoxia, microxia, or dysoxia is also known from coastal areas, including open continental shelves. This is related to eutrophication and oxygen consumption linked with natural environmental factors (e.g. freshwater input, seasonal stratification) or to anthropogenic effects (e.g. nutrient input through fertilizers, sewage outfalls). New York Bight, Chesapeake Bay, Gulf of Mexico, Adriatic Sea, and Orinoco-Paria Shelf are examples of such areas (Boesch and Rabalais, 1991; Malone, 1991; van der Zwaan and Jorissen, 1991). Regarding the effects of anthropogenic activities,

Diaz and Rosenberg (1995) note that 'there is no other environmental variable of such ecological importance to coastal marine ecosystems that has changed so drastically in such a short period as dissolved oxygen.' Aquaculture facilities have also produced localized anoxic areas occurring under fish cages (Schafer *et al.,* 1995). Other areas that were previously only moderately depleted in O_2 have become severely dysoxic or anoxic (e.g. sediments in Norwegian fjords adjacent to paper mills; Nagy and Alve, 1987; Alve, 1991b).

The following narrative is based mainly on published studies regarding Foraminifera from these diverse types of dysoxic to anoxic environments.

12.2   DISTRIBUTIONAL OBSERVATIONS

In a number of studies, benthic Foraminifera recovered from oxygen-depleted sediments were treated with the 'non-vital stain' Rose Bengal (Table 12.2). The interpretations of these data varied. Reliance on the concept that Foraminifera could not be anaerobes led to the conclusion that the occurrence of stained tests in material processed from anoxic deposits simply reflected transport from a favorable into an unfavorable environment (e.g. Douglas, 1981). A contrary interpretation was that the Foraminifera found in these sediments actually inhabited such oxygen-depleted environments. However, given that Rose Bengal is known to stain dead foraminiferal cytoplasm for weeks to months (Bernhard 1988; Hannah and Rogerson, 1997) and, theoretically, for years (Corliss and Emerson, 1990), it was possible that the Rose Bengal stained Foraminifera recovered from oxygen-depleted sediments were dead specimens whose cytoplasm had not yet degraded. Therefore, in order to determine if Foraminifera actually inhabited dysoxic, microxic, and anoxic environments, a more reliable method to distinguish live from dead specimens was required in conjunction with a precise method to determine pore-water oxygen concentrations. The biochemical assay to determine the nucleotide

Table 12.2. Examples of foraminiferal species reported from severely oxygen-depleted samples, and recognized as living by Rose Bengal stain. The species listed were found to be relatively common in their communities. The generic designations of some species are different from those in the cited publications. Oxygen levels: A = anoxic (no detectable O_2); PA = putatively anoxic (from sedimentary or geochemical evidence, O_2 not measured); M = microxic (<0.1 ml/l O_2); D = dysoxic (0.1–1.0 ml/l O_2).

Area (and reference)	Environment	Water depth (m)	O_2 index	Dominant or characteristic species
California borderland, outer basins (Santa Cruz, Santa Catalina, San Nicolas, and Tanner Basins; Douglas and Heitman, 1979)	OMZ, basin floor	1200–1900	D	*Fursenkoina apertura, F. cornuta, Loxostomum pseudobeyrichi, Buliminella tenuata, Chilostomella ovoidea, Bolivina pacifica*
California borderland, inner basins (San Diego Trough, San Pedro and Santa Monica Basins; Douglas and Heitman, 1979)	OMZ, lower slope	400–550	D	*Bolivina argentea, B. spissa, Loxostomum pseudobeyrichi, Epistominella smithi, Uvigerina curticosta*
	OMZ, basin floor	550–950	M/D	*Fursenkoina apertura, F. bramlettei, F. seminuda, F. cornuta, Spiroplectammina earlandi, Buliminella tenuata*
Santa Monica Basin, California (Mackensen and Douglas, 1989)	OMZ, basin floor	529	D	*Cancris inaequalis, Globobulimina pacifica, Rosalina columbiensis, Planulina ariminensis, Trochammina globigeriniformis, T. pacifica*
Santa Catalina Basin, California (Mackensen and Douglas, 1989)	OMZ, basin	893–897	D	*Bolivina spissa, Globobulimina pacifica*
Santa Catalina Basin, California (Kaminski *et al.*, 1995)	OMZ, basin floor	1202, 1309	D	*Saccorhiza sp., Verneuilinulla sp., Reophax dentaliniformis, R. excentricus, Rhizammina irregularis, Bathysiphon filiformis*
San Pedro Basin, California (Kaminski *et al.*, 1995)	OMZ, basin floor	672–874	D	*Textularia sp., Rhizammina irregularis, Trochammina sp., Cribrostomoides wiesneri, Reophax bilocularis*
Santa Barbara Basin, California (Phleger and Soutar, 1973)	OMZ	575–590	D	*Globobulimina hoeglundi, Suggrunda eckisi, Bolivina seminuda, Nonionella stella*
Santa Barbara Basin, California (Bernhard *et al.*, 1997)	OMZ, lower slope	339, 431	D	*Suggrunda eckisi, Uvigerina juncea, Bolivina argentea, B. seminuda* (Each $>10\%$ of assemblage)
	OMZ, basin floor	522–591	M/PA	*Nonionella stella* ($>30\%$), *Bolivina seminuda, Chilostomella ovoidea, Buliminella tenuata, Spiroplectammina earlandi* (Last 4 species, each 5–10% of assemblage)
Gulf of California (Streeter, 1972; Phleger, 1964b)	OMZ	440–980	D	*Bolivina subadvena, B.* spp.
Baja California (Phleger and Soutar, 1973)	Upwelling	75–100	D	*Bolivina* spp., *Uvigerina* spp., *Bulimina* spp.
Baja California (Phleger and Soutar, 1973)	OMZ	530	D	*Bolivina seminuda, Reophax gracilis*

Table 12.2. (Continued.)

Area (and reference)	Environment	Water depth (m)	O$_2$ index	Dominant or characteristic species
El Salvador (Smith, 1964)	OMZ	435–900	D	*Reophax dentaliniformis, Saccammina* sp. cf. *S. comprima, Globobulimina pacifica, Uvigerina peregrina, Buliminella tenuata*
Peru-Chile Trench (Ingle *et al.*, 1980)	OMZ	135	D	*Bolivina rankini, B. interjuncta, Bulimina elongata, Epistominella exigua*
Sagami Bay, Japan (Ohga and Kitazato, 1997)	OMZ	1450	D	*Textularia kattegatensis, Bolivina pacifica, B. spissa, Bulimina aculeata, Fursenkoina* sp., *Chilostomella ovoidea, Globobulimina* spp., *Uvigerina peregrina, Uvigerina akitaensis*
Northern Arabian Sea (Jannink *et al.*, 1998)	OMZ	495–1000	D	*Bolivina dilatata, B. seminuda, Bulimina excilis, Cassidulina laevigata, Ammodiscus* sp., *Globobulimina affinis, Osangularia culter, Uvigerina peregrina, Recurvoides* sp., *Eggerella* sp.
Green Canyon, Gulf of Mexico (Sen Gupta *et al.*, 1997)	Hydrocarbon seeps, under bacterial mats	543–583	PA	*Bolivina albatrossi, B. ordinaria, Cassidulina neocarinata, Osangularia rugosa, Trifarina bradyi, Gavelinopsis translucens*
Green Canyon, Gulf of Mexico (Sen Gupta and Aharon, 1994)	Hydrocarbon seep bacterial mats	216	M/D	*Bolivina subaenariensis, B. ordinaria, Cassidulina neocarinata, Uvigerina laevis*
Drammensfjord, Norway (Alve, 1990, 1995b)	Silled basin with high anthropogenic organic load	40–60	PA/D	*Stainforthia fusiformis, Bulimina marginata, Spiroplectammina biformis, Ammodiscus? gullmarensis*
Drammensfjord, Norway (Bernhard and Alve, 1996)	Silled basin with high anthropogenic organic load	45	D	*Stainforthia fusiformis, Bulimina marginata, Adercotryma glomerata, Psammosphaera bowmanni*
Northern Adriatic Sea continental shelf (Jorissen *et al.*, 1992)	Seasonal eutrophication and stratification	36	D	*Hopkinsina pacifica, Nonionella turgida, Epistominella vitrea, Stainforthia fusiformis, Bolivina spathulata, B. dilatata*
Louisiana continental shelf (Sen Gupta *et al.*, 1996)	Seasonal dysoxia	9–21	M	*Buliminella morgani, Ammonia parkinsoniana*
Explorers Cove, McMurdo Sound, Antarctica (Bernhard, 1987)	Seasonal dysoxia in small basins	18	PA	*Tolypammina vagans, Polymorphina* sp.
Winter Quarter's Bay, McMurdo Sound, Antarctica (Bernhard, 1989)	Subsurface pore water (1–2 cm below surface)	12	A	*Cassidulinoides porrectus, Globocassidulina* sp. cf. *G. biora, Cribrostomoides jeffreysii, Paratrochammina antarctica, Psammosphaera parva*
Frierfjord, Norway (Alve, 1994)	Subsurface pore water (1–5 cm below surface)	90	PA	*Stainforthia fusiformis*
	OMZ, sediment surface	786, 998	D	*Eggerella* cf. *E. scabra, Brizalina* sp., *Technitella* sp.
California continental slope (Bernhard, 1992)	Subsurface (2–4 cm below dysoxic surface)	786, 998	A	*Globobulimina pacifica, Chilostomella oolina, Uvigerina peregrina, Bolivina* sp.

Table 12.2. (Continued.)

Area (and reference)	Environment	Water depth (m)	O$_2$ index	Dominant or characteristic species
South China Sea (Rathburn et al., 1996)	Subsurface (below detected anoxic/oxic interface)	1095, 2150	A	Astrononion sp., Chilostomella oolina, Bolivinopsis cubensis
Sulu Sea (Rathburn et al., 1996)	Subsurface (below detected anoxic/oxic interface)	4515	A	Valvulineria mexicana, Globobulimina sp.
Nova Scotia continental margin (Corliss and Emerson, 1990)	Subsurface pore water (7 cm below surface)	1575	PA	Globobulimina affinis, Nonion grateloupi, Elphidium excavatum

adenosine triphosphate (ATP) concentration developed by DeLaca (1986b) was judged as one such method (Bernhard, 1989, 1992). In these studies, polarographic microelectrodes originally developed by Revsbech et al. (1980) were employed to determine dissolved-oxygen profiles in sediment pore waters from which the Foraminifera were recovered. The caveat in these studies was that the live Foraminifera could have been inhabiting oxygenated microhabitats around such biogenic structures as macrofaunal burrows and tubes, as suggested by Langer et al. (1989) for infaunal tide-flat foraminiferal assemblages and by Moodley (1990) for deep-infaunal Foraminifera from the North Sea.

The core-embedding method of Frankel (1970) and Watling (1988; see also Grimm, 1992; Pike and Kemp, 1996) was recently refined to preserve Foraminifera in their life position within sediments (Bernhard and Bowser, 1996). This technique approaches the issue of foraminiferal associations with aerated microhabitats by preserving foraminiferal life position in sediments where burrowing and tubicolous fauna are absent. The method combines epifluorescence microscopy and enzymatic activity to distinguish hydrolytically active (i.e. live) Foraminifera with epoxy-resin embedded coring to preserve sedimentary and organism *in situ* positions. The use of this technique shows that Foraminifera inhabit the microxic and anoxic sediments of the silled Santa Barbara Basin

(Fig. 12.4; Bernhard, 1996; Bernhard et al., 1997). These sediments are sulfidic, as evidenced by abundant sulfide-oxidizing bacteria *Beggiatoa*. However, even though such distributional data strongly suggest that Foraminifera can inhabit anoxic environments, only experimental data can provide compelling evidence for this conclusion.

12.3   EXPERIMENTAL OBSERVATIONS

12.3.1   Foraminiferal responses to oxygen depletion

Some experimental studies have been conducted to assess the response of Foraminifera to anoxia. It is important to reiterate here that when working with such low $[O_2]$, it is difficult to ascertain if a supposedly anoxic system is devoid of even trace amounts of oxygen. Furthermore, it is also important to remember that all species of Foraminifera cannot be expected to respond similarly to oxygen depletion; some species may have different physiological abilities than others.

In a behavioral response experiment, infaunal Foraminifera from a periodically dysoxic fjord started migrating upward in the sediment when oxygen in bottom waters decreased below 2 ml O$_2$/l (Alve and Bernhard, 1995); however, the timing of species responses varied. For example, *Bulimina marginata* migrated toward aerated habitats more quickly than *Stainforthia fusi-*
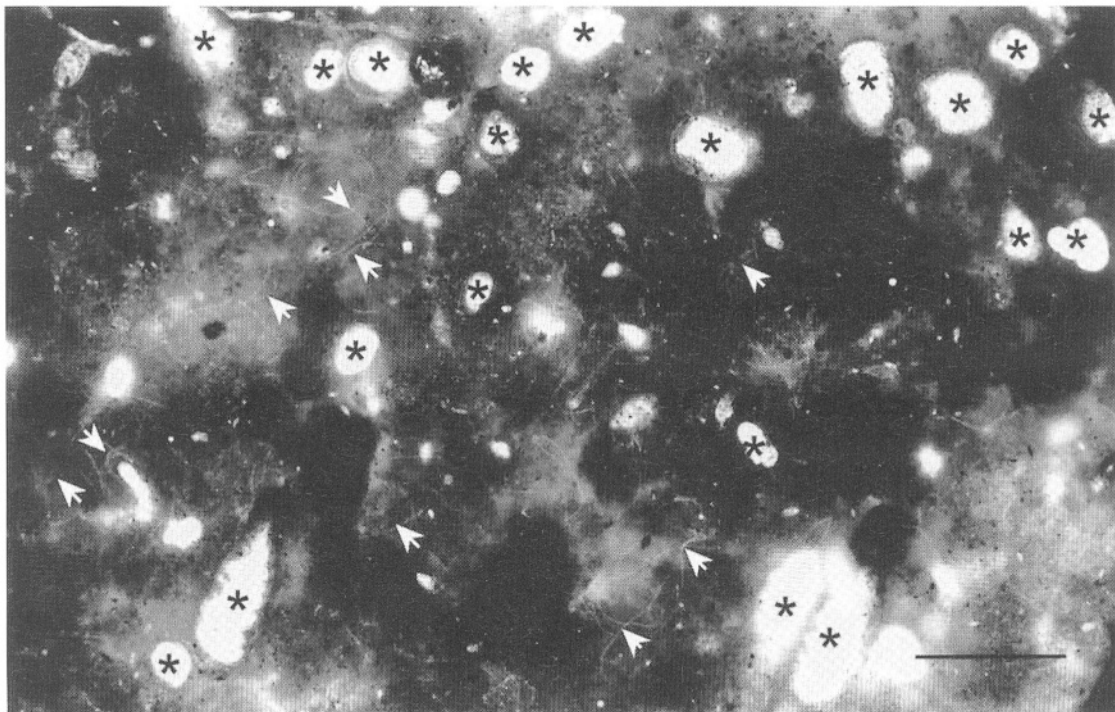
Figure 12.4 Photomicrograph of section through a fluorescently-labeled, embedded core. The light-colored objects are Foraminifera (*) and *Beggiatoa* filaments (white arrows) in their life positions. Light-colored objects without designation are indeterminate organisms such as ciliates, flagellates, or juvenile Foraminifera. Dark objects are sediments (e.g. fecal pellets, clastics). The sample was prepared using the technique of Bernhard and Bowser (1996). Scale bar = 0.5 mm.

formis. Also, *B. marginata* reproduced during the most oxygen-depleted conditions. When bottom waters were re-aerated, some species (e.g. *S. fusiformis*) migrated back into the sediments, presumably tracking a particular geochemical horizon.

Responses of some other species to oxygen depletion have been studied on shorter time scales. In a 7-day experiment, Moodley *et al.* (1998b) observed that while some buried individuals of *Quinqueloculina seminulum* migrated toward aerated sediments, 40–50% remained in presumably anoxic sediments. In the same study, but after a 56-day experiment, the majority (57%) of *Nonionella turgida* remained in sediments that had undetectable O_2, yet the majority of 'soft-shelled' Foraminifera (i.e. allogromiids and saccamminids) migrated into aerated sediments. Considerable numbers (17%) of the soft-shelled Foraminifera,

however, remained in sediments that had undetectable O_2

12.3.2 Survival of Foraminifera exposed to oxygen depletion

The survival of Foraminifera exposed to anoxia has also been studied. Using the concentration of sedimentary particles (food source) around the apertural region as indication of activity, Moodley and Hess (1992) determined that individuals of three infaunal species (*Ammonia beccarii, Elphidium excavatum, Quinqueloculina seminulum*) survived anoxic incubation for at least one day. In the same study, *E. excavatum, Eggerella scabra,* and *Q. seminulum* survived as well as secreted test chambers during a six-day incubation in dysoxic or microxic seawater (i.e. $< 12.5 \, \mu M \, O_2$). Two larger agglutinated Foraminifera, *Pelosina arborescens* and *Astrorhiza limicola,* are known to sur-

vive putative anoxia for ten days (Cedhagen, 1993). The survival period of *Ammonia beccarii* in such an environment may be as long as 1–2 months (Koshio, 1992, in Kitazato, 1994). Incubations in nitrogen-purged seawater for 30 days showed that some Antarctic Foraminifera (e.g. *Cassidulinoides porrectus, Globocassidulina* sp. cf. *G. biora, Reophax subdentaliniformis, Uvigerina bassensis*) are able to survive microxia and possibly anoxia for considerable periods of time (Bernhard, 1993). The results of that study include the observation that ATP concentrations in specimens recovered after an extended exposure to dysoxia were statistically indistinguishable from those of control specimens incubated in aerated seawater.

Since it is possible that Foraminifera become dormant during exposure to adverse conditions such as oxygen depletion, it is of interest to determine ATP concentration ([ATP]) in specimens during their exposure to microxia or anoxia. Bernhard and Alve (1996) incubated Foraminifera for 24 days in a nitrogen-flushed experimental chamber and then extracted their ATP without aeration. Results showed that the [ATP] for specimens of *Psammosphaera bowmanni* were statistically similar between controls (i.e. aeration) and treatments (i.e. microxia). However, the [ATP] of nitrogen-flushed specimens of other species (*i.e., Bulimina marginata, Stainforthia fusiformis, Adercotryma glomerata*) were significantly lower than those of specimens extracted under aerated conditions. Considering all available data from this experiment (i.e. survival rates, [ATP] and ultrastructural observations), Bernhard and Alve (1996) concluded that foraminiferal species respond differently to oxygen depletion. Some species are apparently unaffected, while others may become dormant. If encystment is considered to be a type of dormancy, then independent evidence for such dormancy has been provided by Linke and Lutze (1993), who reported cysts of *Elphidium incertum* from an environment of putative anoxia. Also, Hannah and Rogerson (1997) concluded that Foraminifera buried in an anoxic layer become dormant and would require transport via bioturbation for their return to aerated conditions. In yet another long-term anoxic-incubation experiment, certain foraminiferal species survived putative anoxia for 78 days (Moodley *et al.,* 1997). It should be noted that at some time between 33 and 53 days, the experimental incubations became sulfidic. Thus, the observations concerning survival response to anoxia are somewhat compounded by this change in redox chemistry for approximately the last half to two-thirds of the experiment.

Sulfidic conditions commonly co-occur with anoxia. As noted in the introduction, the term 'postoxic' in this chapter implies anoxia without reducing conditions. The experiments described above addressed postoxic conditions. The few experiments that have been conducted to assess the survival of Foraminifera in anoxic, sulfidic conditions (Bernhard, 1993; Moodley *et al.,* 1998a) show that some Foraminifera tolerate such environments. After 30 days, ATP concentrations in specimens from $500\,nM\,H_2S$/anoxic treatments did not differ significantly from those of aerated controls (Bernhard, 1993). Under higher concentrations ($5\,\mu M\,H_2S$), cytoplasmic movement was observed in Foraminifera after an incubation period of 21 days, but all specimens were dead by the next time point (42 days; Moodley *et al.,* 1998a).

Although experimental results indicate that Foraminifera survive anoxia with or without sulfidic conditions for considerable periods of time, no physiological mechanism responsible for such survival is presently known. It is established, however, that two allogromiid species have an alternative oxidative pathway that may be responsible for their survival in anoxia. Travis and Bowser (1986b) found that the electron-transport inhibitor cyanide did not halt intracellular motility, suggesting that at least some Foraminifera can survive without oxidative phosphorylation. Ultrastructural studies suggest additional possible adaptations and mechanisms to allow foraminiferal survival of anoxia.

12.4 ULTRASTRUCTURAL OBSERVATIONS

A variety of unusual ultrastructural characteristics has been observed in foraminiferal species

that are dominant in oxygen-depleted environments. It is possible that these characteristics reflect adaptations to extreme oxygen depletion, and possibly to sulfidic habitats, but no consistent ultrastructural modification has been observed in species from such environments. Furthermore, the published literature does not include quantitative, comparative studies on the ultrastructure of individuals from anoxic sediments and conspecific individuals from aerated sediments. Such comparisons in the future may elucidate the importance of the various ultrastructural modifications.

Three cases of possible bacterial symbioses have been observed in Foraminifera from oxygen-depleted sediments. Two species from the Santa Barbara Basin have putative endosymbionts. *Buliminella tenuata* has numerous rod-shaped bacteria within its cytoplasm (Fig. 12.5A; Bernhard, 1996). These bacteria do not appear to be a food source, since they are intact in all chambers of this multilocular foraminifer. *Nonionella stella* has bacteria within its test, but these prokaryotes are not intracellular (Bernhard and Reimers, 1991). Lastly, infaunal *Globocassidulina* cf. *G. biora* from shallow Antarctic waters is known to have intracellular rod-shaped bacteria that appear to be associated with pore plugs (Bernhard, 1993). One possible role of these putative symbionts is to oxidize H_2S, thereby detoxifying this pore-water constituent. Given the variance in the morphologic attributes of these three types of bacteria, however, it is likely that they have different metabolic capabilities.

Another ultrastructural feature of some Foraminifera from oxygen-depleted environments (*Stainforthia fusiformis*, *Nonionella stella*, *Nonionellina labradorica*) is that they sequester chloro-
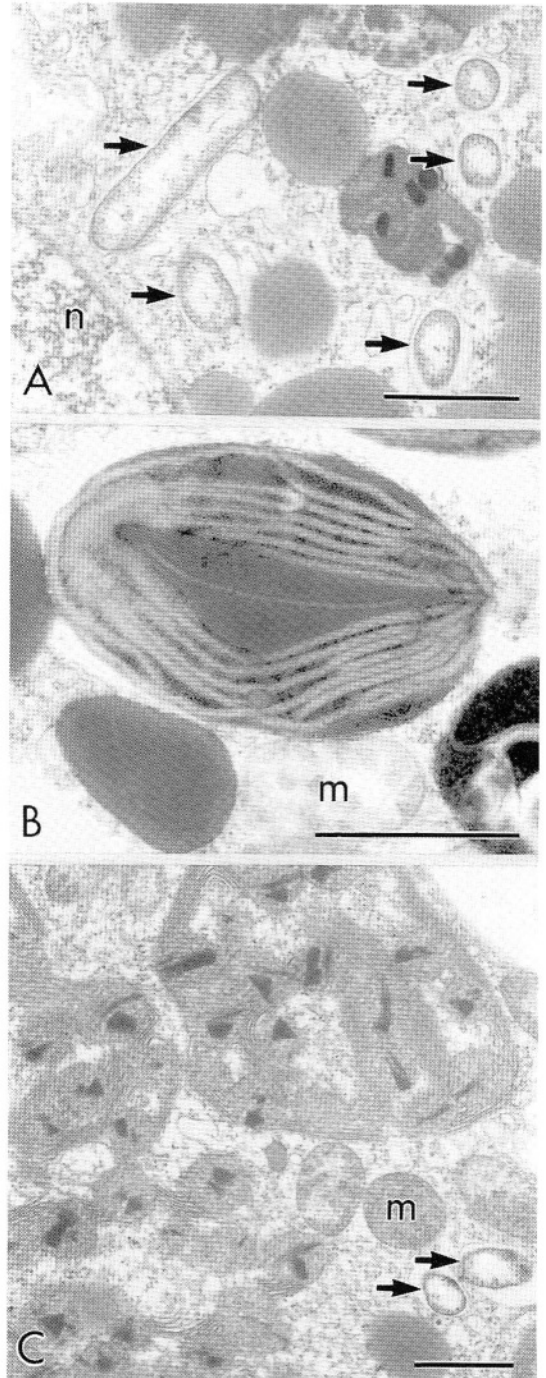
Figure 12.5 Transmission electron micrographs. A. Putative endosymbiotic, rod-shaped bacteria (arrows) in cytoplasm of *Buliminella tenuata*; n = nucleus. B. Sequestered chloroplast in cytoplasm of *Nonionella stella*; m = mitochondria. C. Complex of peroxisome-endoplasmic reticulum in *B. tenuata*; dark polygonal structures are catalase crystals in the core of the membrane bound peroxisomes; stacked membranes linking peroxisomes are the endoplasmic reticulum; m = mitochondria, arrows = putative bacterial symbionts. Scale bars = 1 μm.

plasts (Fig. 12.5B; Leutenegger, 1984; Cedhagen, 1991; Bernhard and Alve, 1996). Such chloroplast husbandry is thought to benefit other protists inhabiting anoxic environments, possibly by providing oxygen to the host (Johnson *et al.,* 1995). A particular complication in interpreting the role of chloroplasts in the cases listed above is that the oxygen-depleted habitats are not in the euphotic zone.

A third ultrastructural feature common to many species from oxygen-depleted environments involves proliferation and aggregation of two typical cellular organelles: endoplasmic reticulum and peroxisomes (P-ER; Fig. 12.5C). Such P-ER complexes have been observed in *Nemogullmia longevariabilis, Gloiogullmia eurystoma, Nonionella stella, Stainforthia fusiformis, Buliminella tenuata,* and *Fursenkoina cornuta* (Nyholm and Nyholm, 1975; Bernhard and Alve, 1996; Bernhard, 1996). The role of these complexes may merely be to break down hydrogen peroxide, which is a byproduct in the anaerobic metabolic pathway of glycolysis. This biochemical avenue has been proposed by Nyholm and Nyholm (1975), although it is not established that Foraminifera rely heavily on glycolysis.

Ultrastructural investigations indicate that organelles which appear to be mitochondria are present in all Foraminifera observed to date, strongly suggesting that these species are aerobes or microaerophiles. In addition, it has been reported that mitochondria of Foraminifera from oxygen-depleted environments are concentrated beneath test pore plugs (Leutenegger and Hansen, 1979). High concentrations of mitochondria, however, have also been observed in apertural cytoplasm (Bernhard and Alve, 1996), which is assumed to form the pseudopodia during network deployment. Optical microscopic examinations (Doyle, 1935; J.M. Bernhard and S.S. Bowser, unpublished data) have shown mitochondrial movements within pseudopods, which can extend to at least ten times the test diameter of a foraminifer (Travis and Bowser, 1991). Thus, it is possible that Foraminifera inhabiting an environment with a steep redox gradient use mitochondrial activity in extended pseudopods to maintain oxidative phosphorylation, even though their tests and cell bodies are located in anoxic sediments.

It is likely that benthic Foraminifera inhabiting anoxic, sulfidic environments use many adaptations in concert to allow survival in such seemingly hostile conditions. The two major chemical barriers are detoxifying H_2S and surviving without or with very little oxygen. As stated earlier, because all Foraminifera examined to date possess organelles that appear to be mitochondria, apparently they are aerobes. We must note, however, that organelles resembling mitochondria in some anaerobic protists are in fact hydrogenosomes (Finlay and Fenchel, 1989). Hydrogenosomes are organelles that perform a variety of functions, most notably (in the context of this chapter) to ferment pyruvate, which is a byproduct of the anaerobic pathway glycolysis. Further enzymatic studies of foraminiferal 'mitochondria' will establish their true identity and functions. Furthermore, it has been shown that mitochondria of certain microaerophilic protists grown under anoxia increase in volume and number, suggesting that these organelles play a role in anaerobic energy metabolism (Bernard and Fenchel, 1996). Additional biochemical studies are required before we can gain a full understanding of foraminiferal physiology during exposure to microxia or anoxia. For further discussion on possible physiological adaptations used by Foraminifera inhabiting oxygen-depleted environments, see Bernhard (1996).

12.5 GENERALIZATIONS ON LOW-OXYGEN FORAMINIFERAL ASSEMBLAGES (LOFAS)

12.5.1 Systematic trends

While the Foraminifera of a number of oxygen-poor environments remain to be investigated, it is useful to make some generalizations about 'typical' assemblages of such habitats. In general, calcareous perforate species dominate LOFAs, but agglutinated species can also occur in con-

siderable abundance. Very few miliolaceans have been found in natural dysoxic, microxic, or anoxic samples. A species of *Pseudotriloculina* was observed in samples from Jellyfish Lake, Palau, where conditions were mildly dysoxic (i.e. $O_2 = 35$–$40\,\mu M$; M. Langer and J.H. Lipps. unpublished data). *Spiroloculina attenuata* and *Edentostomata cultrata* were observed in considerable numbers in black, and therefore presumably microxic or anoxic, sediments of harbor inlets of the Madang Lagoon, Papua New Guinea (M. Langer and J.H. Lipps, unpublished data). Also, a variety of small miliolaceans were common in black sediment samples from mangrove sites of Moorea (M. Langer, pers. comm.). Specimens of *Quinqueloculina stalkeri,* which stained with Rose Bengal, were observed in dysoxic fjord sediments (E. Alve, unpublished data). As noted above, *Q. seminulum* can survive anoxia, but appears to prefer aerated conditions (Moodley *et al.,* 1998b). There are few documented cases of tectinous Foraminifera in oxygen-depleted sediments. Nyholm and Nyholm (1975) noted the occurrence of *Nemogullmia longevariabilis* and *Gloiogullmia eurystoma* in 'low oxygen concentrations' of the Gullmar fjord, but specific $[O_2]$ were not reported. Bernhard (1996) showed an undescribed allogromiid living among *Beggiatoa* filaments (see Bernhard, 1996, Fig. 1). A new species of the closely related testate protist *Gromia* is known to be very abundant at the sediment-water interface in the Arabian Sea OMZ (A.J. Gooday, pers. comm.). Pending a dedicated study, it is highly likely that tectinous Foraminifera and gromids have been overlooked and that they occur in greater abundances in low-oxygen environments than presently thought.

A survey of genus and species distributions, using the data presented in Table 12.2, and some additional information (referenced below), indicates some common features in LOFAs. A brief summary is given here, in terms of major taxonomic groups (see chapter 2 for classification). Among the Order Rotaliida, the Nonionidae and Chilostomellidae (Figs. 12.6A, B, C) are typically common, being represented by seven species of five genera (*Nonion grateloupi, Nonionella stella, N. turgida, Nonionellina labradorica, Chilostomella ovoidea, C. oolina, Astrononion* sp.). The occurrence of *Nonionellina labradorica* in a putatively dysoxic basin was noted by Cedhagen (1991). Other genera from the Order Rotaliida are: Gavelinopsis (Figs. 12.6K, N), *Rosalina, Cancris, Valvulineria, Epistominella, Oscangularia, Polymorphina, Planulina, Ammonia,* and *Elphidium.* The last two genera are represented in dysoxic or microxic habitats by the widely distributed species *Ammonia parkinsoniana* (Figs. 12.6H, L), *A. beccarii* (Kitazato, 1994), and *Elphidium excavatum.*

Members of the Order Buliminida are also conspicuous constituents of LOFAs (Figs. 12.6D, E, F, G, J). The genera include *Bolivina, Fursenkonia, Uvigerina, Bulimina, Globobulimina, Buliminella, Cassidulina, Cassidulinoides, Globocassidulina, Stainforthia, Hopkinsina, Trifarina, Brizalina, Suggrunda,* and *Loxostomum.*

Unilocular agglutinated genera known to be common in dysoxic environments include *Ammodiscus, Bathysiphon, Psammosphaera, Rhizammina, Saccammina, Saccorhiza, Technitella,* and *Tolypammina.* In addition, *Pelosina arborescens* and *Astrorhiza limicola* have been observed in putatively dysoxic environments (Cedhagen, 1993). Multilocular agglutinated genera of LOFAs include *Reophax, Spiroplectam-*

Figure 12.6 Scanning electron micrographs of Foraminifera common in oxygen-depleted environments. A, *Nonionellina labradorica* (Oslo Fjord, Norway); B, *Nonionella stella* (Santa Barbara Basin, U.S.A.); C, *Chilostomella ovidea* (Santa Barbara Basin, U.S.A.); D, *Buliminella tenuata* (Santa Barbara Basin, U.S.A.); E, *Bulimina marginata* (Oslo Fjord, Norway); F, *Stainforthia fusiformis* (Oslo Fjord, Norway); G, *Globobulimina pacifica* (OMZ off Pt. Sur, California, U.S.A.); H, *Ammonia parkinsoniana* (Gulf of Mexico, off Louisiana, U.S.A.), dorsal view; I, *Spiroplectammina earlandi* (Santa Barbara Basin, U.S.A.); J, *Bolivina albatrossi* (hydrocarbon seep, Gulf of Mexico, off Louisiana, U.S.A.); K, *Gavelinopsis translucens* (hydrocarbon seep, Gulf of Mexico, off Louisiana, U.S.A.), dorsal view; L, *Ammonia parkinsoniana* (Gulf of Mexico, off Louisiana, U.S.A.), ventral view; M, *Trochammina pacifica* (Santa Barbara Basin, U.S.A.); N, *Gavelinopsis translucens* (hydrocarbon seep, Gulf of Mexico, off Louisiana, U.S.A.), ventral view. Scale bars = 100 μm. [H and L from Sen Gupta *et al.,* 1996; J, K, and N from Sen Gupta *et al.,* 1997; M from Bernhard *et al.,* 1997; reprinted with publishers' permission.]
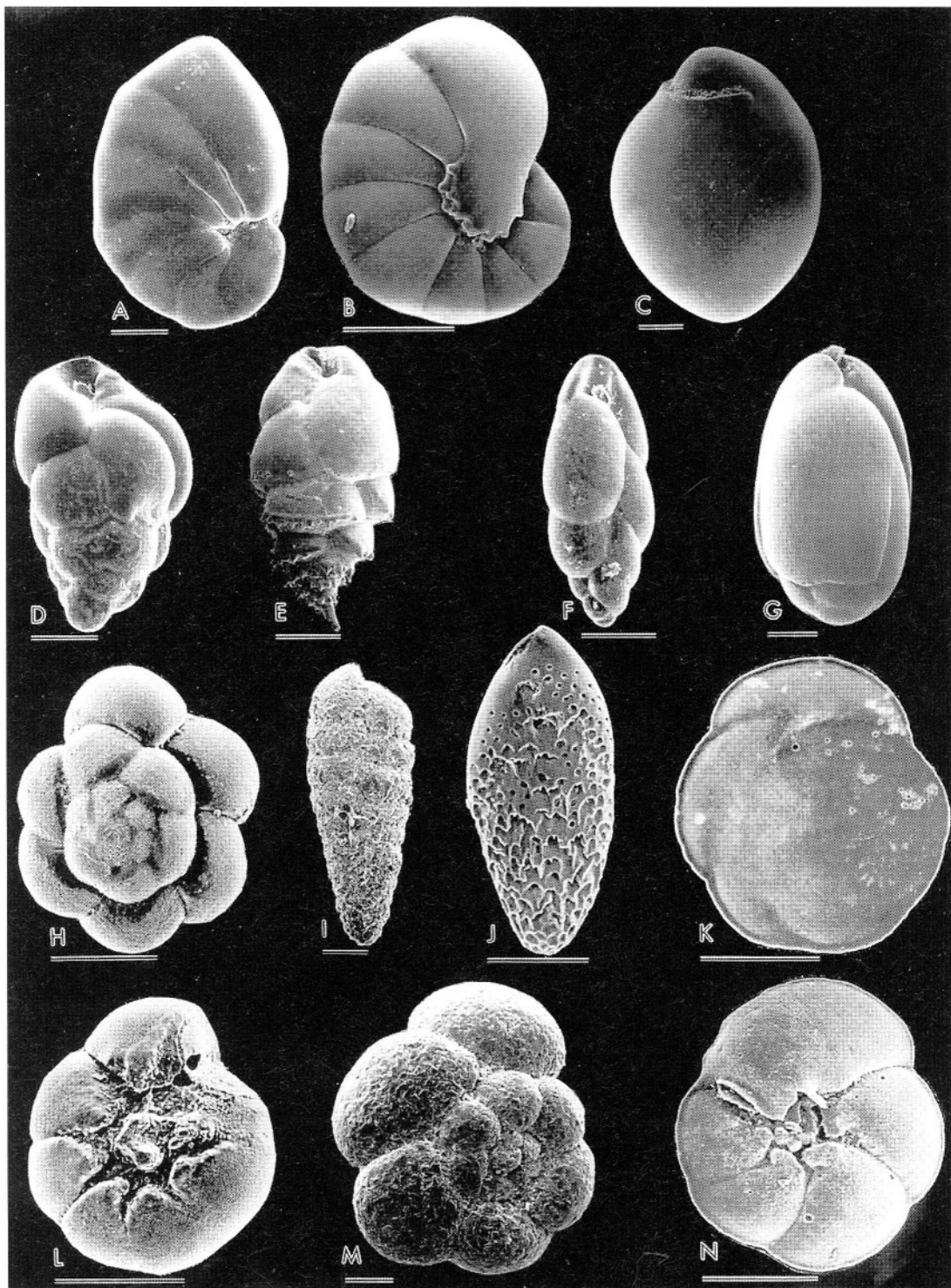
mina (Fig. 12.6I), *Trochammina* (Fig. 12.6M), *Eggerella, Adercotryma, Bolivinopsis, Cribrosto-moides, Portatrochammina, Textularia, Recur-voides* and *Verneuilinulla*. Also, *Ammotium cassis* was observed to inhabit the redox boundary (Linke and Lutze, 1993).

It is crucial to realize that congeneric species also occur in well-aerated environments; not all species of *Bolivina,* for example, are indicative of oxygen depletion. Interestingly, none of the foraminiferal species observed to date in LOFAs is known to live exclusively in anoxic environments. It is possible that certain species are microaerophiles but fine-scale spatial distributional analyses and biochemical studies have not yet been done to confirm this possibility.

12.5.2 Test attributes

It has been suggested that small-sized Foraminifera might survive episodes of oxygen depletion better than larger species, because of less oxygen requirement (Phleger and Soutar, 1973). Indeed, a number of assemblages in microxic environments are dominated by small foraminiferal species. For example, *Nonionella stella* dominates the Santa Barbara Basin (Bernhard *et al.*, 1997), *Stainforthia fusiformis* is common in many dysoxic areas (Alve, 1990, 1994, 1995b; Jorissen *et al.,* 1992), *Epistominella* spp. are common constituents of LOFAs (Ingle *et al.*, 1980; Jorissen *et al.*, 1992) and *Ammonia parkin-soniana* dominates dysoxic inner-shelf areas of the Gulf of Mexico (Sen Gupta *et al.*, 1996). However, a number of taxa comprising LOFAs are not particularly small (e.g. *Globobulimina, Chilostomella,* certain species of *Bolivina*). Because a standard-mesh screen (e.g. 63 μm) has not been used to obtain the sample residue in all studies of LOFAs, it is still uncertain if small species have a competitive advantage over larger species in oxygen-depleted settings. Relatively large-sized (> 1 mm) foraminiferal species are not commonly documented from dysoxic, microxic, or anoxic environments (exceptions being *Astrorhiza limicola* and *Pelosina arbo-rescens*; Cedhagen, 1993). In a recent study, Moodley *et al.* (1997) observed that conclusions

regarding the survival of Foraminifera in anoxia would be significantly different if one considered the > 63-μm fraction rather than the > 38-μm fraction that they used. Thus, they suggest that 38–45 μm should be used as the lower size limit when assessing foraminiferal response to oxygen depletion.

A number of authors (e.g. Harman, 1964; Phleger and Soutar, 1973; Bernhard, 1986) have observed that many calcareous species of LOFAs have thin shells. Miliolaceans of oxygen-depleted environments in the Madang Lagoon also have thin shells (M. Langer and J.H. Lipps, unpublished data). As noted by Sen Gupta and Machain-Castillo (1993), however, not all species from LOFAs are thin-shelled. Given that thin-shelled Foraminifera are more likely to be destroyed during standard laboratory preparation of dry samples, it is possible that the importance of some species has been underestimated. Thus, we suggest that samples to be analyzed for LOFAs should be sieved and picked wet, without prior drying, to prevent excessive damage to thin-shelled forms.

Another trend suggested for LOFA species is that pore size and density are higher in tests from oxygen-depleted environments, compared to those from well-oxygenated environments (Perez-Cruz and Machain-Castillo, 1990; Moodley and Hess, 1992). The proposed explanation for this observation is the widely accepted idea that foraminiferal pores are conduits for oxygen supply to the intracellular milieu (e.g. Berthold, 1976b; Leutenegger and Hansen, 1979), and that larger, more numerous pores could presumably provide more oxygen. As noted above, however, mitochondrial activity in pseudopods may be more important than that associated with pore plugs. In addition, a number of LOFA species (e.g. *Chilostomella ovoidea, Nonionella stella*) have very small pores (J.M. Bernhard, pers. obs.), while the occasion-ally abundant agglutinated species lack pores altogether. Much more detailed study of pore function and pseudopodial activity in Foraminifera are needed to test the significance of pores in the context of microxia.

Lastly, it has been proposed that certain mor-

phologies occur more frequently in Foraminifera from oxygen-depleted environments (Bernhard, 1986), but additional observations do not confirm this trend. The planoconvex morphogroup is rare in most LOFAs observed to date, but some other shapes that were considered indicative of aerated environments are well represented in LOFAs (e.g. spherical: *Chilostomella, Globobulimina, Psammosphaera*).

12.5.3   Abundances

In a number of cases, the reported abundances of Foraminifera in oxygen-depleted sediments are high. Hundreds of stained Foraminifera per cm^3 are documented in Rose Bengal treated samples from different sites (e.g. Phleger and Soutar, 1973; Douglas and Heitman, 1979; Ohga and Kitazato, 1997; Jannink *et al.,* 1998). Bernhard and Reimers (1991) observed up to 2,176 Rose Bengal stained Foraminifera per cm^3 in the microxic Santa Barbara Basin. One reason for such high densities in these habitats is a decrease in predation pressure, because of the severe effect of oxygen depletion on metazoans (e.g. Josefson and Widbom, 1988). There are, however, other cases where oxygen-depleted environments have extremely low foraminiferal densities. In fact, Bernhard and Reimers (1991) found only three Rose Bengal stained specimens per cm^3 during another sampling in Santa Barbara Basin only eight months after observing the extraordinarily high density mentioned above. The reason for this decimation of the assemblage was inferred to be the possible continuation of anoxia for weeks or months. Although it is likely that extended anoxia, in combination with H_2S, prohibits the sustenance of large foraminiferal populations, some previously reported low densities are tied to sample processing methods. We reiterate that a proper census of Foraminifera surviving under dysoxia, microxia, or anoxia has to be preceded by sample washing on appropriately line-mesh sieves (without sample desiccation) and has to include the enumeration of allogromiids.

Taphonomic changes in foraminiferal assemblages are the focus of chapter 16, but it would be worthwhile to make some general comments here on the preservation of Foraminifera in sediments with little or no oxygen. Because calcite dissolution is negligible in some OMZ sediments (Berelson *et al.*, 1996). the calcareous components of the fossil foraminiferal assemblages and the original living assemblages are unlikely to be significantly different in these sediments. On the other hand, calcite dissolution rates are considerable in the mildly dysoxic or oxic sedimentary environments just above and below the OMZ (Berelson *et al.*, 1996). Seasonally dysoxic to anoxic sediments are likely to have substantial rates of calcite dissolution when re-aeration occurs (e.g. Green *et al.*, 1993b). Thus, the calcareous component of these foraminiferal assemblages might be altered greatly from original assemblages.

12.5.4   Application to historical and paleontological records

Understanding the ecology of Foraminifera in oxygen-depleted environments allows interpretations of past environmental conditions from subsurface data. Questions regarding climate change and anthropogenic influence on the environment can be answered using such approaches. For example, using the succession of foraminiferal species observed with respect to bottom-water oxygen concentrations in the Santa Barbara Basin, subsurface data can be analyzed to infer distinctions between $[O_2]$ within a range of dysoxia to microxia (Bernhard *et al.*, 1997). Using this proxy model, data from Ocean Drilling Program station 893, which is located in the Santa Barbara Basin, can be reinterpreted, taking into account that *Nonionella stella* represents the most anoxia-tolerant species.

Analyses of foraminiferal data from subsurface samples have already led to interpretations of oxygen-related environmental changes. For example, faunal changes in a Norwegian fjord foraminiferal assemblage over the last ~ 1,000 years indicate pollution effects superimposed over climatic changes (Alve, 1991b). More specifically, assemblages show a marked decrease in

species diversity and increase in abundance over time, with *Spiroplectammina biformis* dominating just prior to the onset of anoxia about 1970. Another study shows that the foraminiferal record of the Po Delta reflects the environmental history of that area for the last 160 years (Barmawidjaja *et al*., 1995). Strong eutrophication started in 1930, as indicated by the appearance of 'stress-tolerant' species (*Bolivina seminuda, Hopkinsina pacifica,* and *Quinqueloculina stalkeri*), and seasonal anoxia began in 1960, as indicated by the stratigraphic trends of the first two species.

The stratigraphic record of several inner-shelf foraminiferal species of the northwestern Gulf of Mexico demonstrates an overall increase of oxygen stress in the past 100 years. The clues include a decrease in the abundance of *Quinqueloculina* spp. (Rabalais *et al*., 1996), an increase of *Buliminella morgani* (Blackwelder *et al.,* 1996), and a positive trend in the relative dominance of the more tolerant *Ammonia parkinsoniana* over the less tolerant *Elphidium excavatum* (Sen Gupta *et al*., 1996). In this area of strong seasonal oxygen depletion at present, the foraminiferal trends match the overall increasing trend of fertilizer use in the United States in the 20th century, and the consequent higher nutrient input into the Gulf of Mexico by rivers, especially the Mississippi.

12.6   CONCLUSIONS

In summary, certain benthic Foraminifera from various water depths inhabit oxygen-poor and even anoxic environments. It is established that at least some foraminiferal species survive anoxia and even sulfidic conditions for periods up to a few weeks, but the tolerance of most species to oxygen depletion is unknown. Furthermore, the physiological mechanisms enabling foraminiferal species to survive exposure to anoxia and/or sulfidic conditions are not yet identified. The available data suggest, however, that all Foraminifera are aerobic for at least part of their life, and, in all likelihood, some species are facultative anaerobes. Obligate anaerobes have not been identified among foraminiferal species. The information necessary to understand the diverse aspects of foraminiferal adaptation to oxygen-depleted environments must come from experimental studies. Only with such biological information, it will be possible to construct more accurate databases for use in other disciplines such as paleoecology and paleoceanography.

12.7   ACKNOWLEDGMENTS

13

Effects of marine pollution on benthic Foraminifera

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13.1 INTRODUCTION

13.1.1

Population growth and the resultant acceleration
of domestic, municipal, industrial, agricultural,
and recreational activity are the primary causes
of anthropogenic pollution of the marine realm
(Norse, 1993). Such pollution produces numerous
obvious biological effects, including diseases in
plant and animal species (e.g. Lamb *et al*., 1991),
local or complete extinction of some species (Ver-
meij, 1993), changes in community structure
(Bresler and Fishelson, 1994; Suchanek, 1993),
loss or modification of habitat (Nee and May,
1992), and human health complications. The
marine environment, as the ultimate destination
of virtually all terrestrial runoff, is especially
affected by pollution, and the shallow nearshore
marine environment is particularly subject to fre-
quent and extensive industrial and municipal
pollution.

With increasing worldwide awareness of envi-
ronmental problems, ways to detect and monitor
marine pollution over time are the subject of
active research. Numerous studies have demon-
strated the value of various animal species in
detecting dangerous ecosystem contamination
(James, and Evison, 1979; Organization for Eco-
nomic Cooperation and Development, 1987).
Species which occupy key positions in ecosystems
are especially useful biomonitors. Thus, the con-
tinual global biogeochemical cycles of inorganic
and organic compounds are regulated mainly by
biological activity of benthic communities, especi-
ally bacteria and protozoa (Meyer-Reil, 1986;
Santschi, 1988).

Marine protozoa, especially Foraminifera,
play a significant role in global biogeochemical
cycles of inorganic and organic compounds,
making them one of the most important animal
groups on earth (Anderson, 1988; Haynes, 1981;
Lee and Anderson, 1991b). They are ubiquitous
in marine environments. Their tremendous taxo-
nomic diversity gives them the potential for
diverse biological responses to various pollu-
tants, which in turn adds to their potential as
index species for monitoring pollution from
diverse sources. Their tests are readily preserved,
and can record evidence of environmental
stresses through time, thus providing historical
baseline data even in the absence of background

studies. They are small and abundant compared to other hard-shelled taxa (such as mollusks which are often used for pollution monitoring), which makes them particularly easy to recover in statistically significant numbers. They have short reproductive cycles (six months to one year; Boltovskoy, 1964), and rapid growth (Walton, 1964), making their community structure particularly responsive to environmental change. They often show species-specific responses to ecological conditions (Fursenko, 1978). They have biological defense mechanisms (Yanko *et al.*, 1994a) which protect them against unfavorable environmental factors, thus providing detectable biological evidence of the effects of pollution. These characteristics make them powerful tools for continuous *in situ* biological monitoring of marine environments.

Barely forty years have passed since Zalesny (1959) discovered the effects of pollution on foraminiferal distribution in Santa Monica Bay, California. Resig (1958) and Watkins (1961) subsequently suggested the use of benthic Foraminifera as proxy indicators of marine pollution. Since that time, the foraminiferal literature has seen an exponentially rising tide of papers on the behavior of Foraminifera in polluted areas. Brief reviews have been presented by Boltovskoy and Wright (1976), Alve (1991a,b), Culver and Buzas (1995), Yanko *et al.* (1994c) and Alve (1995a).

13.1.2   General locations of studies

The geographic locations of studies on marine pollution and Foraminifera are dictated by two main factors: the distribution of human activities that generate pollution, and the distribution of foraminiferologists with support and interest in the study of pollution. As can be seen from Fig. 13.1, the geographic localities of studies in this field are concentrated primarily in industrialized countries. Studies of the effects of coastal pollution on the Foraminifera are concentrated mainly in the northern Pacific Ocean, with additional studies in the south Pacific and Indian Oceans, and the eastern Mediterranean Sea, northwestern Black Sea and Caspian Sea. Only one study has been undertaken on the Atlantic

coast of the Americas. Pollution in these areas tends to be dominated by municipal sewage, but heavy metals, hydrocarbons, fertilizers, coal and fuel ash, and various other chemical pollutants are also represented.

The study of pollution in bays and harbors (again, mainly by municipal sewage but also by aquaculture, paper mills, heavy metals, fertilizers and chemical pollution) have been undertaken in the North Pacific Ocean, North and South Atlantic Oceans, the Caribbean Sea, the Indian coast, and the Gulf of Mexico. The influence of pollution on Foraminifera in estuaries and lagoons has been studied mainly in the North Atlantic Ocean (Canadian). North Sea, South Atlantic Ocean, and along the Indian coast. Most of these studies focused on pollution from aquaculture, paper mills, fertilizers, heavy metals, domestic sewage, and various chemicals.

13.1.3   Research strategies

The use of Foraminifera as indicators of marine pollution may involve quantitative analysis of: (1) foraminiferal diversity, (2) population density/abundance, (3) assemblage structure, (4) test morphology, including size and prolocular morphology, (5) test ultrastructure, (6) test pyritization, (7) test chemistry, and (8) cytoplasmic/ biological response.

These eight approaches can be complicated by two general factors:

(1) The first complication relates to *covariation* within and among natural and anthropogenic environmental factors. Most toxins enter the marine system from terrestrial sources, primarily through coastal or estuarine ecosystems where steep natural environmental gradients would exert control over foraminiferal distribution patterns even in the absence of anthropogenic effluents. Separating the effects of these two coincident influences can be problematic (e.g. Collins *et al.*, 1995). Moreover, environmental factors (e.g. dissolved organic carbon, especially humic acids, pH, temperature, salinity, ionic strength, rates of biotic pollutant metabolism, and degradation) can modify the toxicity of pollutants (Forstner and Wittmann, 1979; James,
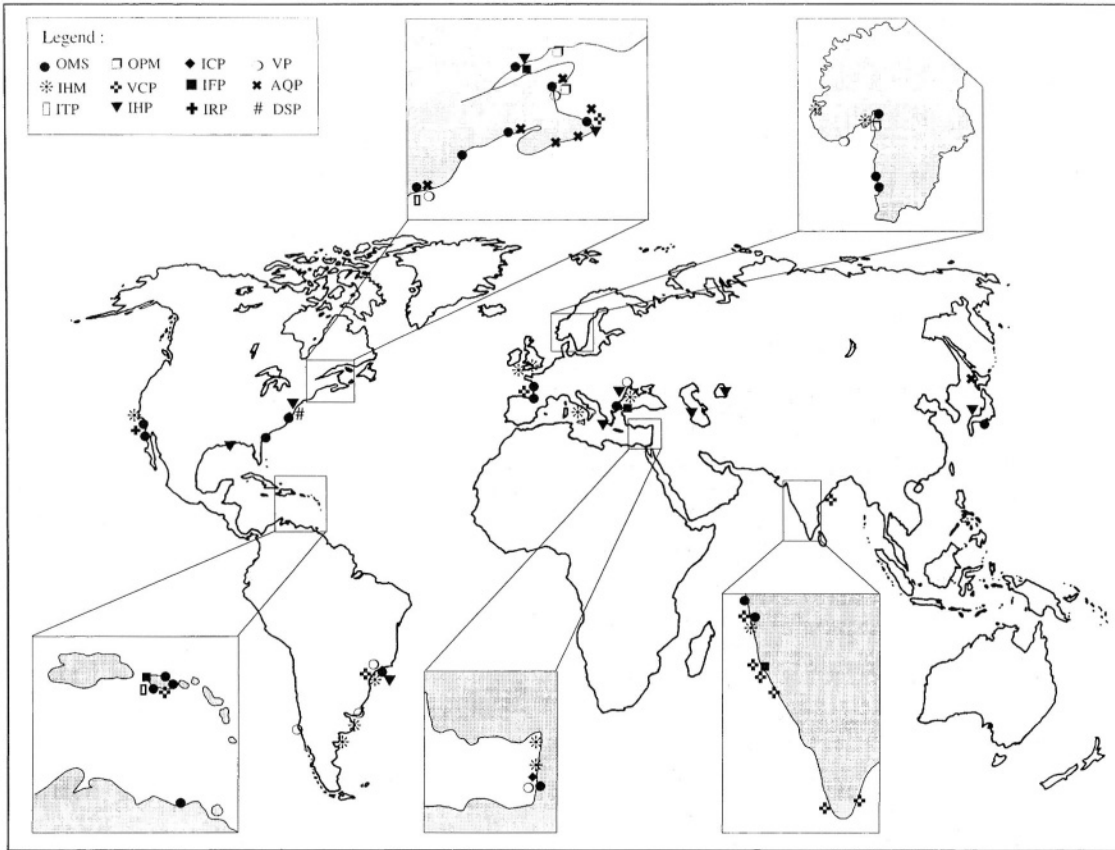
Figure 13.1 Global distribution of studies involving foraminiferal response to pollution. Symbols are as follows: OMS organic pollution by municipal sewage; OPM organic pollution by pulp and paper mills; ICP industrial pollution by coal and fuel ash; IHM industrial pollution by heavy metals; VP various unspecified pollutants; VCP various chemical pollutants, including pesticides; IFP industrial fertilizer pollutants; AQP aquaculture pollution; ITP industrial thermal pollution; IHP industrial pollution by hydrocarbons; IRP industrial pollution by radioactive wastes; DSP dredging and stream discharge pollution.

1989; Paasivarta, 1991; Belfroid *et al.*, 1994; Bresler and Yanko, 1995a,b).

Contaminated estuarine and coastal ecosystems, especially benthic ecosystems, may also contain a broad variety of pollutants. For example, the active components of oil pollution include, as a minimum, numerous polycyclic aromatic hydrocarbons (PAHs), linear hydrocarbons, phenolic compounds, and heavy metals. Active components of fuel ash include various PAHs and heavy metals (Jenner and Bowmer, 1990, 1992; Hamilton *et al.*, 1993). These pollutants may interact to influence toxicity in complex and nonlinear ways (e.g. Green

et al., 1993a). Additionally, some natural constituents in sea water and sediments (e.g. acid-volatile sulfide, dissolved organic carbon, or other organic matter) may also interact with pollutants to modify their toxicity (Versteeg and Shorter, 1992; Bresler and Yanko, 1995b). Sediment-dwelling benthic organisms can also affect the behavior of pollutants as well as the chemical properties of bottom sediments and water (e.g. Huttel, 1990). The biological effects of such complex mixtures can be more (or less) toxic than would be expected from simple additive effects of a single pollutant or several pollutants (Malins and Ostrander, 1993; Newmand and

Jagoe, 1996; Howard, 1997). Moreover, effluent sources – particularly from chemical processing plants – rarely produce only a single toxin, which tends to result in covariation among toxin concentrations; this in turn makes it difficult to determine which toxins are producing the observed effects on foraminiferal populations (e.g. Yanko *et al.*, 1994c). The solution to these covariation problems takes three forms: (i) statistical analysis of faunal distribution patterns and toxin/pollutant concentrations, (ii) laboratory experimentation, and (iii) historical analysis.

The statistical analysis is easier where strong point sources of effluent interrupt natural environmental gradients, but can be complicated by nonlinear causal relationships. For example, intermediate levels of some urban and agricultural organic wastes can cause a 'hypertrophic' zone (Alve, 1995a) of increased foraminiferal productivity, while very high concentrations can result in an 'azoic' (Schafer, 1970a) or 'abiotic' zone (Alve, 1995a). As a general rule, the statistical analysis of complex interactions between numerous species and a large number of environmental factors will require a multivariate approach such as factor analysis (see chapter 5). A particular application of factor analysis, the transfer function discussed in chapters 5 and 7, is a technique that would be particularly well suited to such situations; surprisingly, it has seen little use in the field of foraminferal ecotoxicology.

Laboratory experimentation may identify interactions between species and toxins by growing them under controlled conditions; this allows the researcher to experimentally resolve the problems presented by covariation, if attention is paid to the possibility of interaction among toxins as well as with varying natural conditions.

Historical analysis may be undertaken when there is sufficient stratigraphic accumulation of a pre-industrial foraminiferal record; in that situation it becomes possible to compare modern conditions with preceding unpolluted conditions even without a background study. This approach is complicated by taphonomic effects that themselves may covary with (or indeed be caused by) pollution induced changes in bottom-water chemistry.

(2) A second broad problematic area relates to the *measurement of pollutants.* Effluent concentrations can be measured by extraction from sediments, or by sampling at the sediment-water interface or in the overlying water column, but the biological relevance of such measurements is not well understood. Effluent concentrations can also show considerable temporal variation, depending on the schedules of human activity that produce and release effluents; thus, sampling dates and frequency may have a major effect on results. Additionally, it is not uncommon for effluent concentrations to be taken from published literature rather than measured at the time of sampling for Foraminifera. Further, when toxin concentrations are measured in sediments, the differing properties of sediments must be taken into account. For example, clean sands will interact with toxins in different ways than muds and clays. Toxin concentrations can thus covary with sediment type (*e.g.* Yanko *et al.*, 1998), which, in turn may also influence foraminiferal distributions.

13.2   FORAMINIFERAL RESPONSES TO DIFFERING SOURCES OF POLLUTION

13.2.1

Given the recent emergence of foraminiferal ecotoxicology as a discipline, it is possible to provide a relatively complete account of work on the subject to date. The discussion below is divided into twelve broad categories: municipal sewage, fertilizers, aquacultures, pulp/paper mills, hydrocarbons, heavy metals, fuel ash, chemical pollutants including pesticides, thermal, radioactive, dredging, and stream discharge. References in these areas are grouped accordingly, and are virtually complete through 1997.

13.2.2   Municipal sewage, fertilizers, and aquacultures

Marine ecosystems are sensitive to suspended or dissolved organic matter from municipal

sewage, agricultural fertilizers, and aquacultures. These pollutants can affect marine ecosystems chemically (by depletion of oxygen through oxidation and bacterial decay), biologically (by the introduction of disease-bearing organisms such as viruses, bacteria, and parasitic worms), and physically (warming due to fermentation and reduced photic levels due to turbidity). Dissolved organic material as well as other compounds of phosphorus, silicon, and nitrogen, are usually abundant in such areas, creating artificially high nutrient levels. This organic material is readily metabolized by marine organisms, and can cause an increased foraminiferal abundance (e.g. Watkins, 1961; Bandy et al., 1964a; Seiglie, 1971; Setty, 1976; Yanko et al., 1994c) and diversity (e.g. Resig, 1958, 1960; Yanko et al., 1994c; De Casamajor and Debenay, 1995). Bandy et al. (1964a) discussed a typical example of anomalously high living and dead foraminiferal abundances near a sewage outfall (see chapter 11). Additionally, planktonic Foraminifera were fifty times as abundant in sediment near the outfall as elsewhere at similar depths. Bandy et al. (1964a) also noted that agglutinated species were most abundant among dead tests in the outfall area, which is probably a taphonomic effect related to dissolution in sulfide-rich (Fe_2S) black sediments. Other workers have noted that in some areas polluted by domestic sewage, Foraminifera can have unusually large, well ornamented tests and relatively few deformed tests (e.g. Watkins, 1961; Yanko et al., 1994c). These observations suggest that artificially high levels of nutrients may enhance the general viability of foraminiferal populations.

However, this is not always the case. Clark (1971) found a strong inverse relationship between the density of Foraminifera in the sediment and the production level of nearby aquaculture operations. No live Foraminifera were found by Schafer (1970a) in an 'azoic zone' ('abiotic zone' of Alve, 1995a). Similar observations have been made by others (Bandy et al., 1964b; Schafer and Sen Gupta, 1969; LeFurgey and St Jean, 1975). The azoic zone is usually located in the immediate vicinity of the outfall where bacterial breakdown of extreme concentrations of organic material causes oxygen depletion, eutrophication, and high mortality of Foraminifera (e.g. Bandy et al., 1965b; Schafer et al., 1991).

The existence and spatial distribution of the azoic zone is influenced by the sewage type (activated or treated vs. non-activated or untreated), its geographic location (estuary, bay, or open shelf), hydrodynamic regime (current strength, direction), salinity, temperature, and effluent outfall rates (Bates and Spencer, 1979; Alve, 1995a). For example, in the eastern Mediterranean approximately three miles off Palmahim, Israel, a pipe fitted with a diffuser at its end disposes of $1,400 \ m^3/day$ of domestic sewage in a water depth of 38 m. The activated sludge (after secondary treatment) is composed of 95% water and 5% solids. In addition to the stable biomass, it may contain pathogenic bacteria, inorganic nutrients, and synthetic organic compounds. The lowest foraminiferal abundances were found at the mouth of the distal end of the pipeline, but there was no azoic zone. The highest diversity and abundance were found at stations located to the north and northwest of the sewage outfall, in an open coastal area downcurrent of the outfall with salinities of 39‰ (Yanko et al., 1994c). By contrast, an azoic zone was noted near the Beledune Fertilizer factory in Restigouche estuary, Atlantic Canada, where salinity varied between 21 and 28‰, and currents spread pollutants throughout the entire estuary (Schafer, 1970a). In this situation, the combined effects of water temperature and salinity caused a density-stratified water column that led to reduced overturn and local enhancement of oxygen deficiency (Schafer et al., 1995). This may be an example of the kind of nonlinear interaction that complicates our understanding of the relationship between pollutants and natural environmental factors.

Additional work on organic pollution by municipal sewage includes Alve, 1991a,b; Alve and Nagy, 1986; Bandy et al., 1965a,b; Bonetti et al., 1996; Cato et al., 1980; Collins et al., 1995; Debenay et al., 1997; Eichler et al., 1995; Govindan et al., 1983; Hirshfield, 1979; LeFurgey and St. Jean, 1973, 1976; Latimer et al., 1997; Lidz, 1965, 1966; Matoba, 1970; McCrone and

Schafer, 1966; Nyholm and Olsson, 1973; Nyholm *et al.*, 1977; Resig, 1960; Schafer, 1970b, 1971a, 1973, 1982; Seiglie, 1964, 1968, 1975; Setty, 1982; Setty *et al.*, 1983; Setty and Nigam, 1982, 1984; Scott *et al.*, 1993, 1997; Yanko, 1993, 1994, 1995, 1996a,b; Zalesny, 1959. Additional work on pollution by fertilizers includes Schafer, 1970a, 1992; Seiglie, 1975; Setty, 1976; Yanko and Flexer, 1991. Work on pollution by aquaculture includes Grant *et al.*, 1995; Schafer, 1970b, 1973; Schafer *et al.*, 1993; Scott *et al.*, 1993, 1995, 1997; and Preobrazhenskaya *et al.*, 1991.

13.2.3   Pulp and paper mills

Effluent from pulp and paper mills consists mainly of resistant organic material such as cellulose and lignin, major constituents of wood fibers. The most toxic compounds associated with this effluent are those used to break down wood fibers, rather than the wood fibers themselves. Compounds of mercury are particularly toxic; additionally, sulfides will, under well-oxygenated conditions (usually found downcurrent from the point of discharge), oxidize to sulfates. The presence of sulfides (recognizable by the smell of rotten eggs) normally indicates oxygen-poor conditions, and Foraminifera tend to have low abundances in these areas. Where sulfate levels are high, the environment is usually oxygenated and nutrient-rich, and Foraminifera grow quickly with rapid generational turnover, high productivity, and high abundances. Under these conditions, adult specimens tend to be smaller, probably because of the rapid growth and high reproductive rates characteristic of opportunistic ecological response. However, where sulfate concentrations reach their maximum, foraminiferal abundance is often lower, probably due to coincident high sedimentation rates (Tapley, 1969). In areas surrounded by pulp mills, extreme concentrations of sulfides can create an azoic, reducing environment where coal tar accumulates and Foraminifera are excluded. This variable response to pulp and paper mill effluent is another example of nonlinear faunal response to pollutant concentration.

Additional work on organic pollution by pulp

and paper mills includes Alve, 1994; Alve and Nagy, 1986, 1988; Bartlett, 1966; Buckley *et al.*, 1974; Latimer *et al.*, 1997; Nagy and Alve, 1987; Schafer, 1970a,b, 1971a, 1973, 1982; Schafer and Cole, 1974, 1995; and Schafer *et al.*, 1975. 1991.

13.2.4   Hydrocarbons

In addition to 5–15% alkanes, typical petroleum products contain aromatic hydrocarbons, including monoaromatic hydrocarbons such as benzene and toluene (the most frequently used light petroleum products). Some of these are proven to be carcinogenic (Kennish, 1992). Lethal doses of aromatic hydrocarbons for marine organisms are in the range of 0.00001 to 0.01% for adults, and at the low end of that range for juveniles; doses as low as 10^{-6}% can inhibit physiological activity, and 10^{-7}% can cause pathological reactions (Bokris, 1982; Rubinin, 1983). Depending on the fraction and molecular weight, the hydrocarbons may form a film on the surface of the water, or heavier oil suspensions and tar may sink to blanket the seafloor.

The small amount of work that has been done on the effect of hydrocarbons on Foraminifera has produced conflicting results. Lockin and Maddocks (1982) reported that petroleum operation at Louisiana offshore petroleum platforms had only a minor negative effect on benthic Foraminifera. Similar results were noted around Ekofisk and Forties petroleum platforms in the North Sea (Murray, 1985). Dermitzakis and Alafousou (1987) suggested that meteoric rainfall intensified the effect of terrestrial oil seeps on the offshore marine environment near Zakynthos Island (Greece), possibly due to changes in pH. Vénec-Peyré(1981, 1984) studied the consequences of the Amoco Cadiz incident (March 16–17, 1978) on benthic Foraminifera in Cale du Dourduff, south of Roscoff, northwestern France, and concluded that it did not affect relative abundances or diversity; however, the accident did cause morphological abnormalities in foraminiferal tests. In contrast, a pronounced negative effect of oil on benthic Foraminifera was noted by Mayer (1980) in the

northern Caspian Sea and by Yanko and Flexer (1991) in Odessa Bay where foraminiferal abundance and diversity decreased dramatically in oil-polluted areas. Similar negative effects were noted by Witcomb (1977, 1978) in experimental work on calcareous (*Ammonia beccarii*) and agglutinated species (*Allogromia laticollaris*). He found that crude oil inhibited growth and reproduction in both species, and that petroleum products produced narcosis and death of Foraminifera, and speculated that petroleum products might also cause a decrease in nutrient supply (primarily diatoms). A full understanding of the biological causes of this result awaits further research. V. Yanko (unpublished data) noted that respiratory functions of Foraminifera were inhibited in Black Sea sediments with high concentrations of petroleum products. The breakdown of petroleum was accompanied by the release of H_2S, ammonia, and methane, and by pH as low as 6. (Note that Bradshaw, 1961, found *Ammonia tepida*, a common indicator species, to be very sensitive to pH.)

Work on hydrocarbons also includes papers by Akimoto *et al.*, 1997; Bonetti *et al.*, 1996; Buckley *et al.*, 1974; Casey *et al.*, 1980; Latimer *et al.*, 1997; Schafer, 1992; Schafer *et al.*, 1975; Vénec-Peyré, 1981, 1984; and Yanko and Flexer, 1992.

13.2.5 Heavy metals

The biological relevance of temporal variation of heavy metal toxin concentrations, and of heavy metal concentrations in sediments versus in the water column is not fully understood and, although these factors are undoubtedly important, sampling programs have generally not been designed to assess their relative impact on the Foraminifera. Thus, it is prudent to discuss this research by separating three categories based on sampling methods. The first category includes papers concerning the distribution of living/fossil Foraminifera in sediment samples where the concentration of heavy metals was not measured directly but taken from literature reports. The second group includes information about Foraminifera based on correlation between their

distribution and heavy metal concentrations measured in the same sediment samples. The third set of papers concerns ecotoxicological laboratory experiments on Foraminifera and heavy metals.

Studies based on literature reports of heavy metals. This body of research accounts for much of the early pioneering work in the area of foraminiferal ecotoxicology. Boltovskoy (1956) described a stunted fauna (small in size, lacking ornamentation, with a tendency to asymmetry and monstrosity) in some lead-polluted areas of the northern Argentinean shelf. McCrone and Schafer (1966) noted that trace elements may affect morphology of benthic Foraminifera in the Hudson estuary. Schafer (1973) found that foraminiferal diversity decreased in an area adjacent to a Pb–Zn smelter outfall. Setty and Nigam (1984) found depauperate (in both abundance and diversity) populations of benthic Foraminifera, with high percentages of abnormal individuals, in the area adjacent to a titanium processing plant (near Trivandrum, west coast of India) where a mixture of sulfuric acid, soluble iron, and other metallic salts were discharged. A similar pattern was discovered by Naidu *et al.* (1985) in the Visakhapatnam harbor area (east coast of India) where marine waters were polluted by domestic sewage and a variety of heavy metals (e.g. Cu, Fe, Pb, Zn, Ni, Cr, As). These papers served to draw attention to the fact that foraminiferal morphology – in addition to abundance and diversity – is affected by heavy metal pollution.

Studies based on heavy metal and foraminiferal analyses of the same samples. This body of research is generally more recent and planned with specific ecotoxicological analysis as the primary goal. Ellison *et al.* (1986) investigated foraminiferal response to trace metal (Zn, Cr, and V) contamination in the Patapsco River and Baltimore Harbor, Maryland. They discovered a very depauperate foraminiferal assemblage (fewer than 10 individuals per g^{-1} of sediment), composed of six species, and dominated by *Ammobaculites crassus*. Alve (1991a) analyzed fossil benthic Foraminifera in two short (170–190cm length) sediment cores taken in

Sorfjo (Norway) at depths of 15–53 m, and found a historical record of foraminiferal populations that were characterized by reduced abundances, dominance of agglutinated species, frequent occurrence of abnormal tests (with seven different modes of deformation), and high concentrations of pyritized specimens in areas polluted by heavy metals. A comprehensive study of Foraminifera as indicators of heavy metal pollution was undertaken by Sharifi (1991) and Sharifi et al. (1991) in Southampton Water, southern England. Of the 67 species found in 250 grab samples, some were able to tolerate pollution, and their relative abundance increased at the discharge point, whereas other species developed test deformities. Banerji (1992) compared distributions of heavy metals (Cd, Co, Cr, Cu, Fe, Mn. Ni, Pb, Zn) in sediments and in foraminiferal tests. His results show that species diversity corresponds positively with Fe, Mn, and Zn concentrations in the sediments and negatively with Co. Ni, and Pb concentrations. He found that although *Ammonia* and *Elphidium* species occur together, the former prefers environments enriched with Fe, Mn and Zn, and that an increase in concentrations of Cd, Co, and Pb was accompanied by a decrease in the abundances of *Ammonia* and *Lagena* spp. Such elements as Cu, Zn, and Cr were more readily absorbed into foraminiferal tests than Ni and Pb. At present, comparative observation suggests that it may be possible to develop a scale of gradational species response to heavy metal contamination by using the Lagenida, various agglutinated species, species of *Spiroloculina*, *Triloculina*, *Quinqueloculina*, *Ammonia*, *Cibicides*, *Poroeponides*, and *Elphidium*, and possibly other indicator species. This body of work supports the conclusion that Foraminifera from areas with high concentrations of heavy metals develop stunted tests with numerous deformities. Coccioni et al. (1997) studied living and non-living benthic foraminiferal distributions at fifteen sites throughout the Goro Lagoon, Italy. The concentrations of eleven elements (V, Cr, Co, Ni, Cu, Zn, Ga, As, Pb, Th, and Cd) and total organic carbon (TOC) in the sediments were measured, and a total of 77 species from 43 genera were identified. Some sites displayed marked enrichment in Cr, Ni, Zn, Pb, and As, with Al-normalized values higher than the average values of nearby unpolluted alluvial plain pelites. These sites also exhibited an increase in TOC, a general reduction in foraminiferal test size, and a decrease of benthic foraminiferal species richness, with a concurrent increased abundance of tolerant and opportunistic species such as *Cribroelphidium translucens*. A similar trend was found by Stubbles (1993) and Stubbles et al. (1996a,b) who studied living and dead benthic Foraminifera in Restronguet Creek, Erme and Fowey estuaries, Cornwall. UK. Using semiquantitative microprobe analysis, they found higher concentrations of several heavy metals, including Cd, in the cytoplasm of deformed Foraminifera than in the cytoplasm of non-deformed individuals. The authors suggest that if heavy metals are responsible for deformation of foraminiferal tests, these metals should be dissolved in the water rather than stored in the sediments. This has opened a potentially important avenue of research that may increase our understanding of the biological relevance of heavy metals that are sequestered in sediments versus those dissolved in the water column. However, due to the semiquantitative nature of the instrumentation, further analysis is required.

Research reported in Yanko (1994, 1995, 1996a,b). Yanko et al. (1992, 1994a,b,c, 1995, 1998), and Yanko, ed. (1995, 1996) was directed at the study of benthic Foraminifera as indicators of heavy metal pollution along the eastern Mediterranean coast. Eighty-seven stations were sampled at one mile intervals on a rectangular grid covering the polluted Haifa Bay coastal area, with the relatively clean coast of nearby Atlit Bay as a control. The responses of benthic Foraminifera to ten heavy metals (Cd. Cr, Cu. Pb, Zn, As, Co, Ni, Ti, V) showed that reduced diversity and abundance, stunting of the tests, pyritization, and the presence of anomalous morphologies are closely related to trace metal contamination (Yanko et al., 1998). According to the experimental results of Bresler and Yanko (1995b), there is significant biological influence

of heavy metals on foraminiferal cytoplasm. Mercury ions that penetrate the cytoplasm readily interact with the sulfhydril groups of proteins by blocking them and inhibiting their function. Intracytoplasmic Cd especially interferes with sites that normally interact with calcium; particularly, Cd can penetrate mitochondria and interfere with respiratory functions. However, the Cd-sensitivity of different species, individuals, and even tissues, varies widely.

In general, it can be concluded that there is a negative correlation between concentrations of heavy metals in sediments and foraminiferal abundance and diversity, and a positive correlation between the abundance of deformed tests and heavy metals.

Work on heavy metal pollution also includes publications by Alve and Olsgard, 1997; Banerji, 1989; Bonetti et al., 1996; Kravchuk et al., 1997; Latimer et al., 1997; Schafer and Cole, 1995; Van Geen et al., 1993; Yanko and Flexer, 1991; Yanko and Kronfeld, 1992; and Yanko and Kravchuk, 1996.

13.2.6   Fuel ash

The influence of coal and fuel ash pollution on benthic Foraminifera has been studied along the coast of Hadera, Israel, near a coal-fired power station (Yanko, 1993, 1994, 1995; Yanko et al., 1994c). Fuel ash particles, derived from the combustion of hydrocarbon fuels, dramatically decreases species richness and reproductive rate in Foraminifera, but does not seem to affect the test size. Agglutinated species are less affected by this kind of pollution than calcareous species. It has been speculated that coal and fuel ash particles decrease the food supply (bacteria and diatoms), and also affect foraminiferal metabolism directly (Yanko, 1994). Furthermore, some trace metals and PAHs, contained in fuel and coal ash in very low concentrations, interfere with defense systems and affect nutrient metabolism in Foraminifera (Yanko, 1994).

Additional papers on pollution by coal and fuel ash include work by Yanko, 1993, 1995, 1996b; and Yanko et al., 1994b,c.

13.2.7   Miscellaneous chemical pollutants including pesticides

There are a number of chemical pollutants, including pesticides, that affect foraminiferal abundance and diversity in much the same ways as heavy metals. Some also may be responsible for erosion and corrosion of foraminiferal tests (e.g. in Thana Creek, Bombay Area, India; Setty, 1982). Following exposure to pesticides, foraminiferal biotas can exhibit biochemical and histological alteration in some specimens. Such exposure can also degrade immune systems and cause mutagenic changes (Komarovskiy et al., 1993).

Additional research in this area includes work by Alzugaray et al., 1979; Banerji, 1977; Bartlett, 1972; Bergsten et al., 1992; Bhalla and Nigam, 1986; Boltovskoy and Boltovskoy, 1968; Bonetti et al., 1997a,b; Bresler et al., 1996a,b; Buckley et al., 1974; Geslin et al., 1997a,b, 1998; Jayaraju and Reddeppa Reddi, 1996b; Kameswara and Satyanarayana, 1979; Naidu et al., 1985; Olsson et al., 1973; Seiglie, 1973, 1975; Setty and Nigam, 1980, 1984; Schafer, 1968, 1970a; Schafer et al., 1975; Varshney et al., 1988; Wright, 1968; and Yanko and Kravchuk, 1992.

13.2.8   Thermal and radioactive waste

Research on thermal and radioactive waste is not extensive. An increase in foraminiferal abundance and a decrease of diversity in the Long Island Sound have been related to a powerplant-induced increase of water temperature (Hechtel et al., 1970). Attempts to relate ^{137}Cs contamination from the Chernobyl reactor accident to foraminiferal indices in Iskenderun Bay (Turkey) yielded inconclusive results (Yanko, ed., 1996).

Other works on industrial thermal pollution include Hechtel et al., 1970, and Seiglie, 1975. Work on pollution by radioactive waste includes Reish, 1983.

13.2.9   Dredging and stream discharge

Although the ecological effects of dredging and stream discharge have not been extensively

investigated, it is likely that they will affect tur-bidity (and therefore photic levels), and mobilize nutrients and pollutants that would otherwise remain sequestered in sediments. It has been suggested that these activities change the habitat and community structure of foraminiferal assemblages (Belanger, 1976), although the mechanisms are not well understood.

Additional work on pollution and Foramini-fera that do not fall in the preceding categories include Alzugaray *et al.*, 1979; Banerji, 1977; Bartlett, 1972; Bergsten *et al.*, 1992; Boltovskoy and Boltovskoy, 1968; Boltovskoy *et al.*, 1991; Boltovskoy and Wright, 1976; Bonetti *et al.*, 1997a,b; Bresler *et al.*, 1996a,b; Culver and Buzas, 1995; Geslin and Devenay, 1998; Geslin *et al.*, 1997a,b; Olsson *et al.*, 1973; Schafer, 1968, 197la, 1973, 1975; Wright, 1968; Yanko, 1997; and Yanko and Kravchuk, 1992.

13.3   SPECIAL PROBLEMS IN FORAMINIFERAL ECOTOXICOLOGY

13.3.1   Opportunistic (resistant) species

Species that are abundant in polluted areas are likely to be tolerant (resistant) to the pollutants found there. However, even in these species toxins may produce detectable effects in their cytoplasm and test (Bresler and Yanko, 1995b; Yanko *et al.*, 1998). Species that are sensitive to pollution often express that sensitivity through their absence.

Species identified as resistant in coastal zones, bays, harbors, estuaries and lagoons include approximately 11 agglutinated and 47 calcare-ous species (Table 13.1). The highest number of agglutinated species (6) was found in estuaries while the highest number of calcareous species (33) was noted in coastal zones (Table 13.1). This may be an example of covariation between a natural gradient (salinity) and foraminiferal distribution patterns in an area affected by pollution.

Most eurytopic species are geographically widespread, living within a broad range of lati-tudes, and many can tolerate a wide range of

salinity and depth. For example, *Ammonia tepida* is distributed in the Black Sea from the Danube delta (depth 3–5 m, salinity l–3‰) to the Bosph-orus area (102 m, 26‰) (Yanko and Troitskaja, 1987; Yanko, 1990a,b). In the eastern Mediterra-nean, this species is widely distributed on the shelf at salinities in the range of 39‰ (Yanko *et al.*, 1994a). There are also several taxa (e.g. buliminids, bolivinids, uvigerinids) which can tolerate the oxygen-deficient conditions that often accompany pollution. The dominance of agglutinated Foraminifera in areas close to domestic outfalls (e.g. Bandy *et al.*, 1964a) may be more closely related to fresh-water input than to discharge of pollutants or dissolution of cal-careous forms (Alve, 1995a).

Alve (1995a) concluded that, in general, those species that are most abundant and geographi-cally widespread are most tolerant of environ-mental pollution. If Alve's conclusion is generally valid, then these eurytopic species offer the possibility of comparative studies in widely separated geographic areas – an aspect of fora-miniferal ecotoxicology that has not yet been explored.

13.3.2   Morphological deformity of foraminiferal tests

13.3.2.1   Distribution and correlation

Morphological deformities in fossil foraminiferal tests have been noted by researchers since the last century (e.g. Carpenter, 1856; Rhumbler, 1911). In recent years, reports of deformities in modern Foraminifera have become increasingly common, and further documentation of deformed fossils has been made (e.g. Bogdanow-ich, 1952, 1960; Pflum and Frerichs, 1976). Most of the available data on deformities were sum-marized by Boltovskoy and Wright (1976), Haynes (1981), and Boltovskoy *et al.* (1991), who noted that deformities may be attributed to mechanical damage or environmental stress. but concluded that there is no consensus as to the underlying causes of most deformities. Deformed tests of Foraminifera have been reported from areas contaminated by heavy

Table 13.1 Pollution tolerant species and the environments in which they have been studied.

Species	Coastal zone	Bay and harbor	Estuary	Lagoon
Ammobaculites crassus	+			
A. salsus		+		+
Ammomarginulina fluvialis			+	
Eggerella advena	+	+	+	
Eggerelloides scabrus		+		
Miliammina earlandi?				+
M. fusca	+	+		
Reophax arctica	+			
Spiroplectammina biformis			+	
Trochammina inflata			+	
T. pacifica	+	+		
Ammonia annectens	+			
A. beccarii	+	+		
A. caspica	+			
A. dentata	+			
A. sobrina	+			
A. tepida	+	+		+
Ammonia sp.			+	
Amphistegina lobifera	+			
Bolivina vaughani	+			
Buccella frigida	+	+	+	
Bulimina marginata denudata	+			
B. striata	+			
B. subornata	+			
Buliminella elegantissima	+	+		
Cibicides aknerianus	+			
C. advenum	+			
Cribroelphidium translucens				+
Discorbis columbiensis	+			
Elphidium articulatum	+			
E. bartletti	+			
E. caspicum (=gunteri)	+			
E. clavatum/incertum group		+	+	
Elphidium excavatum	+	+		
E. lidoense	+			
E. margaritaceum			+	
E. norvangi	+			
E. orbiculare		+		
E. poeyanum	+			
E. translucens	+			
Florilus boueanum (=Nonion boueanum)	+			
F. grateloupi (=Nonion grateloupi)	+			
F. scaphus	+	+		
Fursenkoina pontoni	+	+		
Haynesina depressula			+	
Martinottiella communis	+			
Miliolinella subrotunda	+			
Protelphidium paralium (=Haynesina germanica)	+			
Pseudotriloculina subgranulata	+			
Quinqueloculina rhodiensis		+		+
Q. seminulum	+	+		
Rutherfordoides cornuta	+			
Spiroloculina excavata	+			
Stainforthia fusiformis			+	
Triloculina brevidentata		+		
T. marioni	+			
Uvigerina dirupta	+			
U. peregrina	+			

metals, domestic sewage, and various chemicals, including liquid hydrocarbons. See Boltovskoy *et al.* (1991), Alve (1995a), Yanko *et al.* (1998) for detailed reviews of deformities and their probable reasons. Examples of deformed tests from polluted environments can be seen in Fig. 13.2.

Measures of deformity rely on the kind, degree, frequency, and species-specificity of deformity, but the frequency is the easiest measure to quantify. The percentage of deformed Foraminifera can increase dramatically in polluted areas (e.g. Lidz, 1965) where Foraminifera display a wide variety of deformities, including extreme compression, double apertures, twisted coiling, aberrant chamber shape, and protuberances. Various other workers have catalogued similar lists of deformities, but the genesis of specific deformities is often an unresolved matter. Some deformities undoubtedly result from weak calcification or subsequent damage to areas that are weakly calcified. Other deformities (e.g. twisted keels, distortion of equatorial plane) may result from repair and overgrowth by subsequent whorls that cover such damage, resulting in distortion of the normal shell geometry (Röttger and Hallock, 1982; Wetmore, 1998). Thus, deformities that have quite different appearances may have the same underlying physiological cause. Other deformities (e.g. multiple apertures or twinning) are clearly different in nature and may be attributable to differing responses to different toxins. Yanko *et al.* (1995), using sulfaflavine fluorescence and chlortetracycline fluorescence, were able to distinguish morphological deformities caused by mechanical damage from those caused by pathological morphogenesis.

Compared with other pollutants, it appears that trace metals have the most conspicuous deleterious effect upon Foraminifera. Like many other kinds of pollutants, heavy metals often cause reduced population density and diversity, and stunting of tests, but increased frequency of deformed tests is a common aspect of virtually all studies of heavy metal toxicity. Yanko *et al.* (1998) report that at least 30% (65 species from 20 calcareous families and one agglutinated family) of all foraminiferal specimens living on the northern Israeli continental shelf exhibited one of 11 distinct types of morphological deformity in their tests. High proportions of deformed tests in living Foraminifera (up to 10% of the entire assemblage) were also found at all sites showing high metal concentrations in the Goro Lagoon, Italy. This contrasts with observations of 1 % or fewer deformed specimens in natural populations. The types of deformity include: abnormal coiling, aberrant chamber shape and size, poor development of the last whorl, twisted chamber arrangement, supernumerary chambers, protuberances, multiple apertures, irregular keel, twinning, lateral asymmetry, and lack of ornamentation (Coccioni *et al.*, 1997). A similar pattern was found in Sorfjord, Western Norway (Alve, 1991a). and in Southampton Water, southern England (Sharifi *et al.*, 1991). Deformed Foraminifera are represented among the porcelaneous, hyaline, and agglutinated suborders, among various modes of life (epifaunal, infaunal, attached, epiphytic, symbiotic, mud-dwelling, sand-dwelling), and among different morphotypes (milioline, trochospiral, planispiral, flattened, etc.) (Setty and Nigam, 1980; Banerji, 1989; Vénec-Peyré, 1981). Thus, morphological deformities do not show differential

Figure 13.2 Examples of test deformities in live Foraminifera found in Haifa Bay region, Israeli shelf, eastern Mediterranean. 1, *Eggerella advena* (Cushman), specimen with twisted chamber arrangement; 2, *Adelosina pulchella* d'Orbigny, specimen with twisted chamber arrangement of the first whorl and aberrant chamber shape; 3, *Nonionella atlantica* Cushman, specimen with aberrant chamber shape and size; 4–6, *Ammonia compacta* Hofker, specimens with aberrant shape of the last three chambers (4), twisting of the test (5), and non-development of test (6); 7–9, *Ammonia tepida* (Cushman), anomalous protuberance on dorsal side (7), twisting of the entire side (8), and twinning of two specimens by ventral side (9); 10, *Adelosina intricata* (Terquem), specimen with wrong coiling, twisted chamber arrangement, aberrant chamber shape, and double aperture; 11, *Vertebralina striata* d'Orbigny, specimen with additional chamber, and aberrant shape of chambers and aperture; 12, *Peneroplis planatus* (Fichtel and Moll), twinning of two specimens; 13, *Triloculina marioni* Schlumberger, severely deformed specimen; 14, *Cycloforina villafranca* (J. and Y.Le Calvez), severely deformed specimen; 15, *Pararotalia spinigera* (Le Calvez), twinning of two specimens by dorsal side.
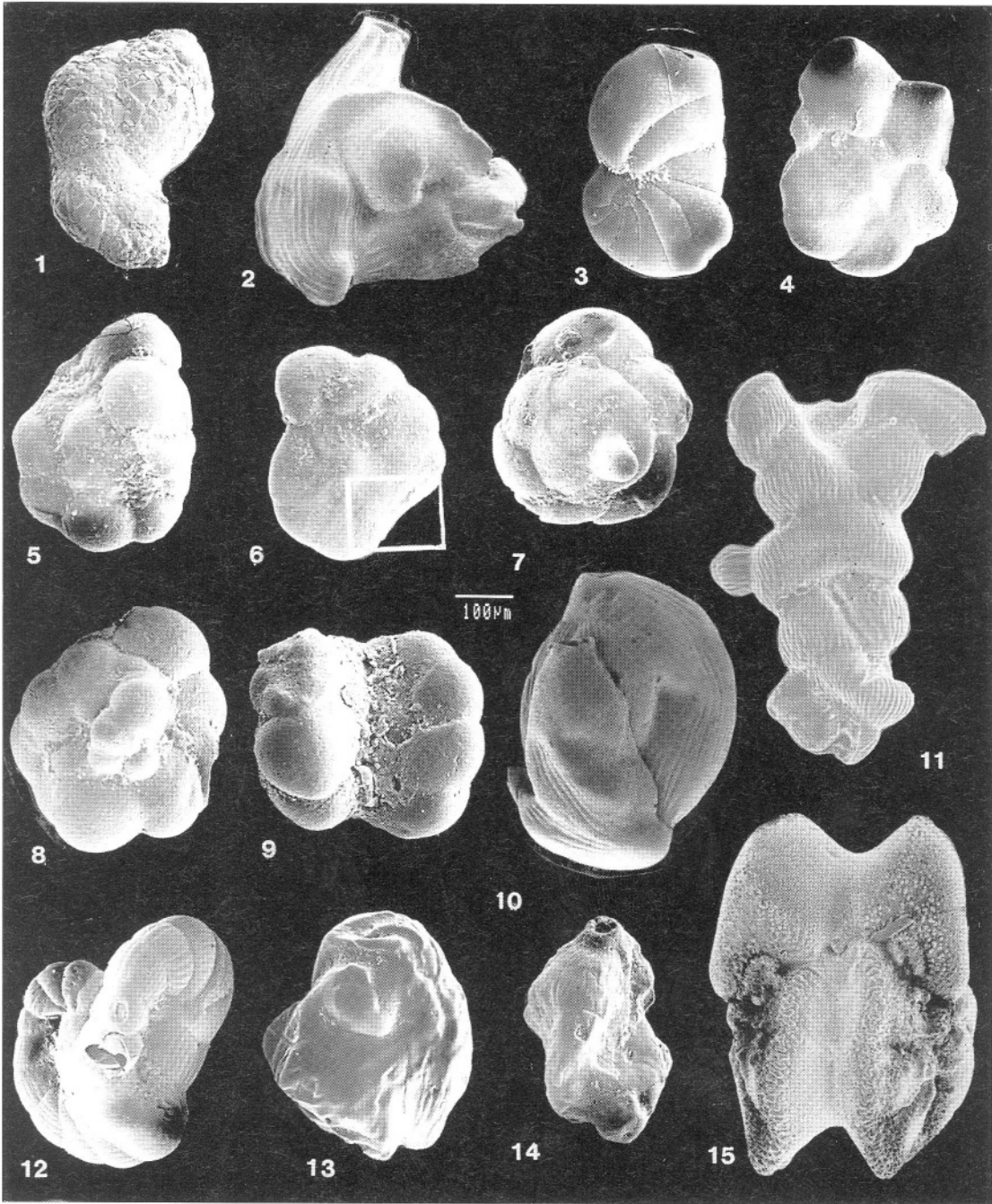
representation based on taxonomic affinity, feeding strategy, or test morphology.

There are indications, however, that some types of environmental stress may cause species-specific deformity. For example, *Adelosina cliarensis* exhibits increased frequency of deformation in response to low salinity, while *Amphistegina lobifera* appears to show an increased incidence of deformity in response to increased Cd concentrations, *Cibicides advenum* seems responsive to Cr, and *Pseudotriloculina subgranulata* to Ti.

High frequencies of test deformity of living benthic Foraminifera are generally regarded to be sensitive *in situ* indicators of marine pollution by heavy metals. However, the biochemical and crystallographic mechanisms of the development of such deformities remain to be studied by culture experiments under controlled conditions and known heavy metal concentrations.

13.3.2.2   Wall texture of deformed tests

The study of the wall texture of abnormal tests, as a possible explanation of deformation related to biomineralization processes, is a new research domain. Geslin *et al.* (1998) have studied ultrastructural deformation in the genus *Ammonia* using scanning electron micrographs. Abnormalities consistently observed in the walls of these deformed tests involve either disorganization of the wall texture due to changes in crystallite arrangement and orientation (Debenay *et al.,* 1996), or the presence of interlamellar cavities.

Normal tests of *Ammonia tepida* are made of crystallites arranged in elongate calcitic elements normal to the wall. These elements are roughly continuous from one lamella to the other. In places, large cleaved crystals may form, with cleavages regularly oblique to the test surface. In deformed tests, calcitic elements may be oriented irregularly. This 'crystalline disorganization' may result from introduction of alien elements in the crystalline framework during calcification; Sharifi *et al.* (1991) showed that the deformed tests contain a high proportion of metals such as Cu and Zn, and Yanko and

Kronfeld (1993) found that the deformed tests exhibit an increased Mg/Ca ratio. Interlamellar empty cavities were also observed in some deformed specimens, even when crystalline organization was normal. Such cavities were reported by Vénec-Peyré (1981). On a different scale, these cavities may be compared with the interlamellar cavities formed in the abnormal shells of some bivalves, particularly of the oyster *Crassostrea gigas* by the hypersecretion of a jelly (Héral *et al.*, 1981, *in* Alzieu, 1991). The organic process leading to these secretions may result from a metabolic perturbation.

Early exploratory research has led to several hypotheses regarding anthropogenic causes of morphological deformity in Foraminifera. Four general explanations are suggested. Test deformity may be caused by (1) direct physiological or metabolic interference of heavy metal pollutants; (2) pollution-induced changes in physical and chemical environmental parameters indirectly resulting in pathological morphogenesis; (3) poor nutritional state in Foraminifera, perhaps due to the effect of habitat damage on other organisms in the food web; and (4) anthropogenic intensification of the normal (low-level) background causes of test deformity seen in natural populations. It is clear that in the near future, controlled laboratory experimentation will play a central role in assessing these hypotheses before a full understanding of the relationship between foraminiferal test deformity and pollution is developed.

13.3.2.3   Morphometry and cytology

Morphometric and cytological studies of normal and abnormal *Amphistegina lobifera* tests from the north Israeli coast have been undertaken to distinguish and describe tests with varying morphologies and to understand the pathogenesis of abnormalities (Yanko, ed., 1995; Yanko *et al.*, 1995). Although only a single index of deformity was used, the deformed and undeformed populations of specimens were statistically distinct. A normal test of *A. lobifera* may be described as a bi-convex lens. Several categories of shell deformation were identified that

caused distortion of that natural shape. These deformities include dorso-ventral asymmetry, loss of a segment of the peripheral margin, lateral asymmetry, irregular keel, abnormal aperture, and various other miscellaneous deformations.

Of these types of deformation, only one (loss of a segment of the periphery) was associated with an increase of sulfaflavine fluorescence (which measures protein content in the shell), and only in the immediate area of the defect. These data indicate that segment loss may have a different pathogenesis than other abnormalities; namely, segment loss is likely to be a result of shell damage and regeneration. During regeneration, especially in the early stages of this process, the protein/Ca ratio increases in the new part of the shell, probably due to intensification of protein synthesis. This suggests that the other remaining test deformities may be the result of pathological morphogenesis rather than of damage and subsequent repair. While the cytoskeleton may play an important role in normal and pathological morphogenesis in metazoan and protozoan cells (Albrecht-Buchler, 1977; Anderheide *et al*., 1977; Brandle and Gabbiani, 1983), the synthesis of shell-building proteins and their calcification is not apparently involved in pathological morphogenesis of the shell.

It has been proposed that trace metal pollutants weaken the Foraminifera and enable bacteria to attack their cytoplasm (Alve, 1991a). This is readily apparent from stunting of the test and morphological deformities (Alve, 1991a; Yanko *et al*., 1994c), and is probably related to the fact that heavy metals (e.g. Cd) dramatically increase membrane permeability and mortality of Foraminifera (Bresler and Yanko, 1995b).

The extent to which Foraminifera are protected from pollutants is also a factor deserving some attention, since it will increase our understanding of the factors controlling distribution patterns. Research in this area suggests several potential biological defense systems; they include (1) a mucopolysaccharide coat that forms an additional diffusion barrier and binds some cationic xenobiotics; (2) a membrane carrier-mediated transport system for elimination of anionic xenobiotics from the cytoplasm; (3) active intralysosomal accumulation and isolation of some cationic xenobiotics; and (4) haloperoxidases that transform xenobiotics to their haloderivatives (Bresler and Yanko, 1995a).

13.3.3 Pyritization

Pyritization has been found in living Foraminifera as well as in fossils, though the percentage of pyritized tests is significantly higher in empty tests than in tests with protoplasm. Two taxa, *Ammonia tepida* and *Porosononion martkobi ponticus*, are regularly pyritized in the Black Sea (Yanko and Kravchuk, 1992). The degree of pyritization of living individual tests ranged from 2% to 50%, and sometimes higher. The reasons for pyritization in marine sediments and foraminiferal tests are not completely clear. Some have suggested that it is connected to chemical processes that result in metabolization of organic matter under anaerobic conditions by sulfate-reducing bacteria, diffusion of sulfide into sediments, or concentration and reactivity of the iron minerals. The process is clearly connected to the redox conditions and the concentration of H_2S High percentages of pyritized foraminiferal tests have also been found in oxygen-deficient polluted areas. The frequency of pyritized foraminiferal tests may therefore show promise as a parameter to indicate certain types of polluted environments.

13.3.4 Asexual reproduction

Foraminifera can reproduce by both sexual and asexual modes (see chapter 3). Fursenko (1978) has suggested that under stressful conditions Foraminifera preferentially revert to the asexual part of their life cycle. The causes of stress can include, for example, hyposalinity (Yanko, 1989, 1990a) and decreased nutrient levels (Fursenko, 1978). Trace metal pollution may also stress the Foraminifera by causing cellular injury and subsequently lead to a decrease in the efficiency of metabolism and protein synthesis (Ganote and Vander Heide, 1987). Life-supporting metabolic

systems then function at a reduced level (Bas-erga, 1985) and the energetic cost of meiosis may be too great compared to mitosis (Effrussi and Farber, 1975). This hypothesis is supported by the observation that megalospheric forms of *Ammonia tepida* are strongly dominant where toxic trace metal pollution is prevalent (Yanko *et al*., 1994c). If a high percentage of megalospheric forms is characteristic of stressed environments, then this characteristic, in conjunction with other indices, may prove a useful tool in monitoring marine pollution.

13.3.5 Chemistry of deformed tests

Several studies have been undertaken to determine whether elevated concentrations of heavy metals in sediments affect test chemistry and morphology (Sharifi, 1991; Sharifi *et al*., 1991; Yanko and Kronfeld, 1993). The primary result of these studies is that deformed Foraminifera show elevated Mg/Ca ratios when compared to non-deformed Foraminifera, especially in severely polluted areas. Deformed tests of all studied species are characterized by increased Mg concentration in their tests, so it is unlikely that this is a species-specific effect. Several hypotheses might be suggested to explain this observation: One is that heavy metals directly affect the crystal structure of the calcite shell, or foraminiferal cytoskeleton, or both. Another is that heavy-metal toxicity affects foraminiferal metabolism in ways that influence Mg/Ca ratios indirectly during calcification. A third is that other pollution-associated environmental effects mediate Mg/Ca ratios. The process of shell calcification includes the development of a glycoprotein organic matrix, *anlagen*, followed by mineralization by Ca^{++} and bicarbonate in the glycoprotein centers (Fursenko, 1978; Hemleben *et al*., 1977). Other cations (e.g. Ba and Cd) can also be included in the crystal structure of the test (Fritz *et al*., 1992; Lea and Boyle, 1989). It is likely that the biochemical transport systems and sites for the Ca^{++} binding cannot easily distinguish between these ions. Trace metals may also affect the ratio of the major element (Ca and Mg) uptake (Yanko and Kronfeld.

1992, 1993). Any of these factors may affect the crystal structure and cause strong morphological deformities in foraminiferal tests. The cytoskeleton, which defines the shape of the organism, may also be affected by heavy metals as has already been shown for the ciliates (Anderheide *et al*., 1977).

13.3.6 Cytology

Organisms have numerous adaptive biological defense mechanisms that protect them against foreign chemicals in their environment (xenobiotics). If these anti-xenobiotic defense mechanisms fail to protect the organisms, the results will be expressed as a pathological disruption of biological structures on various molecular to ecosystemic levels of hierarchical organization. Even if the biological effect of a single toxic compound is simple and well-understood in isolation, the behavior of the same pollutant in complex natural ecosystems inevitably becomes complicated and nonlinear. Understanding this complexity will require the application of cross-disciplinary new methodologies. An example is the use of fluorescent microscopy and fluorometry to study the cytoplasmic response of Foraminifera to pollution (Bresler and Yanko 1994b. 1995a,b; Bresler *et al*., 1995, 1996a, 1997). If the 'health' of foraminiferal species can be objectively characterized by biological parameters (e.g. biophysical, morphophysiological, histopathological, cytogenetic, physiological, and biochemical bioindicators) and measured using vital/supravital microfluorometry, then changes in these parameters can be used as early response indicators of exposure to environmental pollutants. Fluorescent probes allow the scientist to visualize and examine quantitatively the structural and chemical organization of cells and their organelles, including specific functions, such as genetic activity or carrier-mediated transport and metabolism, with great precision and sensitivity. Such techniques would enable us to: (1) assess the interaction of pollutant and antixenobiotic biological defense mechanisms; (2) determine the effect of pollutants on structures and metabolic reactions; and (3) predict

the future behavior of a given species under polluted conditions. Accordingly, the following objectives can be set: (1) to examine the health of pollution-tolerant species (e.g. *Ammonia tepida*) under natural conditions; (2) to examine the response of the these species to a spectrum of natural conditions (varying temperature, salinity, concentrations of natural xenobiotics, and dissolved organic matter); and (3) then to examine how varying levels of a contaminant can modify these natural responses to yield pathological and pre-pathological changes that could serve as indicators of the degree of pollution. As with other organisms, Foraminifera have a number of defense mechanisms that can protect them against xenobiotics (Bresler and Yanko, 1995a; Yanko *et al.*, 1994a). For example, carrier-mediated System of Active Transport of Organic Anionic xenobiotics (SATOA) eliminates many endo- and xenobiotics from the cytoplasm. Therefore, the quantitative study of SATOA in Foraminifera can be used for early ecological monitoring and prediction of the impact of anthropogenic pollution on ecosystems, as well as for retrospective analysis of paleoecosystems.

All these parameters can be examined by the use of biophysical, cytophysiological, biochemical, and morphological vital microfluorometrical techniques, including fluorescent analysis at the microscopic level (Bresler and Nikifirov, 1981). New devices for vital biophysical studies, especially contact fluorescent microscopes and microspectrofluorometers, can be used to examine, *in situ*, various biological parameters at the molecular and cellular levels and their distribution at higher levels of biological organization. The main parameters (and methods) of interest are the following:

(1) Monitoring of respiration and metabolic state of mitochondria by measurement of inherent blue fluorescence of reduced nicotinamide adenine dinucleotide (NAD) and green fluorescence of oxidized flavine adenine dinucleotide (FAD) in living cells and tissues.

(2) Detection of conformation changes of tryptophan-containing proteins by inherent ultraviolet (UV) fluorescence. For example, inherent UV fluorescence of some tryptophan-

containing proteins has been used to study their binding with copper ions (Engel and Breawer, 1987; Bresler and Yanko, 1995b).

(3) Determination of enzyme activity *in situ* by using corresponding fluorogenic substrates and microfluorometry. The activity of some intracellular enzymes also may be sensitive indicators of cell viability (Bresler and Yanko, 1994).

(4) The study of activity and kinetics of transport systems used for the elimination of xenobiotics, such as the system of active transport of organic anions (SATOA) and multixenobiotic resistance (MXR) transporter, by using marker fluorescent substrates of SATOA or MXR, specific inhibitors, and microfluorometry (Bresler *et al.*, 1975, 1979, 1983, 1985, 1990; Bresler and Fishelson, 1994; Bresler and Yanko, 1995a,b; Fishelson *et al.*, 1996).

(5) The examination of cell cycle phases, functional state of nuclear chromatin, DNA concentration and aneuploidy (DNA variability in individual nuclei), and DNA damage by using versatile probe acridine orange (AO) and two-wavelength microfluorometry (Darzynkiewicz 1990; Fishelson *et al.*, 1996).

(6) Cell chemistry, i.e. content of DNA, RNA, proteins, mucopolysaccharides and carbohydrates, lipids, thiol groups, and intra- and extracellular ions (especially calcium), can be studied with special fluorescent probes and microfluorometry.

(7) Permeability of plasma membranes, epithelial layers, or histohematic barriers can be examined by using various fluorescent markers, especially fluorescein, and microfluorometry (Bresler and Fishelson, 1994; Bresler and Yanko 1995).

(8) Cell viability can be studied by using vital staining with AO or neutral red, fluorescent microscopy of their intralysomal, and microfluorometry (Bresler and Fishelson 1994; Bresler and Yanko, 1995b). This approach is often used in ecotoxicology to distinguish living and dead cells and tissues.

(9) Cell and tissue morphology and pathomorphology can be examined by using contact fluorescent microscopy and epi-microscopy to detect early signs of pathology, to identify the

type of pathology, and to identify specific target organelles, cells, and organs. In the field of ecology and ecotoxicology of aquatic animals, especially invertebrates, environmental pathology is clearly underdeveloped as compared with mammalian ecology and ecotoxicology (Hinton *et al.*, 1992; Cotran *et al.*, 1989; Wester and Vos, 1994). The field of foraminiferal pathology lags even farther behind. Contact epi-microscopy in incident light and contact fluorescent microscopy are promising tools for aqueous ecotoxicology (Bresler and Fishelson, 1994; Bresler and Yanko, 1994a,b, 1995a,b; Fishelson *et al.*, 1996).

(10) Cytological indications of genotoxicity and clastogenicity, especially micronucleus tests employing contact fluorescent microscopy, contact epi-microscopy, or conventional microscopy are the most universally useful and sensitive methods for detecting environmental genotoxicity produced by chemical or physical factors (Fishelson *et al.*, 1996).

13.4   CONCLUSIONS

An environmental event could be characteristically transient, resulting in varying rates of foraminiferal recovery that may range from rapid species-specific ecological opportunism to more delayed recovery and even to permanent local extinction. Even when an environmental insult is continuous rather than transient, some species may respond by showing a positive preference for the new conditions, others by showing varying levels of tolerance or intolerance. These kinds of behavior are reflected in shifting patterns of foraminiferal dominance and abundance that are not well understood – partly because the time scale of environmental insult is rarely well documented, partly because foraminiferal responses are often complex and nonlinear, and partly because biotic patterns often covary with natural and anthropogenic environmental gradients that can be difficult to distinguish. Although these questions are posed here in the specific context of foraminiferal response to pollutants, it is unavoidable that they will touch on more fundamental issues relating to the nature

of opportunism, and the meaning of ecological specialization or generalization in other taxa. This is one area in which basic scientific research on Foraminifera is inseparable from the otherwise pragmatic issues of detection, monitoring, and remediation of pollution.

At the organismal level of analysis, we find that ecophenotypic responses among Foraminifera can range from test deformity to subtle changes in size and age distribution. Some of these responses are almost certainly pathological and species-specific, and some may be toxin specific as well. Some biological causes of morphological test deformity may be fundamentally genetic, or due to disruption of normal metabolic processes such as calcification, leading to weak, damage-prone test walls. Controlled laboratory experimentation and detailed cytological studies will certainly play a major role in resolving some of these questions.

Coal miners once used canaries to warn them of toxic atmospheric conditions; they did so without any understanding of the cellular biology of canaries. One might suppose that, as a purely practical expedient, we could take similar advantage of the Foraminifera as environmental indicators without understanding the underlying reasons for their ecological responses, but this is not the case. Foraminifera not only behave differently in different circumstances, but indicator species are rarely so obliging as to conveniently and consistently manifest themselves wherever they are needed to assist in our efforts at monitoring and detection of pollution. Thus, not only are species unique, but virtually every locality is unique as well, and generalization becomes difficult under the best of circumstances. For this reason, we are unlikely to identify species that have the simple, straightforward utility of the canary; instead, we will have to rely on a deeper understanding of biological and ecological processes if the Foraminifera are to achieve their full potential as environmental indicators.

13.5   ACKNOWLEDGMENTS

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PART III:
GEOCHEMISTRY
OF SHELLS

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14

Stable oxygen and carbon isotopes in foraminiferal carbonate shells

Eelco J. Rohling and Steve Cooke

14.1 INTRODUCTION

Analyses of stable oxygen and carbon isotopes from foraminiferal shells have played a pivotal role in paleoceanography since the pioneering efforts of Emiliani (1955) who, building on work of Urey (1947), McCrea (1950) and Epstein *et al.* (1953), interpreted the isotopic record from deep-sea cores as a proxy for a series of Pleistocene climate/temperature cycles. Cores from various locations in the Atlantic, Pacific and Indian Oceans provided isotopic records showing similar trends. Shackleton and Opdyke (1973) correlated the isotope stratigraphy with magnetic stratigraphy, dating 22 recognizable isotopic stages. Analyzing not only records for planktonic Foraminifera, but also for deep-sea benthic Foraminifera – which avoid the 'noise' imposed by short-term temperature and salinity fluctuations – Shackleton and Opdyke (1973) demonstrated that the $\delta^{18}O$ signal predominantly reflects fluctuations in global ice volume, while temperature plays a secondary role. This discovery started widespread use of $\delta^{18}O$ records in global stratigraphic correlations (e.g.

Imbrie *et al.*, 1984b, 1992). Turning attention to downcore $\delta^{13}C$ variations, Shackleton (1977a) showed their potential significance in studying water mass movement and paleoproductivity, and postulated a connection between climatically induced changes in the terrestrial biosphere with observed carbonate dissolution cycles and the flux of dissolved CO_2 in the oceans.

Detailed age control for $\delta^{18}O$ records around the world has been established by 'stacking' a great number of records in various ways to form a global curve for comparison with models of astronomically forced ice volume fluctuations (Imbrie *et al.*, 1984b; Pisias *et al.*, 1984; Prell *et al.*, 1986; Martinson *et al.*, 1987; Imbrie *et al.*, 1992). Consequently, oxygen isotope stratigraphy has become not only a global correlation tool, but also an established dating tool (Fig. 14.1). In addition, the primary ice-volume control on (benthic) oxygen isotope records has led to their use in the approximation of past sea level variations after calibration with studies of other sea level indicators (e.g. Chappell and Shackleton, 1986; Shackleton, 1987; Bard *et al.*, 1996; Linsley *et al.*, 1996; Rohling *et al.*, 1998).
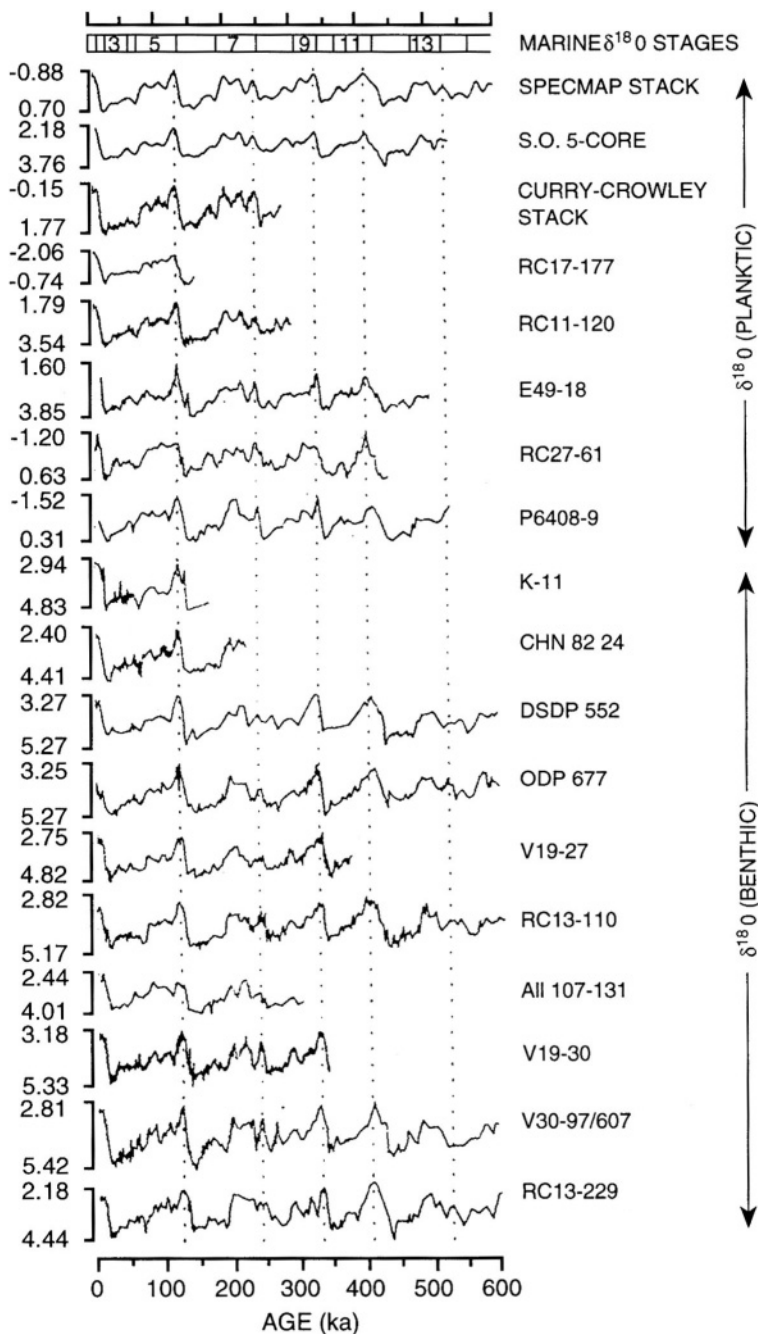
Figure 14.1 Overview of Quaternary oxygen isotope records from various locations, illustrating their potential in global correlation and dating through recognition of Marine Isotope Stages and a standard chronology (after Imbrie *et al.*, 1992). For location map and further details about the cores, see Imbrie *et al.* (1992).

There are three stable isotopes of oxygen: ^{16}O, ^{17}O, and ^{18}O, with relative natural abundances of 99.76%, 0.04%, and 0.20%, respectively. Research on oxygen isotopic ratios normally concerns $^{18}O/^{16}O$ ratios. There are two stable isotopes of carbon: ^{12}C (98.89%) and ^{13}C (1.11%). Basically, molecules consisting of light isotopes react more easily than those consisting of heavy isotopes. Partitioning of isotopes between substances is called fractionation. If R_A and R_B are the heavy/light ratios for any two isotopes (e.g. $^{18}O/^{16}O$) in exchanging chemical compounds A and B, then the fractionation factor is defined as $\alpha_{A-B} = R_A/R_B$. Fractionation mainly results from isotopic exchange reactions and kinetic effects. The former are also known as 'equilibrium isotope fractionation' processes and are essentially temperature dependent. Kinetic effects cause deviations from equilibrium due to different rates of reaction for the various isotopic species. Important kinetic effects are associated with diffusion. Detailed accounts on the physico-chemical behavior of isotopes, and on equilibrium and kinetic fractionation may be obtained from Craig *et al.* (1963), Craig and Gordon (1965), Ehhalt and Knott (1965), Merlivat (1978), Merlivat and Jouzel (1979), Garlick (1974), Stewart (1975), Gonfiantini (1986), Knox *et al.* (1992), Hoefs (1997), and references therein.

While absolute abundances of minor isotopes (such as ^{18}O and ^{13}C) cannot be determined accurately, it is still possible to get quantitative estimates by comparing results for a known external standard (*std*) with those for the unknown sample (*sam*). These differences in isotope ratios are defined as: $\delta_{sam}\text{‰} = 10^3 \times (R_{sam} - R_{std})/R_{std}$. A positive δ value indicates enrichment in the heavy isotope, relative to the standard, and conversely, depletion is shown by a negative δ value.

Stable isotopes of oxygen and carbon in carbonates are analyzed by mass spectrometric determination of the mass ratios of carbon dioxide (CO_2) obtained from the sample by reaction of carbonate with phosphoric acid: $CaCO_3 + H_3PO_4 \rightleftharpoons CaHPO_4 + CO_2 + H_2O$ (see McCrea, 1950), with reference to a standard CO_2

of known isotopic composition. The standard for both oxygen and carbon in carbonates is referred to as PDB (Pee Dee Belemnite), having $\delta^{18}O = 0$ and $\delta^{13}C = 0$, by definition (Epstein *et al.,* 1953). The PDB standard (no longer available) is a guard from *Belemnitella americana,* a Cretaceous belemnite from the Pee Dee Formation in North Carolina, U.S.A.

Various international standards have been run against PDB for comparative purposes. Two are commonly used and distributed by the National Institute of Standards and Technology (NIST) in Gaithersberg, Maryland, U.S.A., and the International Atomic Energy Agency (IAEA) in Vienna, Austria. They are: (a) NBS–18 (carbonatite), for the analysis of carbonates with $\delta^{13}C$ and $\delta^{18}O$ in per mil (‰) difference from Vienna Pee Dee Belemnite (VPDB) or Vienna Standard Mean Ocean Water (VSMOW) and (b) NBS-19 (limestone), for $\delta^{13}C$ and $\delta^{18}O$ analysis of carbonates, used to define the VPDB scale (Coplen, 1988; 1994). The isotopic compositions of these reference materials, as given by NIST (1992) are listed in Table 14.1. To convert VPDB to VSMOW, use $\delta^{18}O_{VSMOW} = 1.03092 \; \delta^{18}O_{VPDB} + 30.92$ (NIST, 1992; also Coplen *et al.,* 1983).

Some further corrections are needed. The Isotope Ratio Mass Spectrometer (IRMS) measures two ratios: mass $45/44$ ($= \delta 45$), and mass $46/44$ ($= \delta 46$). The final results required are $\delta^{13}C$ and $\delta^{18}O$ relative to VPDB, and a correction for the ^{17}O contribution is applied. A further complication results from fractionation between $\delta^{18}O$ in carbonate and in the CO_2 produced by reaction with phosphoric acid, which mainly depends on the temperature at which that reaction takes place. The analyzed $\delta^{13}C$ is corrected for this effect. The correction is determined by experiment to suit the technique used to gener-

Table 14.1 Isotopic compositions (in ‰) of reference materials (National Institute of Standards and Technology, 1992).

	$\delta^{13}C_{VPDB}$	$\delta^{18}O_{VPDB}$	$\delta^{18}O_{VSMOW}$
NBS-18	−5.04	−23.05	17.66
NBS-19	1.95	−2.20	28.65

ate CO_2. There is no similar fractionation effect on carbon (Swart *et al.,* 1991).

Major contributions of $\delta^{18}O$ and $\delta^{13}C$ to paleoceanography in the applied sense are captured in Emiliani (1955), Shackleton and Opdyke (1973), Shackleton and Kennett (1975), Savin *et al.* (1975), Shackleton (1977a,b), Keigwin (1979), Savin *et al.* (1981), Duplessy *et al.* (1984), Imbrie *et al.* (1984b), Vergnaud-Grazzini (1985), Chappell and Shackleton (1986), Kennett (1986), Berger and Labeyrie (1987), Shackleton (1987), Woodruff and Savin (1989), Savin and Woodruff (1990), Imbrie *et al.* (1992), Zachos *et al.* (1994), and Sarnthein *et al.* (1995), and are reviewed in, for example, Haq (1984), Kennett (1982), Crowley and North (1991), Frakes *et al.* (1992), and Broecker (1995). We, instead, review the fundamental controls on $\delta^{18}O$ (section 14.2) and $\delta^{13}C$ (section 14.3) in foraminiferal carbonate. Several have only recently been discovered, and we aim to offer an overview, with pointers to the relevant specialist literature. Since isotope ratios in carbonates to a great extent reflect those in the ambient water, the following sections first evaluate the processes governing $\delta^{18}O$ and $\delta^{13}C$ in seawater, and then those causing fractionation during carbonate formation. To facilitate evaluation of the paleoceanographic value of $\delta^{18}O$ and $\delta^{13}C$, section 14.4 summarizes the various controls and highlights analytical strategies to minimize complications.

14.2   OXYGEN ISOTOPES

14.2.1   Oxygen isotope ratios in seawater

Seawater $\delta^{18}O$ is intimately linked with the hydrological cycle, consisting of evaporation, atmospheric vapor transport, and return of freshwater to the ocean via precipitation and runoff, or iceberg melting. Furthermore, long-term freshwater storage in aquifers and (especially) ice sheets significantly affects seawater $\delta^{18}O$ (Fig. 14.2). Seasonal sea ice formation and melting impose strong local variability. Finally, the spatial $\delta^{18}O$ distribution in the oceans depends on advection and mixing of water masses from different source regions.

14.2.1.1   Evaporation

Isotopic exchange at the sea-air interface is given by $H_2^{16}O_{liquid} + H_2^{18}O_{vapor} \rightleftharpoons H_2^{18}O_{liquid} + H_2^{16}O_{vapor}$. Because of higher vapor pressures, the lighter molecular species are preferentially enriched in the vapor phase. The fractionation factor for equilibrium exchange is $\alpha_{l-v} = [^{18}O/^{16}O]_l/[^{18}O/^{16}O]_v$. The most commonly used relationship between α_{l-v} and temperature is $\alpha_{l-v} = \exp\{(1.137T^2) \times 10^3 - (0.4156T^{-1}) - 2.0667 \times 10^{-3}\}$, with T in Kelvin, illustrating a decrease in fractionation with increasing temperature (Majoube, 1971). The $\delta^{18}O$ difference between seawater and vapor then equals $10^3 \ln(\alpha)$‰, which at 20°C amounts to 9.8‰. The equilibrium enrichment factor ε equals $\alpha - 1$, and is reported as a ‰ value.

In addition, there is kinetic fractionation during molecular diffusion within the boundary layer between the water-air interface and the fully turbulent region where no further fractionation occurs (e.g. Craig and Gordon, 1965; Ehhalt and Knott, 1965; Stewart, 1975; Merlivat and Jouzel, 1979; Gonfiantini, 1986). The magnitude of kinetic enrichment depends on relative air humidity in the turbulent region, changing by about 0.7‰ for every 5% change in relative humidity (Gonfiantini, 1986), and to a lesser extent on roughness of the water-atmosphere interface, with a threshold around near-surface mean wind speeds of $7\,m\,s^{-1}$ (Merlivat and Jouzel, 1979). In exceptional settings, this roughness threshold may have been persistently exceeded in the geological past (e.g. Rohling, 1994). Finally, the $\delta^{18}O$ of newly evaporated water also depends on that of the surface water, and of the vapor already present in the turbulent region of the atmosphere (full set of equations in Gonfiantini, 1986).

Preferential uptake of lighter isotopes during evaporation increases $\delta^{18}O$ values in the remaining surface waters. Because factors such as relative humidity are difficult to assess for the geological past, geological studies best consider
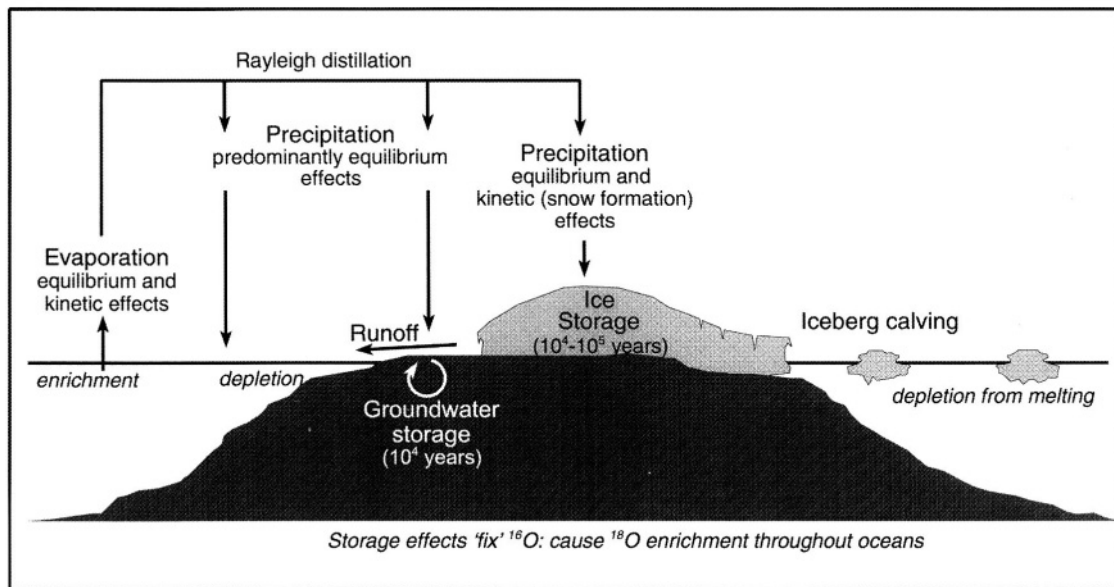
Figure 14.2 Schematic presentation of the influences of the hydrological cycle on oxygen isotope ratios. Effects on seawater are described in italics.

equilibrium fractionation and a constant value for kinetic fractionation, using likely ranges of change in kinetic fractionation to determine confidence intervals.

14.2.1.2 Precipitation and atmospheric vapor transport

Fractionation during condensation is basically the same as during evaporation, but acts in opposite sense. Normally, kinetic effects are negligible, so that droplets are near equilibrium with atmospheric vapor (Ehhalt and Knott, 1965; Stewart, 1975). The isotopic compositions of original vapor, precipitation, and remaining atmospheric vapor are related through basic Rayleigh distillation (Dansgaard, 1964; Garlick, 1974). Consequently, the first precipitation has a similar $\delta^{18}O$ to the original seawater, while longer pathways from the source region, with progressively more rain out, cause increasing depletion in vapor and associated new precipitation (Fig. 14.3). Successive condensations during transport towards colder regions cause a quasi-linear relationship of $0.69\%_0$ C^{-1} between $\delta^{18}O$ of precipitation and temperature (valid between

-40 and $+15°C$). Consequently, high latitude precipitation is significantly more depleted than that in the tropics (reaching $-60\%_0$ or less in Antarctica; Lorius, 1983; Rozanski *et al.*, 1993). Above $+15°C$, the so-called 'amount effect' dominates, with $1.5\%_0$ depletion in the $\delta^{18}O$ of precipitation for every 100 mm increase in rainfall. For further reading, see Dansgaard (1964), Craig and Gordon (1965), Jouzel *et al.* (1975), Stewart (1975), Rozanski *et al.* (1982, 1993), Merlivat and Jouzel (1979), Joussaume and Jouzel (1993), Hoefs (1997), and Hoffmann and Heimann(1997).

Changes in $\delta^{18}O$ of precipitation affect oceanic surface waters through addition of the fresh water, either directly, or via run-off. Whereas arid areas show the evaporative surface water ^{18}O enrichment, regions in reasonable proximity to a river mouth are affected by the volumetrically weighted average isotopic composition of precipitation over the catchment basin. A high-latitude river imports freshwater with generally lower $\delta^{18}O$ values than a low- latitude river, e.g. Arctic McKenzie $\delta^{18}O \approx -20\%_0$, (pre-Aswan dam) Nile $\delta^{18}O \approx -2\%_0$, and Parana (Argen-
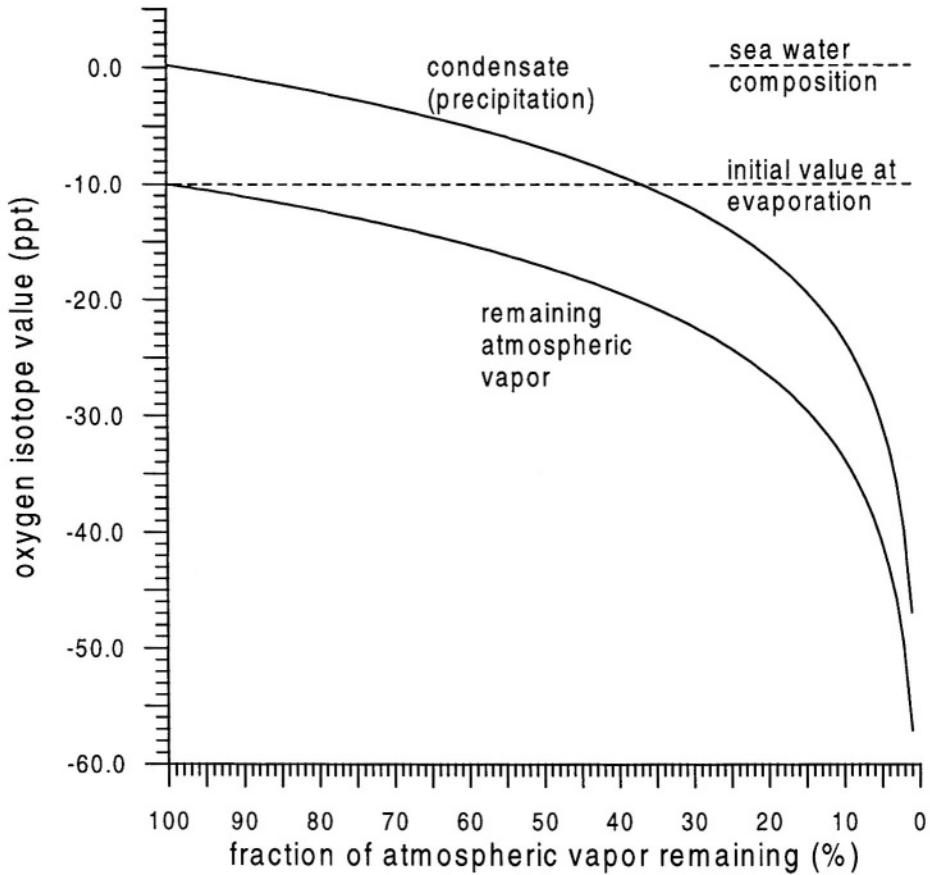
Figure 14.3 The relationships between isotope compositions of atmospheric vapor and precipitation, relative to evaporation, with an original composition of $-10‰$ and fractionation at constant temperature of $15°C$.

tina) $\delta^{18}O \approx -4‰$ (overview in Rohling and Bigg, 1998).

Long-term storage of precipitation causes two main delayed responses. Icebergs calving from continental icesheets import continental freshwater with fossil isotopic signatures. Ice cores in the Greenland and Antarctic ice sheets include ice older than 100,000 years (Lorius *et al.*, 1985; Taylor *et al.*, 1993; Grootes *et al.*, 1993; Jouzel *et al.*, 1993) to even 400,000 years (Petit *et al.*, 1997), so that the isotopic signatures of bergs from those icesheets should not be considered as a result of the modern freshwater cycle. Similarly, but less importantly, aquifers may accumulate waters as old as 35,000 years (e.g. Rozanski, 1985), and at later stages contribute to discharge.

14.2.1.3   Glacial ice-volume

Apart from delayed return of fossil signals to the ocean, long-term storage in glacial icesheets and, to a lesser extent, in major aquifers, also affect the global $\delta^{18}O$ budget. Because storage time-scales in the order of $10^4–10^5$ years exceed those of ocean ventilation (in the order of 10^3 years), the storage effects influence $\delta^{18}O$ values equally in surface and deep waters.

The most important fluctuations are related to the volume of glacial ice sheets. These are built up by high latitude precipitation at very low temperatures towards the end of the Rayleigh distillation (Fig. 14.2), and so record extremely low $\delta^{18}O$ values (Fig. 14.3). Preferential sequestration of ^{16}O in ice sheets leaves the

oceans enriched in ^{18}O. At the same time, build up of ice volume lowers global sea level. Research on $\delta^{18}O$ changes in fossil carbonate, with accurate constraint of sea level variations from fossil coral reef studies, illustrates that the relationship between sea level lowering and mean oceanic $\delta^{18}O$ increase approximates $0.012 \pm 0.001‰\,m^{-1}$ (Aharon, 1983; Labeyrie et al., 1987; Shackleton, 1987; Fairbanks, 1989). Although this relationship provides a sound working model for well matured ice sheets, the processes behind it may invoke a more nonlinear relationship for growing or recently matured icesheets (see Mix and Ruddiman, 1984).

14.2.1.4   Sea ice freezing and melting

Newly formed sea ice is $2.57 \pm 0.10‰$ enriched relative to seawater $\delta^{18}O$ (Macdonald et al., 1995). This difference imposes a distinct seasonal fluctuation associated with ice formation and melting (cf. Strain and Tan, 1993). These seasonal influences do not necessarily cancel out in the long term, since increases in surface-water salinity due to sea ice formation may lead to convection and transport of existing surface waters into the ocean interior; the replacement waters likely were not affected as much by freezing processes (Rohling and Bigg, 1998). Large errors may arise in interpretations of oxygen isotopic change near (present or past) sea-ice margins when freezing/melting effects are overlooked.

14.2.1.5   Advection

Advection and mixing of water masses from different source areas are very important for the basic $\delta^{18}O$ composition at any site. Each source area concerns a basin or region, which may be very remote from the study site, where surface waters are imprinted with a certain $\delta^{18}O$ composition by the freshwater cycle, freezing/melting of sea ice, etc. This pre-set composition behaves as a virtually conservative property for the newly formed watermass, provided this watermass does not come into contact with further $\delta^{18}O$ sinks or sources. In practice, therefore, $\delta^{18}O$ is a useful conservative tracer for watermass transport and mixing in the subsurface ocean (e.g. Weiss et al.,

1979; Fairbanks, 1982; Paren and Potter, 1984; Kipphut, 1990; Frew et al., 1995).

The $\delta^{18}O$ of a mixing endmember is a volumetrically weighted average of the $\delta^{18}O$ compositions of its components. Hence, any change in the relative proportions or isotopic compositions of the mixing components affects the basic endmember $\delta^{18}O$. Changes in $\delta^{18}O$ at any site must, therefore, be viewed within the broader context of water mass formation and mixing on basin-wide scales, instead of being ascribed purely to local changes in surface forcing (e.g. freshwater budget). Emphasizing the importance of advection, Rohling and Bigg (1998) and Schmidt (1998) called for caution when interpreting past $\delta^{18}O$ variations; after the necessary correction for ice volume effect, surface forcing processes of both local (direct) and remote (through advection mixing) origin need to be considered. This contrasts with the classical paleoceanographic interpretation that deals with local processes only.

14.2.2   Oxygen isotope ratios in foraminiferal carbonate

Equilibrium fractionations between water and the various carbonate species ($CaCO_3$, H_2CO_3, HCO_3^-, CO_3^{2-}) determine an important temperature influence on the $\delta^{18}O$ of foraminiferal carbonate. In addition, several processes cause deviations from equilibrium, both in planktonic Foraminifera (e.g. Shackleton et al., 1973; Fairbanks and Wiebe, 1980; Duplessy et al., 1981; Bouvier-Soumagnac and Duplessy, 1985) and in benthic Foraminifera (e.g. Duplessy et al., 1970; Woodruff et al., 1980; Vincent et al., 1981; Wefer and Berger, 1991).

14.2.2.1   Equilibrium fractionation.

The overall reaction for precipitation of carbonate is: $Ca^{2+} + 2HCO_3^- \rightleftharpoons CaCO_3 + CO_2 + H_2O$. Between 0 and 500°C, the equilibrium fractionation factor α_{c-w} between calcite and water changes according to $\alpha_{c-w} = \exp\{(2.78T^{-2}) \times 10^3 - 3.39 \times 10^{-3}\}$, with T in Kelvin (O'Neil et al., 1969). Recently, Kim and O'Neil (1997) showed a more detailed relationship where

the $\delta^{18}O$ change with temperature is more pronounced at low temperatures (up to $0.25‰ \, °C^{-1}$) than at higher temperatures (around $0.2‰ \, °C^{-1}$). The temperature dependence of fractionation fueled initiatives to develop 'isotopic paleothermometers' or 'paleotemperature equations' (e.g. Urey, 1947; McCrea, 1950; Epstein *et al.*, 1953; O'Neil *et al.*, 1969; Shackleton, 1974; Erez and Luz, 1983). A comprehensive summary, including new calibrations using data from cultured Foraminifera, was presented by Bemis *et al.* (1998).

Since temperature decreases with increasing depth in the surface ocean, vertical migrations influence equilibrium fractionation. Many planktonic foraminiferal species show a $\delta^{18}O$ increase with growth that suggests calcification in progressively deeper, colder, waters (among others, Emiliani, 1954; Berger, 1971; Emiliani, 1971; Berger *et al.*, 1978; Fairbanks *et al.*, 1982; Bouvier-Soumagnac and Duplessy, 1985; Kroon and Darling, 1995). There are, however, also suggestions that a species like *Globigerina bulloides* calcifies at depth as a juvenile and later migrates to shallower waters (Spero and Lea, 1996; Bemis *et al.*, 1998).

14.2.2.2 Deviations from equilibrium $\delta^{18}O$ in foraminiferal calcite

14.2.2.2.1 Research is beginning to link $\delta^{18}O$ disequilibrium in foraminiferal shells to variations in seawater chemistry and depth-specific habitats, but the reports are largely descriptive. Five main causes of disequilibrium have been identified: the ontogenic effect; the symbiont photosynthesis effect; the respiration effect; the gametogenic calcite effect; and the effect of changes in $[CO_3^{2-}]$. The various effects may operate in opposite ways, masking one another. All are important for planktonic Foraminifera, but a great variety of deviations from equilibrium also exists in deep-sea benthic Foraminifera (e.g. Duplessy *et al.*, 1970; Woodruff *et al.*, 1980; Vincent *et al.*, 1981; Wefer and Berger, 1991). Since these benthic species live in an environment with very stable low temperatures and a complete absence of photosynthetic activity, the disequilibria suggest

an important role of microhabitat differentiation combined with pore water chemistry and food supply. The various effects are not strictly separate, and there may be considerable overlap between their regulating processes.

14.2.2.2.2 Ontogenic effect In laboratory experiments with constant $\delta^{18}O_{water}$ and temperature, *Globigerina bulloides* shows a progressive $\delta^{18}O$ increase of up to 0.8‰ with shell development: juvenile chambers are strongly depleted (around 1.15‰), while the final chamber is less depleted (around 0.30‰), relative to equilibrium (Spero and Lea, 1996). The mass-balanced average of the individual chambers gives a systematic whole-shell depletion of around 0.7‰. Since a similar trend of increasing values through ontogeny was observed in $\delta^{13}C$, an explanation was offered in terms of incorporation of metabolic (respired) CO_2 during calcification. Higher metabolic rates in juveniles would cause the strongest depletions, while adults gradually trend towards equilibrium.

The $\delta^{18}O$ trend is to some extent corroborated by reports of a size-dependent $\delta^{18}O$ trend in *G. bulloides* (e.g. Kroon and Darling, 1995), although the trend in those real-ocean results is a factor of two smaller than that observed under laboratory conditions. Spero and Lea (1996) found a similar difference when comparing laboratory results with data from fossil *G. bulloides* from Chatham Rise, speculating that the reduced signal was caused by vertical migrations from deeper cooler waters during early stages to very shallow, warmer water during later stages (see also Bemis *et al.*, 1998).

14.2.2.2.3 Symbiont photosynthesis In the photosynthetic symbiont-bearing planktonic foraminiferal species *Globigerinoides sacculifer*, Spero and Lea (1993) observed no variations in shell $\delta^{18}O$ with ontogeny within the size range 350–850 μm, supporting earlier conclusions that growth alone does not cause disequilibrium in this species (Erez and Luz, 1982, 1983; Wefer and Berger, 1991). However, a distinct chamber $\delta^{18}O$ decrease is seen with increasing irradiance levels (Spero and Lea, 1993), A similar but weaker

decrease with increasing irradiance occurs in photosynthetic symbiont-bearing *Orbulina universa* (Spero, 1992; Spero and Lea, 1993; Spero *et al.,* 1997). In addition, increased growth rates were observed with increasing light intensities, corroborating observations of light-enhanced calcification rates under elevated irradiance in photosynthetic symbiont-bearing corals (Chalker and Taylor, 1975) and larger Foraminifera (Ter Kuile and Erez, 1984). McConnaughey (1989a) and Wefer and Berger (1991) reported decreasing skeletal $\delta^{18}O$ values with increasing growth rates. The processes involved center around increasing kinetic discrimination against the heavy isotopes during CO_2 diffusion through the skeletal membrane, with rapid $CO_2 + H_2O \rightleftharpoons H_2CO_3$ reaction cycles (McConnaughey, 1989b; Spero and Lea, 1993).

14.2.2.2.4 Respiration Studies on photosynthetic symbiont-bearing corals indicate that the process of photosynthesis *per se* invokes no appreciable fractionation effects for $\delta^{18}O$ (Swart, 1983). Respiration, on the contrary, does cause ^{18}O depletion (Lane and Doyle, 1956). Relative to ambient dissolved oxygen, the oxygen used in respiration is depleted by 21‰ in near-shore, shallow waters (Kroopnick, 1975), and 11‰ in the deep ocean (Grossman, 1987). The $\delta^{18}O$ of ambient dissolved oxygen in surface waters commonly ranges around +24 to +26‰ (SMOW)(Kroopnick *et al.,* 1972; Kroopnick, 1975). In North Atlantic station Geosecs II, preferential respiratory ^{16}O utilization causes a marked $\delta^{18}O$ peak in dissolved oxygen (+31‰ SMOW) around 1000 m depth (Kroopnick *et al.,* 1972). Utilization of depleted respiratory products during calcification (Belanger *et al.,* 1981; Grossman, 1987) might cause skeletal ^{18}O depletion.

14.2.2.2.5 Gametogenic calcite Several planktonic foraminiferal species deposit a veneer of calcite on the surface of their shell at the end of the life-cycle (Bé, 1980; Duplessy *et al.,* 1981; Deuser, 1987; Spero and Lea, 1993; Bemis *et al.,* 1998). *Globigerinoides sacculifer* secretes the additional calcite over a period of up to 16 hours before gamete release (Bé, 1980), and its gameto-

genic calcite layer comprises 18 to 28% of the shell mass (Bé, 1980; Duplessy *et al.,* 1981) (around 26% in *Orbulina universa*; Bouvier-Soumagnac and Duplessy, 1985). Specimens covered by gametogenic calcite are called thick-walled. Gametogenic calcite is ^{18}O enriched relative to earlier (thin-walled) stages of the shell. These layers are, therefore, very important for whole-shell isotopic analyses.

Duplessy *et al.* (1981) speculated that the early stages of *G. sacculifer* are deposited at distinct disequilibrium in warm shallow waters, whereas the gametogenic layer is deposited in colder waters at depths of up to several hundreds of meters, possibly in near equilibrium. Bouvier-Soumagnac and Duplessy (1985) presented similar cases for *O. universa, Neogloboquadrina dutertrei,* and *Globorotalia menardii.* Kroon and Darling (1995) apply such arguments to reconstruct changes between last glacial maximum and Holocene vertical temperature gradients in the Arabian Sea and Panama Basin. Spero and Lea (1993), on the contrary, considered that vertical distribution studies of living planktonic Foraminifera do not support calcification at great depths, so that another, unidentified, mechanism should cause the ^{18}O enrichments in gametogenic calcite. However, in a subsequent study by these and other workers (Bemis *et al.,* 1998), the calcification-at-depth hypothesis was invoked again, without further discussion. Clearly, the nature of the enrichment in gametogenic calcite is yet to be resolved.

14.2.2.2.6 Carbonate ion concentrations Spero *et al.* (1997) subjected specimens of *Orbulina universa* to variations in $[CO_3^{2-}]$ at constant alkalinity, under both high and low irradiance conditions. They observed a constant $\delta^{18}O$ offset between the high and low irradiance experiments, while the ratio of change in shell $\delta^{18}O$ with change in $[CO_3^{2-}]$ remained similar for both groups. A second experiment with manipulation of $[CO_3^{2-}]$ by changes in alkalinity with constant ΣCO_2 corroborated the results of the first experiment. A third experiment concerned *Globigerina bulloides*, which bears no symbionts, and again a change was observed in shell $\delta^{18}O$ with $[CO_3^{2-}]$

variations. Spero *et al.* (1997), therefore, concluded that foraminiferal $\delta^{18}O$ decreases with increasing $[CO_3^{2-}]$, that the magnitude of this response is species-specific, and that symbiont photosynthesis plays no role. These findings for biological carbonates endorse McCrea's (1950) observations on inorganic precipitates, suggesting a common, abiological, kinetic fractionation effect, which may be related to calcification rates and the pH dependent balance between CO_2 hydration and hydroxylation (McCrea, 1950; McConnaughey, 1989b; Usdowski and Hoefs, 1993; Spero *et al.*, 1997; and references therein).

Bemis *et al.* (1998) re-evaluated data on the benthic Foraminifera *Uvigerina* and *Cibicidoides* and found that the epifaunal *Cibicidoides* precipitates its shell close to oxygen isotopic equilibrium with ambient seawater, while *Uvigerina* shows mild ^{18}O enrichment. Those authors speculated that this enrichment might result from a more infaunal habitat with low pore-water pH and decreased $[CO_3^{2-}]$

14.2.2.3   Aragonite versus calcite

Some benthic Foraminifera (e.g. *Hoeglundina elegans*) construct their test of aragonite rather than calcite. *H. elegans* is enriched relative to the equilibrium value for calcite by $0.78 \pm 0.19‰$ (Grossmann, 1984a). This agrees well with experimental observations that, at room temperature, inorganically precipitated aragonite is about 0.6‰ enriched relative to inorganically precipitated calcite, while theory suggests an enrichment of 0.79‰ (Tarutani *et al.*, 1969). The temperature dependence of the aragonite-water fractionation is similar to that of the calcite-water fractionation (Grossman and Ku, 1986).

14.3   CARBON ISOTOPES

14.3.1   Carbon isotopes and the global carbon cycle

There are two main carbon reservoirs: organic matter and sedimentary carbonates. For comprehensive schematics of fluxes within the global carbon cycle, see Compton and Mallinson

(1996), Mackenzie (1998), and references therein.

The organic carbon cycle revolves around CO_2 fixation into organic biomass through photosynthesis, in both the marine and the terrestrial biospheres: $CO_2 + H_2O + energy$ (sunlight) $\rightarrow CH_2O + O_2$. Respiration under the presence of oxygen follows the reverse reaction. The organic carbon cycle acts on a wide range of time scales, from alteration between daytime photosynthesis and night-time respiration within plants to cycles in the order of 10^8 years. where organic carbon is stored in sediments, only to become exposed and oxidized much later.

Weathering of most ordinary types of exposed or uplifted rocks also draws down CO_2 from the atmosphere. Schematically representing the rocks as calcsilicates ($CaSiO_3$), the weathering reaction follows: $CaSiO_3 + CO_2 \rightarrow CaCO_3 + SiO_2$. The $CaCO_3$ dissociates in water, utilizing more CO_2 (see below). Long-term cycles of orogeny and weathering (of order 10^8 years), therefore, cause fluctuations of atmospheric CO_2 concentrations, which also equilibrate with total dissolved inorganic carbon in the oceans.

The inorganic carbon pool in the oceans is governed by the carbonate reactions. Most of the CO_2 in water is contained in HCO_3^- (the bicarbonate ion), due to $H_2O + CO_2 \rightleftharpoons H^+ + HCO_3^-$, while a further (weak) reaction may dissociate HCO_3^- according to $HCO_3^- \rightleftharpoons H^+ + CO_3^{2-}$. At normal seawater pH of 7.8–8.3, HCO_3^- dominates and there are only small amounts of CO_3^{2-}. Total dissolved inorganic carbon (DIC) consists of HCO_3^-, CO_3^{2-}, and dissolved CO_2. Calcium carbonate, biogenic and abiogenic, interacts with the inorganic carbon pool via the precipitation/dissolution equation $2HCO_3^- + Ca^{2+} \rightleftharpoons CaCO_3 + CO_2 + H_2O$.

The average $\delta^{13}C$ of the carbonate reservoir is around 0‰, while the organic carbon reservoir averages around –25‰ (Fig. 14.4; also Hoefs, 1997). Extremely depleted values are known from methane in the form of gas-hydrates within the continental slope, with typical values between –35‰ and –80‰. Seepage of gas-hydrates (clathrates) may cause consider-
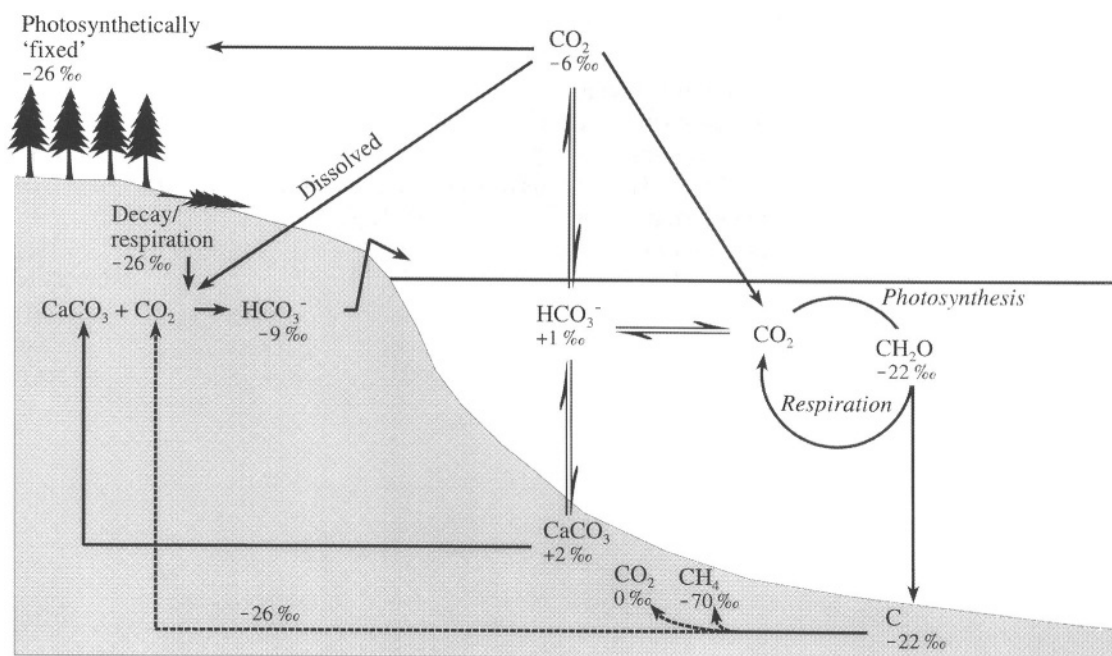
Figure 14.4 Main interactions between the terrestrial and marine organic and inorganic carbon cycles, with general mean carbon isotope values for the main phases (after Garlick, 1974). This diagram depicts these interactions in highly simplified form; no effort has been made to incorporate a correct stoichiometry. Values are only rough approximations. Double arrows indicate isotopic equilibration.

able $\delta^{13}C$ depletions in infaunal benthic Fora-minifera (Wefer) *et al.*, 1994).

There is a clear distinction between the $\delta^{13}C$ depletions in terrestrial ($-26‰$) and marine organic matter ($-22‰$) (Fig. 14.4). Swart (1983) argued that dissolved CO_2 is the main carbon species involved in photosynthesis in the oceans, with HCO_3^- and CO_3^{2-} utilized only at lower efficiencies. Since dissolved CO_2 is strongly ^{13}C depleted relative to HCO_3^-, and not much different from gaseous CO_2 (Fig. 14.5), Swart proposed that the heavier $\delta^{13}C$ signature of marine algae stems from different CO_2 assimilation mechanisms in ter-restrial and aquatic plants, and absence of translocation processes in the non-vascular algae. The ability to utilize HCO_3^-, however, was later found to differ between phytoplank-ton taxa, compromising Swart's arguments (e.g. Morel *et al.*, 1994; Riebesell and Wolf-Gladrow, 1995).

14.3.2 Carbon isotopes in seawater.

14.3.2.1 Photosynthesis, respiration, export productivity, and surface-deep $\delta^{13}C$ gradients

Photosynthesis is strongly discriminative in favor of ^{12}C, and marine phytoplankton forms organic matter with $\delta^{13}C$ values of -20 to $-23‰$ relative to ambient water. Photosynthe-sis is restricted to the euphotic layer and due to the preferential uptake of ^{12}C during photosyn-thesis, the dissolved carbon in suface waters is relatively enriched in ^{13}C. Through equilibra-tions, this enrichment affects surface water HCO_3^- and the carbonates formed thereof (Fig. 14.6).

As organic matter is remineralized, its low $\delta^{13}C$ values are released into the water column, again equilibrating with HCO_3^- and so affecting carbonates. Where remineralization occurs within the mixed layer, this effect to some extent offsets the enrichment due to photosynthesis.
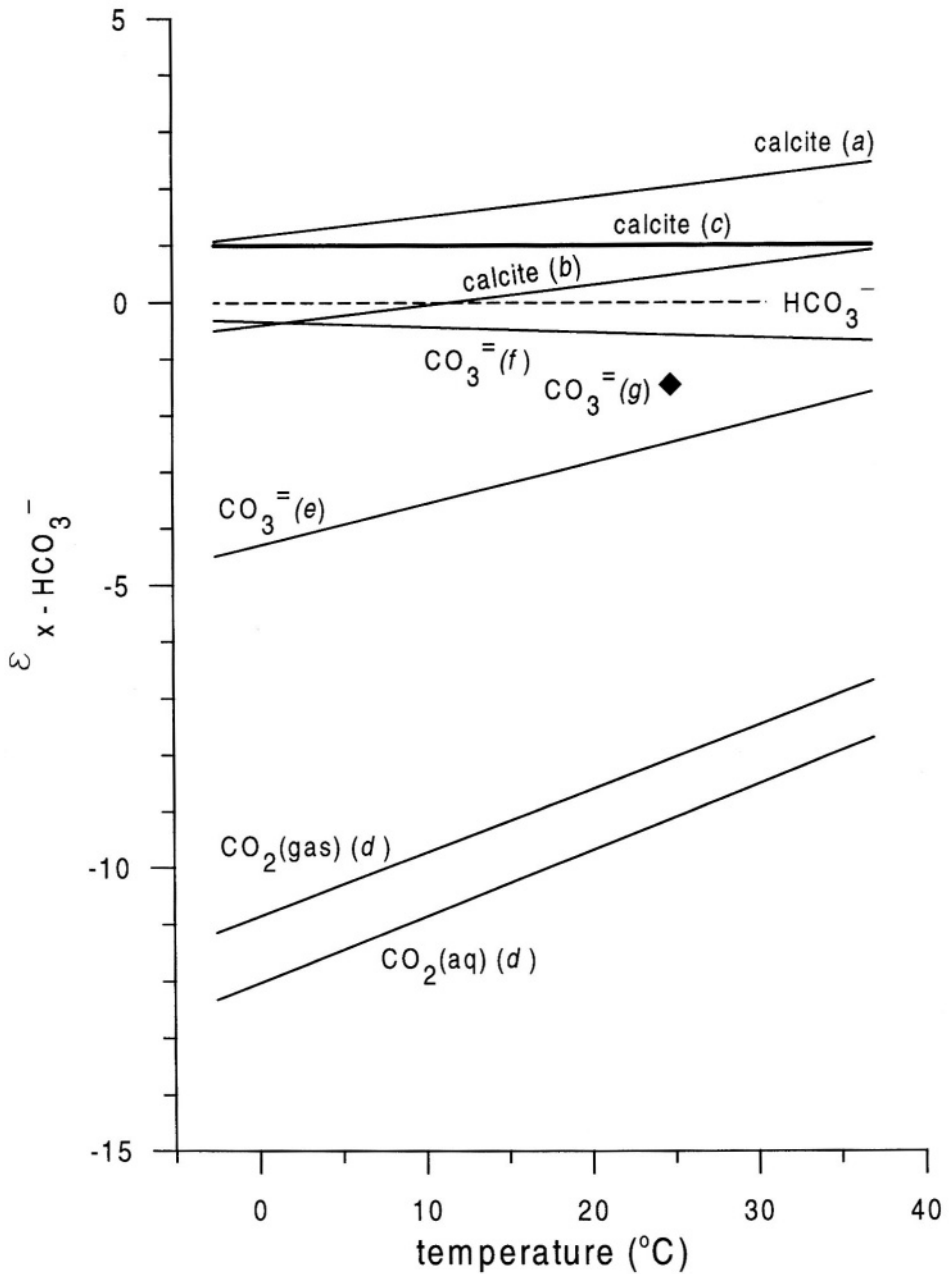
Figure 14.5 Temperature dependence of the carbon isotope enrichment factor ϵ (‰) relative to HCO_3^-. Sources: (a) Emrich *et al.* (1970); (b) Grossman (1984b); (c) Romanek *et al.* (1992); (d) Mook *et al.* (1974); (e) Swart (1983); (f) Freeman and Hayes (1992); (g) Turner (1982; at pH > 9).

However, export production from the mixed layer constitutes a loss of ^{13}C depleted marine organic matter to deeper waters. Upon reminer-alization at depth, an effective transfer of ^{12}C has occurred from surface to deep water. Hence, increases in export productivity will enhance gradients between increased $\delta^{13}C$ in surface waters and decreased values in deep waters,
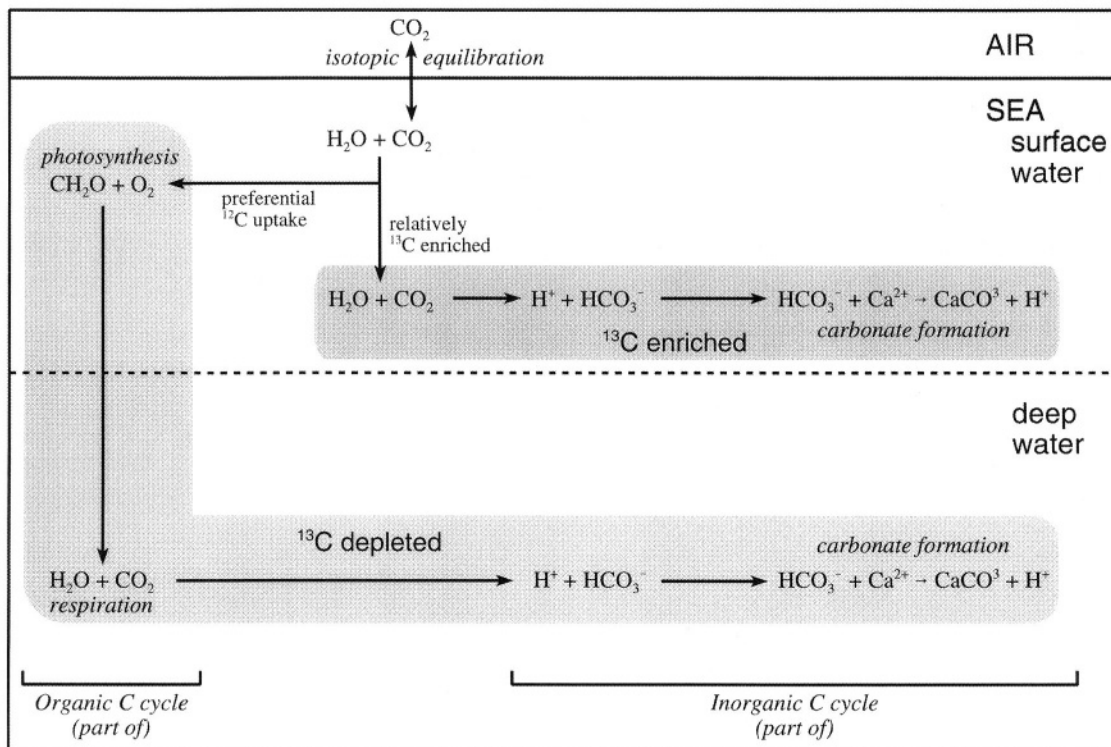
Figure 14.6 Schematic presentation of the generation of a carbon isotope gradient between the sea surface and deep water due to export production and interactions between the marine organic and inorganic carbon cycles. There was no effort to incorporate a correct stoichiometry.

which will be recorded in calcareous fossils (Figure 14.6).

Remineralization at depth releases not only ^{13}C depleted CO_2, but also nutrients, into deep water. Consequently, enhanced ^{13}C depletion in the present-day oceans correlates well with enhanced nutrient concentrations, where the expected relationship between $\delta^{13}C$ (in ‰) and phosphate concentrations (in $\mu mol\,kg^{-1}$) is -0.93‰ per $\mu mol\,kg^{-1}$ (see Broeker, 1982; Broecker and Peng, 1982, pp. 308 and 309). There are similar relationships between $\delta^{13}C$ and nitrate concentrations (Ortiz et al., 1996). If sufficient validation is possible from independent evidence, this $\delta^{13}C$:nutrient correlation has great potential in paleoceanographic applications, as demonstrated by the applications of paired $\delta^{13}C$ and Cd/Ca analyses pioneered by Boyle and Keigwin (1982; 1985/86; 1987) and Boyle (1986).

Lateral gradients in deep water $\delta^{13}C$ may be used to trace the history of deep water from its source area. The deep water $\delta^{13}C$ reflects; (1) time of exposure to organic matter decay (true age); (2) the amount of organic matter decayed within the deep water (i.e. export production along its pathway); and (3) the rapidity of organic matter decay, which is temperature dependent (respiration rates roughly double for each 10°C temperature increase; Swart, 1983). This technique of deep water tracing is often called 'ageing' of deep water, where age obviously is just a relative concept. The age of deep water provides a powerful tool for reconstruction of ocean circulation. For example, the relatively high $\delta^{13}C$ values in the present-day deep North Atlantic ($+1.0$‰, with average surface waters at $+1.6$‰; Kroopnick et al., 1972) correctly identify it as a basin with active deep water formation and consequently young deep

waters. Low North Pacific deep water $\delta^{13}C$ values ($-0.2‰$, with average surface waters at $+1.5$ to $+2.0‰$; Broecker and Peng, 1982; p. 308) successfully identify these waters as old, derived from remote source-regions. Lynch-Steiglitz and Fairbanks (1994) used Cd/Ca ratios to deconvolve $\delta^{13}C$ signals into a part related to the age of deep water (associated with nutrient enrichment) and a part related to the air-sea exchange defined in the deep water formation area (see Broecker and Maier-Reimer, 1992). Thus, likely glacial deep water source areas were identified that are very different from those of today.

Geographic shifts of deep water sources greatly affect the world ocean's surface-deep $\delta^{13}C$ gradients, which are low in actively over-turning basins and high in non-overturning basins with old deep waters. Such ocean-wide patterns should, therefore, be established before past local/regional variability in surface-deep $\delta^{13}C$ gradients can be used to quantify export production.

14.3.2.2   Interactions with $\delta^{13}C$ of atmospheric CO_2

Interactions between $\delta^{13}C$ of atmospheric CO_2 and the marine reservoir (Fig. 14.6) depend on: (1) spatial variability in the equilibration between atmospheric CO_2 and dissolved inorganic carbon, and (2) geographically widespread temporal variability in the $\delta^{13}C$ of atmospheric CO_2. For atmospheric signals to be recorded in the marine reservoir, a signal of sufficient magnitude and duration is needed. Because the atmospheric CO_2 reservoir is orders of magnitude smaller than the marine reservoir, a recordable signal transmitted by the atmosphere should involve the terrestrial biosphere and/or lithosphere.

Differences in photosynthetic pathways cause C_3 plants to become much more $\delta^{13}C$ depleted than C_4 plants (Kelly *et al.*, 1993). Cerling *et al.* (1993) argued that the late Miocene saw an increase in dominance of C_4 plants, which include many grasses, relative to C_3 plants, of which most trees are a subset (Leavitt, 1993).

This would have reduced the mean relative atmospheric ^{13}C enrichment caused by ter-restrial plants. This signal, anchored in the ter-restrial biosphere, was sufficiently strong and long-lived to help explain the late Miocene shift to lower $\delta^{13}C$ values in marine carbonates (Derry and France-Lanord. 1996). Because of its long-term characteristic, the signal affected surface and deep waters equally, in contrast with export production or deep water age fluctuations that influence gradients between surface and deep waters.

14.3.2.3   Carbon burial and global isotope shifts

14.3.2.3.1   Organic carbon On the long term, the water column is in steady state, so that the particulate transport of ^{13}C depleted organic matter is matched by upwelling of nutrient-rich, ^{13}C depleted waters. However, some periods in geological history were characterized by higher than average organic matter preservation and removal from the system by inclusion in sediments. Such a situation not only constitutes a sink of carbon, so that eventually the atmospheric CO_2 concentration should drop, but simultaneously causes a residual ^{13}C enrichment throughout the oceans and atmosphere. This line of reasoning was developed to explain the 'carbon shift' associated with the widely documented Middle Miocene cooling (Vincent and Berger, 1985), where the appointed organic carbon sink was the deposition of the Monterey Formation of California.

14.3.2.3.2   Inorganic carbon Weathering of the total sedimentary carbonate reservoir reflects its mean $\delta^{13}C$, which during the Neogene was very stable around $1.8 \pm 0.2‰$ (Derry and France-Lanord, 1996). The stability of this value allowed these authors to develop relatively straightforward isotopic balance equations to estimate the fractions of organic carbon in the total eroded carbon and in the total carbon burial flux. These relationships center around Δ_E, the mean isotopic difference between the sedimentary carbonate and organic carbon being eroded, and Δ_B, the mean isotopic differ-

ence between carbonates and organic carbon deposited at time t. If we use a rough approximation that $\Delta_E \approx \Delta_B$, the relationships indicate that the ratio between mean carbonate $\delta^{13}C$ and $\delta^{13}C$ of carbonate formed at time t depends mainly on the difference between the fractions of organic carbon eroded and buried at time t. This would imply that variations in the organic carbon pool drive global $\delta^{13}C$ fluctuations, while the inorganic carbon pool instead monitors or records the changes.

14.3.3 Carbon isotope ratios in foraminiferal carbonate

14.3.3.1 Equilibrium fractionation

14.3.3.1.1 Equilibrium between carbonate and dissolved inorganic carbon
Grossman (1984b) analyzed $\delta^{13}C$ for both calcitic and aragonitic (*Hoeglundina elegans*) benthic Foraminifera, evaluated the results against inorganic precipitates, and presented new equilibrium equations for aragonite and calcite. The isotopic enrichment factor for calcite (c) versus bicarbonate (b) was $\varepsilon_{c-b}(\permil) = 10.51 - 2980T^{-1}$, with T in Kelvin. Grossman's (1984b) equation for calcite returns values about 1.5‰ lower than that of Emrich *et al.* (1970), which concerned a mixture of aragonite and calcite (see also Fig. 14.5). Romanek *et al.* (1992) reported a different, temperature independent, relationship between the $\delta^{13}C$ values of equilibrium carbonate and bicarbonate: $\delta^{13}C_{eqcarb} = \delta^{13}C_{HCO_3^-} + 1.0$. Aragonite shows a weak inverse relationship with temperature (Grossman, 1984b; Grossman and Ku, 1986; Wefer and Berger, 1991).

Often, carbonate $\delta^{13}C$ equilibrium is reported relative to the $\delta^{13}C$ of total dissolved inorganic carbon (i.e. the $\delta^{13}C$ of $\Sigma CO_2 = \delta^{13}C_{DIC}$), rather than relative to the $\delta^{13}C$ of bicarbonate. This is because the value for $\delta^{13}C_{DIC}$ can be either analytically determined (Kroopnick, 1974), or estimated from apparent oxygen utilization rates (Kroopnick, 1985), whereas the $\delta^{13}C$ of bicarbonate can only be obtained indirectly from calculations using $\delta^{13}C_{DIC} = (f\delta^{13}C)_{HCO_3^-} + (f\delta^{13}C)_{CO_3^{2-}} + (f\delta^{13}C)_{CO_2^{aq}}$, where f indicates the mole fraction per dissolved inorganic species. The mole fraction for CO_2^{aq} is very small at normal seawater pH of 7.8–8.3, so that $\delta^{13}C_{DIC}$ is only slightly (0.2 to 0.4‰) lower than $\delta^{13}C_{HCO_3^-}$ due to dominance of HCO_3^- over CO_3^{2-}. Information on pH and the concentrations of the various inorganic carbon species is essential for accurate evaluation of the equilibrium state of carbonate precipitation, which is not a trivial problem when sampling natural environments.

14.3.3.1.2 Apparent disequilibria: differential depth habitats or microhabitat effect
Changes in depth of calcification during growth and differences among preferred depths of different planktonic foraminiferal species may cause apparent $\delta^{13}C$ deviations from surface water equilibrium, because the gradient in $\delta^{13}C_{DIC}$ is steep between the surface and the thermocline (Kroopnick *et al.*, 1972; Garlick, 1974; Kroopnick 1985; Tan, 1989). Hence, these calcification depth preferences must be taken into account before decisions are made on the degree of disequilibrium and its potential causes (e.g. Bouvier-Soumagnac and Duplessy, 1985; Wefer and Berger, 1991; Ravelo and Fairbanks, 1995; Ortiz *et al.,* 1996). Since temperature drops in the oceans with increasing depth, there is also a strong $\delta^{18}O$ relationship with calcification depth (see section 14.2.2.1). Covariations between increasing $\delta^{18}O$ and decreasing $\delta^{13}C$ with growth in several planktonic Foraminifera suggest that calcification at later growth stages occurs well below the mixed layer (Bouvier-Soumagnac and Duplessy, 1985). Ravelo and Fairbanks (1995) assessed the potential of these covariations for reconstructions of past surface water hydrography, concluding that non-spinose species offer the greatest potential because they are less affected by biological fractionation effects.

Concerning benthic Foraminifera, the question of equilibrium should be viewed within the context of ambient pore water $\delta^{13}C$ at the species' preferred living depth or microhabitat (Woodruff *et al.*, 1980; Belanger *et al.*, 1981: Grossman, 1984a,b; 1987; McCorkle *et al.*, 1985;

1990; Zahn *et al.*, 1986; Wefer and Berger. 1991; Loubere *et al.*, 1995). McCorkle *et al.* (1990) consistently found lower δ^{13}C values in deep dwelling taxa than in shallow dwelling taxa. Pore-water δ^{13}C gradients may reach 1‰ depletion per cm depth within sediment due to decomposition of sedimentary organic matter (Grossman, 1984a,b; McCorkle *et al.*, 1985; Grossman, 1987). There are additional intraspecific controls on the depletions by the amount (Zahn *et al.*, 1986; Loubere, 1987) and mechanisms (Loubere, 1987) of food supply within the sediment. The epibenthic species *Cibicides wuellerstorfi* (also described under *Cibicidoides, Planulina,* and *Fontbotia)* forms its test nearest to equilibrium and so provides the best measure for bottom water δ^{13}C$_{DIC}$ variations through time (e.g. Woodruff *et al.,* 1980; Graham *et al.*, 1981; Zahn *et al.*, 1986; Grossman, 1987; Wefer and Berger, 1991; Mackensen *et al.*, 1993), but see Chapter 10 for possible complications.

14.3.3.2   Deviations from equilibrium δ^{13}C in foraminiferal carbonate

14.3.3.2.1   Foraminiferal δ^{13}C disequilibrium may be caused by: (1) utilization of metabolic CO_2 during shell formation, (2) photosynthetic activity of symbionts, (3) growth rate, and (4) variation in carbonate ion concentrations in ambient waters. The effects are not strictly separate; there may be strong overlaps between regulating processes. For detailed overviews, see Grossman (1987), Ravelo and Fairbanks (1995), Spero *et al.* (1991; 1997), and references therein.

14.3.3.2.2 Respiratory CO_2: 'vital' effects Vital effects are reflected in the incorporation of isotopically light metabolic CO_2 into the carbonate skeleton (among others Keith and Weber, 1965; Weber and Woodhead, 1970; Vinot-Bertouille and Duplessy, 1973). The vital effect magnitude is proportional to the amount of metabolic CO_2 within the organism's internal CO_2 pool (Erez, 1978), which, in turn, reflects the organism's ability for gas-exchange with ambient water. Organisms from oxygen minimum zones around the world show the least influence of vital effects, suggesting that they are specially adapted for efficient gas-exchange (Leutenegger and Hansen, 1979; Grossman. 1984a. 1987).

Respired products are ^{18}O depleted relative to unused oxygen (section 14.2.2.2.4) while the food source (sedimentary organic matter) would cause likely ^{13}C depletions in metabolic CO_2 (see Lane and Doyle, 1956; Degens *et al.*, 1968; Kroopnick, 1975; De Niro and Epstein, 1978). Hence, the incorporation of metabolic carbon-oxygen compounds should cause reductions of both skeletal δ^{18}O and δ^{13}C. However, this expected relationship holds only to a limited extent (Grossman, 1987), and laboratory cultures show that large variations in δ^{13}C of food used by *Orbulina universa* and *Globigerina bulloides* cause only negligible shifts in shell δ^{13}C (Spero and Lea, 1993, 1996: see also Ortiz *et al.,* 1996). Ortiz *et al.* (1996) concluded that the major cause for shell δ^{13}C fluctuations is not food δ^{13}C. but metabolic rates controlled by temperature. This is supported by reduced δ^{13}C values in gastropod shells and corals due to enhanced metabolic activity associated with spawning (Wefer and Berger, 1991; Gagan *et al.,* 1994). Photosynthetic symbiont-bearing larger Foraminifera also shift to very low δ^{13}C values in the reproductive period (Wefer and Berger, 1991).

14.3.3.2.3 Symbiont photosynthesis A wide range of photosynthetic (symbiont bearing) organisms that precipitate calcium carbonate display increasing skeletal ^{13}C enrichment with increasing light intensity (McConnaughey, 1989a). Spero and Lea (1993) noted such a relationship in *Globigerinoides sacculifer*, ascribing it to elevated utilization of $^{12}CO_2$ by photosynthetic symbionts, which increases the calcifying microenvironment in $H^{13}CO_3^-$ and so produces ^{13}C enriched chambers. A similar relationship is known for *Orbulina universa*, although the relationship disappears when photosynthetic activity is prevented (Spero and Williams, 1988). At very low light

levels, $\delta^{13}C$ values of *G. sacculifer* shift slightly below equilibrium, suggesting that photosynthetic effects become suppressed and that some respired CO_2 gets incorporated into the shell (to a proportion of 0–3% of shell carbon; Spero and Lea, 1993). Similar values were observed for *O. universa* (Spero, 1992). Influences of light intensity or photosynthetic activity cannot be easily accounted for in data from Foraminifera grown in natural dark-light alternations, unless the proportions are known of the shell fractions deposited during dark and light periods (40 and 60%, respectively, for *O. universa*; Spero *et al.*, 1991).

14.3.3.2.4 Changes with growth Romanek *et al.* (1992) found no significant $\delta^{13}C$ fractionations due to differences in calcification rates alone. However, most Foraminifera experience major physiological changes during growth. In *Globigerinella aequilateralis* and *Orbulina universa*, symbiont density increases with test size (Faber *et al.*, 1985; Spero and Parker, 1985), which in turn increases total gross photosynthesis so that each new chamber shows increasing ^{13}C enrichment. An analysis of whole-shell $\delta^{13}C$ gives an integrated value of the masses and different $\delta^{13}C$ compositions of all individual chambers (Spero *et al.*, 1991), and will therefore be different for the same species in different size-classes. However, progressive increases in $\delta^{18}O$ in *Orbulina universa* in the natural environment suggest migration to progressively deeper habitats with lower light intensity during growth, causing progressive ^{13}C depletion which may (partially) offset the enrichment due to increased symbiont density (Ravelo and Fairbanks, 1995).

In non-symbiont-bearing species, a change with size is expected in the depletion caused by contamination of shell $\delta^{13}C$ with metabolic or respiratory CO_2. Depletions should be strongest in small specimens from early life stages with high metabolic rates, decreasing towards equilibrium in adult stages (cf. Berger *et al.*, 1978; Wefer and Berger, 1991). Bouvier-Soumagnac and Duplessy (1985) reported such trends for *Globorotalia menardii* and *Neo-*

globoquadrina dutertrei. Ravelo and Fairbanks (1995) confirmed the trend in *N. dutertrei*, but observed little to no size-dependent fractionation in *G. menardii, Globorotalia tumida, Globorotalia inflata, Globorotalia crassaformis, Globorotalia truncatulinoides*, or *Pulleniatina obliquiloculata.*

Deep-sea benthic Foraminifera show no significant change in skeletal $\delta^{13}C$ with size (Vincent *et al.,* 1981; Dunbar and Wefer, 1984; Grossman, 1984; 1987; Wefer and Berger, 1991).

14.3.3.2.5 Carbonate ion concentration Similar to $\delta^{18}O$, foraminiferal $\delta^{13}C$ decreases with increasing $[CO_3^{2-}]$. The signal magnitude is species-specific, and symbiont photosynthesis plays no role (Spero *et al.*, 1997). These results combined with abiogenic data (McCrea, 1950) suggest a common, abiological, kinetic fractionation effect (cf. section 14.2.2.2.6).

14.3.3.3 Aragonite versus calcite

The aragonitic benthic foraminifer *Hoeglundina elegans* shows constant $\delta^{13}C$ values with depth in the California borderland study area, whereas $\delta^{13}C_{DIC}$ increases with depth (Grossman, 1984a). This may suggest a negative temperature dependence of bicarbonate-aragonite fractionation (also Grossman, 1984b; Grossman and Ku, 1986). To date, fractionations associated with aragonite formation remain poorly understood.

14.4 SUMMARY

Table 14.2 summarizes the main processes determining seawater $\delta^{18}O$ at any study site, and those determining fractionations between $\delta^{18}O$ of foraminiferal carbonate and of seawater, including typical magnitudes of the isotopic changes due to each effect. Table 14.3 is similar, but for $\delta^{13}C$.

To investigate the main controlling processes and eliminate the noise introduced by minor ones, specific analytical strategies have been

Table 14.2 Summary of the main processes determining seawater $\delta^{18}O$ at any study site (white) and those determining fractionations between $\delta^{18}O$ of carbonate and of seawater (shaded). Ticks indicate predominant influences on surface and/or deep waters, and planktonic and/or benthic Foraminifera. Last column lists typical magnitudes of isotopic change due to given effects.

Oxygen isotopes Process	Deep/ Benthic	Surface/ Planktonic	Impact and typical magnitude
evaporation; ice-volume effect	√	√	global; up to 2‰ (0.012‰ m^{-1} sea level change)
evaporation; 'normal' effect	√ [1]	√	local; surface 1‰, [1]may affect deeper waters through mode water formation
precipitation		√	local; 1‰
runoff		√	local; >1‰ near river mouth or melting ice
sea ice freezing	√ [1]	√	local; surface 1‰, [1]may affect deeper waters through mode water formation
sea ice melting		√	local; 1‰
watermass transport and mixing	√	√	everywhere; magnitudes under investigation
equilibrium fractionation	√	√	everywhere, temperature dependent; 0.2‰°C^{-1}
depth habitat/vertical migrations		√	1‰ depending on local temperature gradient
microhabitat effect	√		1‰ depending on local gradient in pore-water
ontogenic effects	?	√	species specific <1‰
photosynthetic symbiont effect		√	species (or specimen?) specific <1‰
vital effect	√	√	(?) <1‰, not well known for Foraminifera
gametogenic calcite		√	species (?) specific (?) <1‰
changing carbonate ion concentration	√	√	<1‰, poorly known for natural conditions

adopted in paleoceanographic research. The vital effect is commonly considered to be species-specific, and avoided by study of monospecific records. The effects of symbiont density, gametogenic calcite formation, and changes in calcification depth during growth are avoided by analyzing either thin-walled, or thick-walled, specimens of the selected species from similar ontogenic stages, using narrowly constrained size-fractions. No studies have yet established in sufficient detail the temporal changes in oceanic $[CO_3^{2-}]$ to allow assessment of their impact on foraminiferal isotope records.

The ice volume effect exerts by far the most important control on $\delta^{18}O$ records, allowing both global correlations and absolute dating (Figure 14.1). Also very important is the influence of ambient temperature during calcifica-

tion. In a 'glacial world,' this influence is less relevant for deep-sea benthos, since oceanic deep-sea temperature fluctuations are unlikely to exceed 1 to 2°C. However, larger deep-sea temperature fluctuations may have prevailed in previous geological periods when the deep-sea was filled with so-called warm saline deep water, such as is found today in isolated basins like the Red Sea and the Mediterranean. For planktonic foraminiferal $\delta^{18}O$ records, temperature influences are always very important. Temperature effects may be constrained through the use of other paleotemperature indicators, such as transfer functions or geochemical proxies (e.g. alkenone records).

Secondary influences on benthic foraminiferal $\delta^{18}O$ records originate from the microhabitat and $[CO_3^{2-}]$ effects, which likely are related, but

Table 14.3 Summary of the main processes determining seawater $\delta^{13}C$ at any study site (white) and those determining fractionations between $\delta^{13}C$ of carbonate and of seawater (shaded). Ticks indicate predominant influences on surface and/or deep waters, and planktonic and/or benthic Foraminifera. Last column lists typical magnitudes of isotopic change due to given effects.

Carbon isotopes

Process	Deep/ Benthic	Surface/ Planktonic	Impact and typical magnitude
photosynthesis		√	global, but locally variable; $<1‰$
respiration	√	√	local; $<1‰$
export production	— causes gradients —		function of photosynthesis, respiration, 'age' of deep water
'age' of deep water	√		along deep water path; up to $>1‰$
shifts in terrestrial vegetation	√	√	global; $>1‰$
burial/oxidation sedimentary organic matter	√	√	global; $>1‰$
equilibrium fractionation	√	√	everywhere; $<1‰$ to negligible (uncertain!)
depth habitat/vertical migrations		√	up to $1‰$ depending on local temperature gradient
microhabitat effect		√	$1‰$ or more depending on local gradient in pore-water (very strong near gas-hydrate seepage)
growth-related effects		√ (some)	species (or specimen?) specific $<1‰$
photosynthetic symbiont effect		√	specimen specific $<1‰$
vital effect	√	√	species specific $<1\%$, not well known for Foraminifera
changing carbonate ion concentration	√	√	$<1‰$, poorly known for natural conditions

still are not fully understood or quantified. Away from sea-ice margins, secondary controls on planktonic $\delta^{18}O$ records are exerted by local freshwater cycle effects and $[CO_3^{2-}]$ variations. Temporal variations due to the $[CO_3^{2-}]$ effect are not yet sufficiently known. The assumption that, through time, a systematic relationship should exist between salinity and $\delta^{18}O$ due to action of the freshwater cycle has given rise to the term 'salinity effect.' Recent work is casting doubt on this assumption, and thus on the potential of oxygen isotopes in the determination of paleosalinity. Temporal changes in sub-surface water sources, advective pathways, and mixing of water masses appear to complicate interpretation of $\delta^{18}O$ records, especially for planktonic species.

For $\delta^{13}C$, the major controls are: global shifts related to changes in terrestrial vegetation and/ or large-scale burial oxidation of sedimentary organic matter, and the interrelated influences of export production, respiration at depth, and age of deep water. The global effects are established by inter-comparison of a large number of records from various worldwide locations. The effect of export production, etc.. may be estimated from comparison of planktonic records with records for epiphytic benthic species known to calcify near equilibrium. This approach is most successful when paired with analyses of other nutrient proxies, such as Cd/Ca ratios. The age of deep water is assessed similarly, but in a wider geographical context.

Other influences on benthic foraminiferal $\delta^{13}C$ are due to the microhabitat effect, and the $[CO_3^{2-}]$ effect, which likely are related to one

another. Seepage of clathrates may cause very strong anomalies in the δ^{13}C values of infaunal benthic species. Additional control on planktonic foraminiferal δ^{13}C records is exerted by $[CO_3^{2-}]$ fluctuations through time. This effect may be important, but is not yet well quantified.

14.5   ACKNOWLEDGMENTS

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15

Trace elements in foraminiferal calcite

David W. Lea

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15.1 INTRODUCTION

The trace element composition of calcitic fora-
minifer shells has become an important means
by which paleoceanographers deduce past oce-
anic conditions. Pelagic foraminifer shells are
composed of extremely pure calcite, typically
about 99% by weight $CaCO_3$. Trace elements
such as Mg, Sr, Ba and Cd comprise the remain-
ing 1% and occur in calcite foraminifer shells at
individual abundances of 0.25% or less. Trace
elements are incorporated directly from sea-
water during shell precipitation. For this reason,
shell composition reflects both seawater com-
position and the physical and biological condi-
tions present during precipitation.

The idea that chemical signals encoded into
skeletal carbonates could be used to assess past
environmental and climatic information dates
back to at least the early part of the twentieth
century (Clarke and Wheeler, 1922). This idea
did not come to fruition until decades later,
however, when Harold Urey and his group at
the University of Chicago were able to demon-
strate the potential of oxygen isotope variations
for paleothermometry (Epstein *et al.,* 1953; Emi-
liani, 1955). The trace element component of

climate proxy research has always lagged behind
that of isotopic research. This might be due to
the attitude prevalent in the Chicago school that
trace element incorporation was not likely to be
as systematic (S. Epstein, pers. comm., 1992).

The direct investigation of trace elements in fora-
minifer shells was hindered by the difficulty of trace
element determination in the small samples typical
of these shells. The first studies to show real poten-
tial were those of Michael Bender and his students
at the University of Rhode Island, which focused
on using shell Sr, Mg, and Na to establish Cenozoic
ocean chemical histories (Bender *et al.,* 1975;
Graham *et al.,* 1982). Arguably though, trace ele-
ments did not become an important paleoceano-
graphic tool until Edward Boyle's pioneering
studies at the Massachusetts Institute of Technol-
ogy, in which he demonstrated that foraminiferal
Cd could be used to assess past nutrient phosphate
concentrations (Boyle, 1981; Boyle and Keigwin,
1982; Hester and Boyle. 1982). Boyle's research
pushed foraminiferal trace element research into a
new realm because Cd is a unique nutrient proxy
that is integral to defining past ocean circulation
changes (Boyle and Keigwin. 1982, 1985/1986,
1987). In addition, Boyle's findings set new stan-
dards of analysis for the extremely low levels of

metals present and the care with which such determinations had to be made (Boyle, 1981). Trace elements in Foraminifera are no longer just a curiosity needed for chemical bookkeeping but have become a unique tool to understand the past. This paradigm shift drives trace element research today as we endeavor to refine our toolbox of elemental proxies while continuously pursuing new leads for proxy development.

We are currently in the midst of a revolution in the investigation of trace elements in Foraminifera, and our knowledge in this area is increasing rapidly. This is especially true for minor elements like Mg, which appears to have potential as a paleotemperature proxy. This flurry of activity is largely driven by improvements in analytical capabilities and an expansion in the number of laboratories undertaking such investigations. Culturing of live individuals has also played an important role in this proxy development, because the potential usefulness of trace elements can be verified directly by experimentation.

In this review, I focus on the abundance and application of four broad groups of trace elements incorporated in foraminifer shells:

(1) 'nutrient' proxies such as Cd and Ba, which provide information on seawater nutrient, carbon and carbonate levels;
(2) 'physical' proxies such as Mg, Sr, F, and B isotopes, which dominantly reflect physical parameters such as temperature and pressure;
(3) 'chemical' proxies such as Li, U, V, Sr, and Nd isotopes, which provide diverse information on the history of ocean chemistry; and
(4) 'diagenetic' proxies such as Mn, which reflect secondary post-depositional processes.

Naturally, there is some overlap among these broad groups, but the divisions are a helpful way to view the toolbox of elemental proxies available to the paleoceanographer.

15.2   TRACE ELEMENTS IN THE OCEAN

The diverse oceanic behavior and distribution of the trace elements are the key to utilizing elemental variation in foraminifer shells. Chemical oceanographers broadly group elemental behavior in the ocean according to the biogeochemical cycling of the elements in the ocean (Broecker and Peng, 1982; Bruland, 1983). These groups include: (1) nutrient-like elements, those that act as biological nutrients or mimic such behavior; (2) conservative elements, those that occur in fixed proportion to the major salts in seawater and are nearly unaffected by biological cycling; and (3) particle-reactive elements, those that are dominated by solid particle–seawater interactions.

Nutrient-like elements (Cd, Ba, Zn) show large and systematic variations in their seawater chemistry which result from involvement in biological cycling (Bruland, 1983). Minimum nutrient concentrations are found in oligotrophic surface waters due to algal removal of nutrients, whereas maximum concentrations are found in Pacific deep waters due to decomposition of nutrient-rich particulate matter. Deep water masses have unique trace element imprints due to variations in source waters and patterns of oceanic mixing. In the modern ocean, minimum deep-water nutrient concentrations are found in North Atlantic bottom waters and maximum concentrations in Pacific bottom waters. Cd, which follows phosphate, has almost a thousand-fold concentration range in the oceans. Ba and Zn, which follow alkalinity and silicic acid respectively, vary by five to ten fold. The large modern ocean variation in these elements is expected to be reflected in the shell chemistry of Foraminifera calcifying in different hydrographic settings. The impact of physical and/or biological processes on calcification can also influence the presence of these elements in the foraminifer shells (Elderfield *et al.,* 1996).

The ratio of conservative elements (Mg, Sr, B, Li, F, V, U) to Ca is nearly fixed in seawater, and among the three groups, conservative elements have the longest oceanic residence limes. Only V and U are present in seawater at truly trace concentrations ($<10^{-6}$ mol/kg). Any variations in these elements in foraminifer shells found in modern samples must reflect the impact of physical and/or biological processes on calcification.

In shells from older sediments, variations in the abundance of a conservative element relative to Ca might also reflect changes in seawater chemistry, which responds to shifting oceanic source and sink patterns. Both Sr and B have important isotope systems which can be monitored using foraminifer shells (see below).

Particle reactive elements (Mn, Nd) are rapidly cycled and have typically short oceanic residence times They are less regularly distributed in the oceans, and can be enriched in the surface ocean by the dissolution of aeolian particles. Solid phase Mn is released in suboxic (little or no O_2 present) pore-waters by reduction to soluble Mn^{2+}, and this behavior leads to the deposition of Mn in or on foraminifer shells. Nd displays a strong isotopic variation in seawater because the isotopic composition of its sources varies between ocean basins.

15.3 INCORPORATION OF TRACE ELEMENTS IN FORAMINIFERAL CALCITE

15.3.1

The ideal situation from a geochemical point of view is that trace elements are incorporated homogeneously into calcite and regulated by strict physical (thermodynamic) laws. This ideal of pure thermodynamic control is an important concept, because it predicts regular, reproducible behavior for the incorporation of trace elements. There is abundant evidence, however, that the incorporation of trace elements in foraminiferal calcite does not take place in such an ideal, thermodynamic manner. Foraminifera, as living organisms, actively precipitate their shells, affecting both the structure and chemistry of shell calcite. Active precipitation argues for significant biological or kinetic (processes affected by the rate of reactions) controls on trace element substitution.

15.3.2 Thermodynamics of trace element incorporation

A primary goal in interpreting trace element compositions in precipitated minerals is to relate those concentrations to the composition and physical conditions at the time of precipitation. This is most commonly accomplished by the use of a constant that relates mineral composition to fluid composition. The relationship between shell calcite composition and seawater is best expressed by an *empirical partition coefficient D*, which is defined for the specific case of Foraminifera in seawater by the relationship:

$$[TE]/[Ca]_{\text{foraminifer shell}}$$
$$= D \times [TE]/[Ca^{2+}]_{\text{seawater}} \tag{1}$$

where the bracketed concentrations indicate the actual concentration ratios of trace element (TE) to Ca in calcite and seawater (Morse and Bender, 1990; Mucci and Morse, 1990). If D is greater than 1, the trace element is preferentially concentrated in the shell. If D is less than 1, the trace element is preferentially excluded from the shell. It is important to realize that the partition coefficient is not a thermodynamic property of the system, but rather represents an empirical measure of the trace element to calcium ratio in the shell relative to the same ratio in seawater for a specific set of physical and biological conditions.

The partition coefficient is distinct from the thermodynamic equilibrium or *distribution constant* (occasionally termed distribution coefficient) K, which can be derived from an exchange reaction:

$$CaCO_3 + TE^{2+} \Leftrightarrow TECO_3 + Ca^{2+} \tag{2}$$

The equilibrium constant for reaction (2) is defined by:

$$(a_{TECO_3}/a_{CaCO_3})_{\text{calcite}} = K \times (a_{TE^{2+}}/a_{Ca^{2+}})_{\text{seawater}} \tag{3}$$

where a is the activity of solid and solution phases. Activities, which represent thermodynamic or effective concentrations, are not easily measurable and do not relate in any necessarily simple way to bulk measured concentrations. Because the distribution constant K is an intrinsic thermodynamic property of the system, it can be calculated from the thermodynamic properties of the products and reac-

tants. Given that there is no simple way to determine solid phase activities and that the empirical partition coefficient generally does not reflect thermodynamic equilibrium, the best practice is to determine the partition coefficient D by empirical means, and use the thermodynamic constant K as a point of comparison only.

The thermodynamic constant K will change with properties such as temperature if the solubility of the pure trace metal phase changes differentially relative to pure calcite. A documented example of this is the solid solution of $SrCO_3$ in aragonite, for which the solubility of $SrCO_3$ increases to a greater extent with rising temperature than for aragonite, leading to progressively lower Sr/Ca (less solid $SrCO_3$) at higher temperatures. This thermodynamic relationship is exploited as a paleotemperature tool in corals (Beck *et al.,* 1992). The extent to which D will change with environmental parameters is dependent on both thermodynamic and kinetic (biological) factors. Any parameter that changes the rate of calcification also has the potential to change D (Lorens, 1981), although it is not easy to predict the potential magnitude of such changes in biological systems. For example, calcification rate increases with rising pH, which increases the incorporation of Sr in calcite (Morse and Bender, 1990). One of the challenges faced by researchers is sorting out the extent to which thermodynamic and kinetic influences determine the dependence of trace elements such as Mg on temperature. True thermodynamic dependence, such as is observed for oxygen isotopes, is most likely to lead to robust proxies that will not be undermined by unpredictable kinetic influences.

There are two general mechanisms for trace element incorporation in foraminiferal calcite: direct solid solution, in which the trace element substitutes directly for Ca^{2+} in the calcite structure, and trapping, in which the trace element occurs as a discrete phase or absorbed ion (Pingitore, 1986). Substitution by isomorphous solid solution undoubtedly provides the more robust mechanism for trace element incorporation, because it is most likely to be primarily regu-

lated by thermodynamics. Trace elements with ionic radii compatible with the Ca^{2+} site and chemical structures isomorphous with calcite are most likely to exhibit regular ionic substitution into foraminifer shells (Reeder, 1983) (Table 15.1). Trace element occurrence by trapping is far less likely to lead to homogeneous mineral composition, and trapping is more likely to be affected by kinetic factors such as precipitation rate. It must also be recognized that some trace elements might be incorporated by a combination of factors, in which case the element might be uniformly distributed by solid solution but also concentrated preferentially in some parts of the crystal by trapping.

15.3.3 Biology of trace element incorporation and role of live culturing

Foraminifera are living organisms, and, therefore their biology influences the precipitation of shell calcite. Geochemists have termed this the 'vital effect,' a term that generally encompasses the sum of biological influences without attempting to unravel their causes. Comparison of empirical partition coefficients (D) with predicted thermodynamic distribution constants (K) indicates that the biology of calcification offsets foraminifer shells from equilibrium values (Elderfield *et al.,* 1996). Shell calcification is relatively rapid, variable in time, and influenced by external factors, all of which contribute to non-equilibrium precipitation (Lea *et al.,* 1995).

Empirical partition coefficients are most commonly determined by calibrating foraminiferal shell chemistry from core-top sediments with estimates of seawater chemistry and physical conditions (Hester and Boyle, 1982; Lea and Boyle, 1989; Boyle, 1992; Rosenthal *et al.,* 1997b). These calibrations implicitly include all vital effects, as well as any possible post-depositional factors. Core-top calibrations, however, cannot be used to separate and attribute individual biological influences or determine how vital effects might vary spatially, especially through the secondary influence of oceanographic parameters.

Live culturing is an important means by

Table 15.1 Trace element abundance in foraminiferal calcite. The values quoted for planktonic and benthic Foraminifera are the normal observed ranges of shell abundances. The values quoted for seawater concentration are the normal observed ranges of total element concentration in the pelagic surface and deep ocean. The partition coefficient is the ratio of metal/Ca in the foraminifer shell to metal/Ca in seawater. Proxy indicates the mostly closely allied seawater property for each trace element. Ionic radii from Shannon (1976), crystal structures from Speer (1983). Calcite is rhombohedral, aragonite is orthorhombic. Foraminiferal data and partition coefficients from sources cited in text. Seawater data from Bruland (1983).

Element	Ion in calcite	Ionic radius (Å)	Crystal structure	Planktonic (mol/mol Ca)	Benthic (mol/mol Ca)	Seawater concentration (mol/kg)	Partition coefficient D	Proxy
Calcium	Ca^{2+}	1.00	rhombohedral	1	1	10.3×10^{-3}		
Carbon	CO_3^{2-}	2.50	rhombohedral	1	1	2–2.5×10^{-3}		
Magnesium	Mg^{2+}	0.72	rhombohedral	0.5–5×10^{-3}	0.5–10×10^{-3} (neritic = 0.13–0.15)	53.2×10^{-3}	0.1–1×10^{-3}	temperature
Sodium	Na^{+}	1.02		4–7×10^{-3}		468×10^{-3}	10×10^{-6}	?
Strontium	Sr^{2+}	1.31	orthorhombic	1.2–1.6×10^{-3}	0.9–1.6×10^{-3} (neritic = 2–2.4×10^{-3})	90×10^{-6}	0.11–0.19	seawater chemistry, pressure?
Fluorine	F^{-}	1.33		0.5–3×10^{-3}	0.3–4×10^{-3}	68×10^{-6}		
Boron	$B(OH)_4^{-}$			60×10^{-6}	60×10^{-6}	0.416×10^{-3}		pH
Lithium	Li^{+}	0.76		10–30×10^{-6}		25×10^{-6}	0.01	seawater chemistry
Manganese	Mn^{2+}	0.83	rhombohedral	1–100×10^{-6}	1–500×10^{-6}	0.2–3×10^{-9}	2?	diagenesis
Zinc	Zn^{2+}	0.74	rhombohedral	10–75×10^{-6}	1.5–6×10^{-6}	0.05–9.0×10^{-9}		silicic acid
Barium	Ba^{2+}	1.47	orthorhombic	0.5–$2 (10) \times 10^{-6}$	1.5–5×10^{-6}	32–150×10^{-9}	0.15–0.4	alkalinity
Iron	Fe^{2+}?	0.78	rhombohedral	$<0.1 \times 10^{-6}$	$<0.1 \times 10^{-6}$	0–2.5×10^{-9}		diagenesis?
Copper	Cu^{2+}	0.73	rhombohedral	$<0.1 \times 10^{-6}$	$<0.2 \times 10^{-6}$	0.5–6×10^{-9}		nutrient
Neodymium	Nd^{3+}	0.98	orthorhombic	$<0.1 \times 10^{-6}$		5–35×10^{-12}	<100	seawater chemistry
Cadmium	Cd^{2+}	0.95	rhombohedral	0.002–0.1×10^{-6}	0.02–0.25×10^{-6}	0.001–1.1×10^{-9}	1.3–3.0	phosphate
Vanadium	HVO_4^{2-}			20–40×10^{-9}	112×10^{-9}	20–35×10^{-9}	2–32×10^{-3}	seawater chemistry
Uranium	UO_2^{2+}	3.46	orthorhombic?	5–10×10^{-9}		13.6×10^{-9}	7–8×10^{-3}	seawater chemistry

which such biological effects can be unraveled. For example, factors that are known to influence Foraminifera, such as light (via its influence on symbiotic dinoflagellates), temperature, salinity, and pH, can be varied systematically by experimentation. Since the early 1980s, live culturing of Foraminifera has become an important tool to assess trace element incorporation in shells. Culturing offers the advantage of direct experimentation, which removes much of the ambiguity associated with calibration by indirect means. To date most culturing studies have focused on spinose planktonic Foraminifera, but some activity has been directed towards culturing benthic species and non-spinose planktonic species (Bé et al., 1977a; Hemleben et al., 1989; Chandler et al., 1996).

Pioneering studies conducted by Peggy Delaney and Allan Bé assessed Cd, Mg, Sr, Na, and Li incorporation in tropical spinose Foraminifera (Delaney et al., 1985; Delaney, 1989). Subsequently, different research groups have investigated Ba, Cd, B, and Ca uptake (Lea and Spero, 1992; Lea and Spero, 1994; Lea et al., 1995; Sanyal et al., 1996; Mashiotta et al., 1997), U and V uptake (Russell et al., 1994; Hastings et al., 1996b), and Mg uptake (Nürnberg et al., 1996; Mashiotta et al., in press). Culturing studies are beginning to reveal the detailed biological influences on trace element uptake. One example of such an influence is the observation that symbiotic dinoflagellates sequester Cd, thus reducing the Cd content of shell calcite (Mashiotta et al., 1997).

15.4   SAMPLE PREPARATION AND ANALYTICAL TECHNIQUES

Many of the trace elements determined in foraminifer shells are in very low abundances, and the presence of extraneous phases which contain high trace element levels can obscure the determination of the primary material. It is therefore necessary to purify the foraminifer shells by both physical and chemical steps. Rigorous purification procedures were developed by Edward Boyle to determine the very low levels of Cd in shells (Boyle, 1981; Boyle and Keigwin, 1985/1986). These consist of alternate steps of physical agitation to remove detrital grains and chemical treatment, including oxidation of organic matter, reduction of Fe and Mn oxides, and acid leaching of adsorbed ions. Boyle's purification techniques, with various degrees of modification depending on individual circumstances for each element, are the accepted standard for preparing foraminifer shells for trace element determination. Modifications of this purification cleaning method have been made for foraminiferal Ba (Lea and Boyle, 1993) and improved Cd determination (Rosenthal et al., 1997a).

Given the range of trace elements determined in foraminifer shells, it is not surprising that there are a number of methods used to make measurements. Because trace elements have been routinely determined in foraminifer shells only since about 1980, the analytical techniques are less standardized than for stable isotope determinations. Among the predominant analytical techniques are:

Atomic Absorption Spectrophotometry (AAS): AAS has been used to determine Ca, Mg, Na, Sr, Li, Mn, Cd, and Zn in foraminifer shells (Boyle, 1981; Delaney et al., 1985). AAS relies on the unique atomic absorption spectra of each element; trace element abundances are quantified by comparing the absorption of a sample to that of a known standard. Graphite furnace AAS (GFAAS) is an extremely sensitive technique which is used to determine the very low levels of Cd and Zn in foraminifer shells.

Inductively Coupled Plasma Mass Spectrometry (ICP-MS): ICP-MS has been used to determine Ca, Mg, Sr, Mn, Ba, Cd, U, and V in foraminifer shells (Lea and Boyle, 1993; Russell et al., 1994; Hastings et al., 1996b; Lea and Martin, 1996; Rosenthal et al., 1997b). ICP-MS uses a quadrupole or magnet to directly differentiate the masses of individual isotopes ionized in a plasma. Trace element abundances are quantified by either isotope dilution, internal standardization, and/or reference to gravimetric standards. ICP-MS is comparable in sensitivity to GFAAS but offers the advantage of simultaneous determination of elements.

Thermal Ionization Mass Spectrometry (TIMS): TIMS has been used to determine Sr, Sr isotopes, B, B isotopes, Ba, U, and V (DePaolo and Ingram, 1985; Russell *et al.,* 1994; Hastings *et al.,* 1996b; Sanyal *et al.,* 1996). TIMS uses a magnet to differentiate the masses of individual isotopes ionized from a solid filament. Trace element abundances are quantified by isotope dilution; isotope ratios are quantified by reference to standards with known ratios. TIMS is a relatively slow technique but offers superior precision by a factor of 10–1000 over ICP-MS and AAS.

A technique likely to become important in the near future is *High Resolution Multi-Collector ICP-MS*. This technique combines the precision of TIMS with the rapid throughput of ICP-MS (Halliday *et al.,* 1998). It is likely that in the future, geochemists will be able to determine both low level trace elements such as Cd and high precision isotope ratios such as $^{87/86}Sr$ by this technique.

15.5 ABUNDANCE OF TRACE ELEMENTS IN FORAMINIFERAL CALCITE

Abundances of trace elements in Foraminifera are commonly presented in molar units (mol element per mol Ca) or sometimes in weight units (usually ppm, which denotes μg of the trace element per g of calcite). Molar units are preferable because they can be directly related to elemental ratios in seawater. To convert between units, use the following equation:

ppm = mol element/mol Ca

$\qquad$ × atomic weight/100 g

example:

0.1 μmol Cd/mol × 112.411 g Cd/mol/100 g

$\qquad$ = 0.112 ppm = 112 ppb

Fifteen trace elements have been sufficiently documented so that their actual presence in shell calcite (as opposed to in extraneous phases such as organic compounds, oxides, or clays) is rea-

Trace elements in foraminifer shells
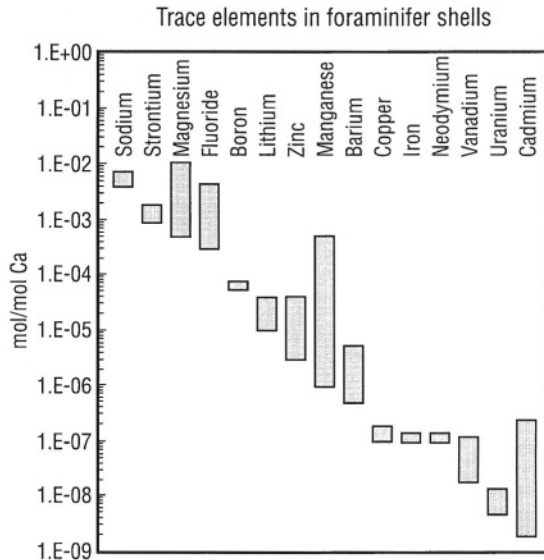
Figure 15.1 Trace element abundances in foraminifer shells in moles of element per mole Ca. The ranges are the minimum and maximum observed concentrations (Table 15.1). Data sources are listed in the text.

sonably certain (Table 15.1; Fig. 15.1). Four elements, Mg, Na, Sr, and F, are present at abundances of greater than 10^{-3} mol/mol Ca. Because these elements occur at levels of up to 0.25% by weight, they are often termed *minor elements*. Five of the trace elements, B, Li, Mn, Zn, and Ba are present at abundances between 10^{-3} and 10^{-6} mol/mol. The remaining six trace elements, Fe, Cu, Nd, Cd, V, and U are present at abundances between 10^{-6} and 10^{-9} mol/mol. The metals Mg, Sr, Mn, Zn, Ba, Fe, Nd, and Cd are known to form solid solutions isomorphous with either calcite or aragonite (Table 15.1) (Speer, 1983). Therefore these metals are most likely to be directly interpretable in terms of their chemical behavior in shells.

15.6 NUTRIENT PROXIES: Cd AND Ba

15.6.1

The most developed and well understood trace element proxies are those used to assess past nutrient concentrations, mainly Cd and Ba. Understanding the concentration and distribu-

tion of nutrients and carbon in ancient oceans is a prime problem in paleoceanography (Boyle, 1990). Using planktonic and benthic Foraminifera, nutrient proxies can be used to reconstruct nutrient and carbon chemistry in surface and deep waters. Levels of surface water nutrients are directly linked to the cycle of carbon dioxide and oceanic productivity by Redfield ratios (Broecker and Peng, 1993). Because the distribution of nutrients in the deep ocean is a direct reflection of the thermohaline flow of abyssal waters, deep-water nutrient distributions can in turn be used to deconvolute water mass mixing or to fingerprint source waters.

15.6.2   Cadmium

The oceanic behavior of Cd closely mimics that of phosphate in the water column, and Cd is the most direct nutrient analog available (Fig. 15.2a) (Boyle, 1976, 1988a). Cd also forms a solid solution with calcite, and therefore, Cd is expected to exhibit systematic behavior when incorporated into shells. Cd occurs at very low concentrations in the oceans, ranging from

Figure 15.2 Foraminiferal Cd as a paleoceanographic proxy. (a) The correlation between Cd and phosphate, a primary limiting nutrient, in present-day seawater (Boyle, 1988a). The most nutrient-depleted oceanic surface waters are similarly low in Cd and P; the most nutrient-rich Pacific deep waters are similarly enriched in Cd and P. Reprinted from Boyle, 1988a. (b) Core-top calibration of Cd in benthic Foraminifera versus estimated bottom water Cd concentrations (from Boyle, 1988a). Species plotted include *Uvigerina* spp., *Cibicidoides kullenbergi*, *Nuttallides umbonifera*, and *Cibicides wuellerstorfi*. The data demonstrate that the benthic foraminifer shells take up Cd with a partition coefficient of 2.9 ± 0.6, and that there are no significant differences in Cd uptake among species. (c) Culturing calibration of Cd uptake in the planktonic species *Globigerina bulloides* and *Orbulina universa* (Mashiotta *et al.*, 1997). Foraminifera were cultured in seawater enriched with the rare stable isotope [111]Cd. The results demonstrate that the shells of symbiont-barren *G. bulloides* take up Cd with a partition coefficient of 1.9 ± 0.2, similar to benthic species. In contrast, symbiont-bearing *O. universa* incorporates very little Cd in shells ($D = 0.095 \pm 0.021$), presumably because the symbiotic algae deplete the calcifying environment of Cd. Reprinted from *Geochimica et Cosmochimica Acta*, 61, Mashiotta, T.A. *et al.*, Experimental determination of Cd uptake in shells of the planktonic foraminifers *Orbulina universa* and *Globigerina bulloides*: Implications for surface water paleoreconstructions, 4053–4065, Copyright 1997. with permission from Elsevier Science.
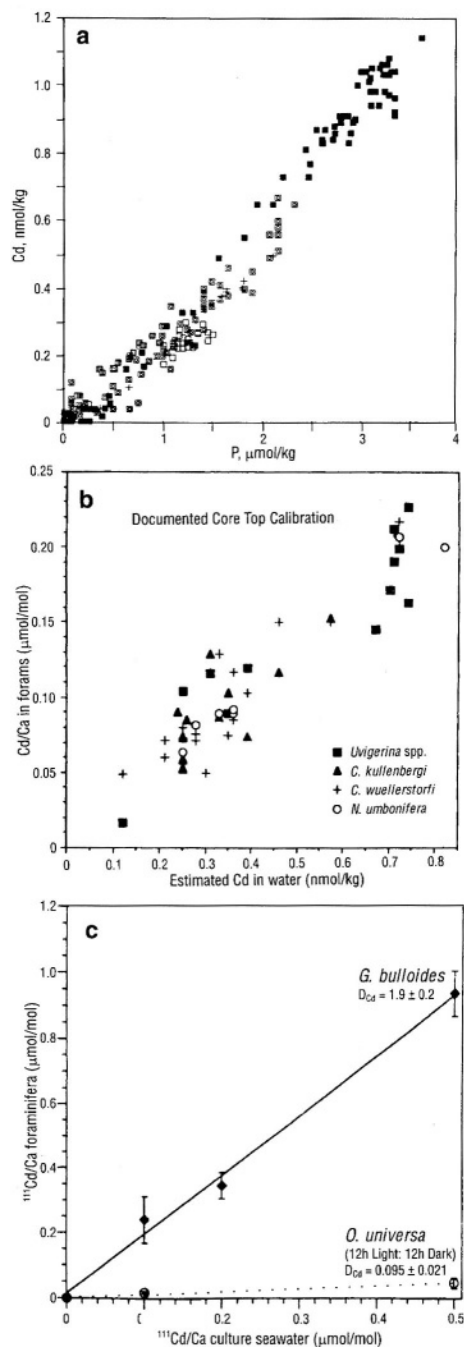
10^{-12} mol/kg in the most nutrient depleted surface waters to 10^{-9} mol/kg in the most nutrient-enriched deep waters (Bruland, 1983). It follows that the abundance of Cd in foraminifer shells is also very low, ranging from 0.001 μmol/mol in tropical spinose planktonic species such as *Globigerinoides sacculifer* and *G. ruber* to 0.250 μmol/mol in benthic genera *Cibicidoides* and *Uvigerina* from the Pacific. The low levels of shell Cd make shell purification particularly critical and Cd analysis challenging.

Regular uptake of Cd into foraminifer shells has been demonstrated by comparing the Cd/Ca of core-top benthic Foraminifera to bottom water Cd concentrations (Fig. 15.2b) (Hester and Boyle, 1982; Boyle, 1988a, 1992). These studies demonstrate that the partition coefficient *D* for Cd in benthic foraminifer shells is between 1 and 3. Research indicates a depth (pressure?) effect on Cd incorporation, and Boyle has proposed that this effect can be corrected by interpolating between *D* values of 1.3 (at depths < 1150 m) and 2.9 (at depths > 3000 m) (Boyle, 1992). There are insignificant differences in D among calcitic species. Potential complications in using benthic Cd include: (1) the diagenetic addition of sedimentary Cd trapped or added by Mn-carbonate overgrowths (see below) (Boyle, 1983); (2) influence of pore water Cd on benthic Foraminifera, particularly those with infaunal modes of life (McCorkle and Klinkhammer, 1991; Martin *et al.*, 1996); and (3) a possible dissolution effect on shells deposited below the lysocline (McCorkle *et al.*, 1995).

The vast majority of effort in studying shell Cd has been directed at determining bottom water concentrations of Cd, mainly with the objective of assessing shifts in abyssal circulation. Cd records were instrumental in establishing that the flux of North Atlantic Deep Water (NADW) was weaker during cold glacial climate periods (Figs. 15.3a, b) (Boyle and Keigwin, 1982, 1985/1986, 1987; Boyle, 1990, 1995; Boyle and Rosener, 1990; Boyle and Rosenthal, 1996; Rosenthal *et al.*, 1997a). Boyle used Cd to establish the 'deepening' of nutrients during glacial episodes, which might have contributed to the atmospheric pCO_2 drawdown (Boyle, 1988b,c),

and to assess changing mean ocean nutrients (Boyle, 1986, 1992). Boyle's findings have been verified and extended by other workers (Lynch-Steiglitz and Fairbanks, 1994; Ohkouchi *et al.*, 1994; Oppo and Rosenthal, 1994; Bertram *et al.*, 1995; Lea, 1995; Martin and Lea, 1998; Lynch-Steiglitz *et al.*, 1996; van Geen *et al.*, 1996). The use of Cd has been extended to the aragonitic genus *Hoeglundina* for studies of intermediate waters (Boyle *et al.*, 1995; Marchitto *et al.*, 1998), and to neritic benthic species to reconstruct paleo-upwelling in the California Current (van Geen *et al.*, 1992: van Geen and Husby, 1996). Some attempts have been made to investigate Cd in pre-Pleistocene sediments, but the potential for diagenetic influence is recognized as considerable (Delaney and Boyle, 1987; Delaney, 1990).

There has been less progress in utilizing Cd signals in planktonic Foraminifera. Boyle's early work showed that Cd could be measured in planktonic species and that differences in Cd/Ca between species tracked known depth preferences (Boyle, 1981). Because the limited surface water Cd range makes it difficult to do core-top calibrations, Cd uptake in planktonic species is best assessed by culturing studies (Fig. 15.2c) (Delaney, 1989; Mashiotta *et al.*, 1997). These studies demonstrate uptake of Cd with a partition coefficient of about 2. Mashiotta *et al.* (1997) further demonstrated that certain symbiont-bearing species have much lower uptake coefficients (0.1 to 0.4), most probably due to sequestration of Cd by symbiotic dinoflagellate algae. Published down-core work has mostly been confined to the polar species *Neogloboquadrina pachyderma* (Boyle, 1988b; Keigwin and Boyle, 1989), with recent work demonstrating significant sub-Antarctic nutrient shifts in *N. pachyderma* and *Globigerina bulloides* records (Mashiotta and Lea, 1997; Rosenthal *et al.*, 1997a).

15.6.3 Barium

Barium behaves like a nutrient in the oceans. In contrast to Cd, Ba is less readily regenerated
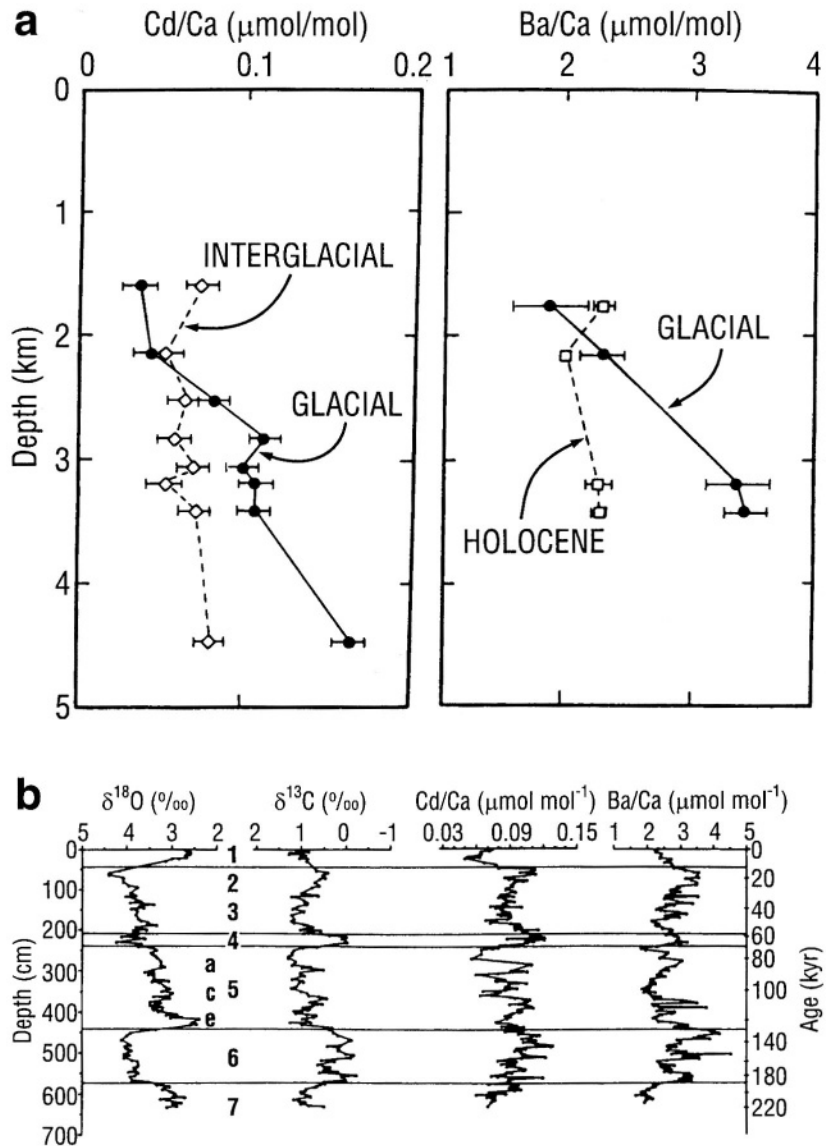
Figure 15.3 Paleoceanographic time series and hydrographic reconstruction using the paleo-nutrient proxies Cd and Ba. (a) Comparison of Holocene and glacial (20 kyr BP) depth profiles for Cd and Ba in the North Atlantic, as reconstructed from the composition of benthic foraminifer shells (Boyle and Keigwin, 1987; Lea and Boyle, 1990b). The data demonstrate that during the last glacial maximum, the Cd and Ba (and hence nutrient) content of abyssal Atlantic waters rose appreciably in response to a decline in the production rate of North Atlantic Deep Water. In contrast, the nutrient content of intermediate waters (<2 km water depth) was lower. Reprinted from *The Glacial World According to Wally*, Eldigio Press, Palisades, NY, Copyright 1993. (b) Time series of oxygen and carbon isotopes, Cd/Ca, and Ba/Ca in benthic Foraminifera from core CHN82–24–4PC in the North Atlantic at 42°N, 33°W, 3427 m water depth (Boyle and Keigwin, 1985/1986; Lea and Boyle, 1990a). The data demonstrate synchronous changes in the nutrient proxies (δ^{13}C, Cd/Ca, and Ba/Ca) that are clearly correlated to the waxing and waning of the continental ice sheets, as indicated by δ^{18}O. Differences between the proxies reflect their unique geochemistry. Reprinted by permission from *Nature* (Lea and Boyle, 1990a), Copyright 1990 Macmillan Magazines Ltd.

from sinking particles and therefore is most similar to the refractory properties alkalinity, sum of excess base, and silicic acid (Lea and Boyle, 1989, 1990b; Lea, 1993). Ba is depleted in surface waters through the precipitation of barite, $BaSO_4$ (Bishop, 1988). Deep waters are enriched by the dissolution of this barite, which predominantly dissolves on the seafloor (Chan *et al.*, 1977). The oceanic distribution of Ba reflects a combination of biogeochemical cycling and abyssal circulation, with concentrations ranging from 30×10^{-9} mol/kg in the nutrient depleted Pacific surface waters to 150×10^{-9} mol/kg in the most nutrient-rich waters of the north Pacific (Ostlund *et al.*, 1987).

Benthic Foraminifera reflect the distribution of bottom water Ba concentrations, ranging from about 2 µmol/mol in the North Atlantic to about 5 µmol/mol in the North Pacific (Lea and Boyle, 1989). They take up Ba with a partition coefficient of about 0.35, with small differences among species. A partition coefficient less than 1 indicates that Ba is discriminated against during precipitation, probably because it has an ionic radius sufficiently large to favor incorporation in the more open orthorhombic structure (Table 15.1). Foraminiferal Ba concentrations are about 20 times higher than Cd, but shell purification requirements are still considerable, because of the potential for barite contamination (Lea and Boyle, 1991, 1993). Ba incorporation in shells might also be affected by dissolution in sites below the lysocline, or alternatively by pressure affects (McCorkle *et al.*, 1995).

The paleoceanographic application of Ba has focused on reconstructing circulation changes and alkalinity shifts. Downcore records from the Atlantic ocean indicate that Ba increased in bottom waters by about 50% during glacial episodes (Figs. 15.3a,b) (Lea and Boyle, 1990a,b). In contrast, Ba was only 10–20% higher in glacial Circumpolar Deep Water (CPDW) and about 20% lower in glacial Pacific deep waters (Lea and Boyle, 1990b; Lea, 1993, 1995). The implication of these changes is that reduced production of NADW during glacial episodes essentially eliminated the large gradient in bottom

water Ba that exists today between the Atlantic and Pacific. The picture of glacial abyssal circulation derived from benthic Ba is somewhat different than that from Cd and $\delta^{13}C$, and current research focuses on understanding these differences and how they provide clues to shifts in physical, chemical and biological factors between glacial and interglacial episodes (Martin and Lea, 1998). Ba has also been used to estimate alkalinity changes in Antarctic waters. Results from the glacial sections of Southern Ocean cores suggest that alkalinity shifts due to circulation changes are too small to account for the glacial drawdown in atmospheric pCO_2 (Lea, 1993, 1995).

Culturing results and core-top determinations demonstrate that Ba is incorporated into spinose planktonic shells with a partition coefficient of 0.15, less than half of D for benthic shells (Lea and Boyle. 1991; Lea and Spero, 1992, 1994). This difference presumably relates to calcification rate differences between planktonic and benthic Foraminifera. There is evidence that non-spinose species incorporate considerably more Ba, although an explanation is wanting. Downcore Ba records from planktonic Foraminifera have not revealed climatically significant shifts (Lea and Boyle, 1990a, 1991)

15.7   PHYSICAL PROXIES: Mg, Sr, F, AND $^{10}B/^{11}B$

15.7.1

Physical proxies are those elements for which shell variability is primarily mediated by physical factors such as temperature, salinity, pressure, or pH. The best candidates are those elements that behave conservatively in the oceans, and therefore occur in nearly constant proportion to calcium in seawater. (Boron isotopes are unique among the physical proxies; see below.) The controls on shell chemistry might occur through the direct influence of physical factors on the trace element partition coefficient, or alternatively, occur indirectly through the effect of physical parameters on

biological factors such as calcification rate. The influence of calcification rate on trace element incorporation is probably related to shifts in mass transport and surface reaction kinetics (Morse and Bender, 1990). Paleoceanographers are inclined to establish relationships between shell trace elements and physical parameters by empirical means, and leave the details of the chemical and biological controls to future studies. But if Mg, Sr, and F incorporation is mediated by a complex indirect pathway involving calcification rate, it is less likely that these elements will be robust proxies of physical changes in the past. One area of particular concern is that there is a general relationship between Mg and Sr in shells, suggesting that their incorporation might be linked (Carpenter and Lohmann, 1992).

15.7.2   Magnesium

The study of Mg in carbonate fossils (including Foraminifera) has been an area of geological interest for almost a century (Clarke and Wheeler, 1922). At that time it was already recognized that carbonate shells precipitating in warm water tended to contain higher levels of Mg than their counterparts in cold waters. Two down-core records from the subantarctic Indian Ocean first indicated that planktonic shell Mg variations correlate with climate change in the late Quaternary, with higher levels of Mg associated with warm climate periods (Cronblad and Malmgren, 1981). However, early systematic attempts to isolate temperature as a controlling factor on planktonic foraminiferal Mg, using core-top, sediment trap, sediment, and cultured samples, failed to yield an unambiguous relationship between Mg and inferred growth temperature (Savin and Douglas. 1973; Bender et al., 1975; Delaney et al., 1985).

Mg/Ca in planktonic Foraminifera varies from about 0.5 to 5 mmol/mol, with a increase in Mg from cold to warm waters. Surface-dwelling spinose species contain more Mg than their deeper-dwelling non-spinose counterparts, presumably because of temperature control (Savin and Douglas, 1973; Bender et al., 1975; Delaney et al., 1985; Rosenthal and Boyle. 1993). Benthic foraminifer Mg/Ca ranges from 0.5 to 10 mmol/mol, with the highest values in shells from the shallowest (warmest) sites (Izuka, 1988; Rathburn and Deckker, 1997; Rosenthal et al., 1997b). Given that seawater Mg/Ca is 5.17 mol/mol (Bruland, 1983), the partition coefficient for foraminifer shells is of order 0.001, indicating that shell precipitation strongly discriminates against Mg.

Interest in using shell Mg as a proxy of sea surface temperature (SST) has intensified in the 1990s. Culturing and surface sediment studies have demonstrated a strong dependence of both planktonic and benthic shell Mg/Ca on growth temperature (Figs. 15.4a,c), while down-core studies suggest that systematic oscillations in shell Mg with climate change do exist in the deep-sea record (Nürnberg, 1995; Nürnberg et al., 1996; Mashiotta et al., in press; Rathburn and Deckker, 1997; Rosenthal et al., 1997b). Parallel studies, however, have suggested that

Figure 15.4 Magnesium and Sr in foraminifer shells. (a) Compilation of Mg/Ca in core-top and cultured planktonic Foraminifera versus actual or inferred growth temperature (Nürnberg et al., 1996). The closed circles indicate results from cultured specimens of *Globigerinoides sacculifer*. Most of the data describe an exponential relationship between shell Mg/Ca and seawater temperature. Shell Mg/Ca doubles for every 8°C increase in temperature. Reprinted from *Geochimica et Cosmochimica Acta*, 60, Nürnberg, D. *et al.*, Assessing the reliability of magnesium in foraminiferal calcite as a proxy for water mass temperatures, 803–814, Copyright 1996, with permission from Elsevier Science. (b) Magnesium/Ca and Sr/Ca in core-top specimens of *Globorotalia tumida* from the Ontong Java Plateau plotted versus water depth (Brown and Elderfield, 1996). The calcite saturation horizon is at about 3200 m; the foraminiferal lysocline is at about 3400 m. The data indicate that post-depositional dissolution of the shells leads to decreases in Mg/Ca and Sr/Ca. Apparently, the portion of the *G. tumida* shells enriched in Mg and Sr is the most likely fraction to be removed by dissolution. Reprinted from Brown and Elderfield, 1996. (c) Magnesium/Ca and Sr/Ca in core-top specimens of *Cibicidoides* and *Cibicides* from broad oceanic regions plotted versus water depth (Rosenthal et al., 1997b). The data demonstrate that Mg/Ca in benthic foraminifers follows water temperature. In contrast, Sr/Ca shows a linear decrease with depth, which might reflect the influence of pressure. Reprinted from *Geochimica et Cosmochimica Acta*, 61, Rosenthal, Y. *et al.*, Temperature control on the incorporation of Mg, Sr, F and Cd into benthic foraminiferal shells from Little Bahama Bank: prospects for thermocline paleoceanography, 3633–3643, Copyright 1997, with permission from Elsevier Science.

a Mg/Ca$_{observed}$ (mol/mol) vs T(°C)

- ● G. sacculifer (Nürnberg *et al.*, 1996)
- ○ N. pachyderma sin., South Atl. (Nürnberg, 1995)
- ■ N. pachyderma sin., North Atl. (Nürnberg, 1995)
- + N. dutertrei (Rosenthal & Boyle, 1993)
- ○ G. ruber (Rosenthal & Boyle, 1993)
- × G. sacculifer (Rosenthal & Boyle, 1993)
- ▲ G. sacculifer (Delaney et al., 1985)
- ★ G. menardii (Delaney et al., 1985)
- ○ G. sacculifer (Delaney et al., 1985) sed. trap.
- ＊ G. memardii (Delaney et al., 1985) sed. trap.

Mg/Ca = 0.00047 * exp(0.082*T)

b Water depth (m)

Mg/Ca (mmol/mol) — *G. tumida*

Sr/Ca (mmol/mol) — *G. tumida*

c Depth (m)

Mg/Ca (mmol mol^{-1}) — *Cibicidoides*

Sr/Ca (mmol mol^{-1}) — *Cibicidoides*

- ◆ Little Bahama Bank
- ◇ Atlantic Ocean
- ○ Equatorial Pacific

Temperature °C

there are strong post-depositional effects on shell Mg in some species, most likely due to preferential dissolution of Mg-enriched portions of the shells (Fig. 15.4b) (Savin and Douglas, 1973; Hecht *et al.,* 1975; Lorens *et al.,* 1977; Rosenthal and Boyle, 1993; Russell *et al.,* 1994; Brown and Elderfield, 1996).

Sorting out the controls and potential usefulness of Mg is a most important contemporary problem in foraminiferal trace element research. If shell Mg can be used for paleothermometry, it would become a critical tool in paleoceanographic and paleoenvironmental research. Because shell Mg and $\delta^{18}O$ can be measured in the same phase, it is possible to calculate the $\delta^{18}O$ composition of the water from which the shell precipitated, if Mg can be converted to temperature (Mashiotta *et al.,* in press). Benthic Mg/Ca might be the best information on the history of deep-water temperatures. Research will be required on many fronts, including: (1) establishing why shell Mg varies with temperature (i.e. thermodynamic control versus kinetic or biological factors); (2) why different species have different shell Mg/Ca, and how that relates to foraminiferal habitat; and (3) what secondary factors might influence Mg, including post-depositional dissolution, and how these effects vary from species to species.

15.7.3   Strontium

Strontium is a conservative element in seawater with a long residence time of about 5 My. In similar fashion to Mg studies, systematic attempts to isolate the factors controlling foraminiferal Sr, using core-top, sediment trap, sediment and cultured samples, have failed to yield unambiguous relationships (Bender *et al.,* 1975; Delaney *et al.,* 1985). These studies, however, demonstrate that Sr/Ca is much more uniform than Mg/Ca in planktonic Foraminifera, varying from about 1.2 to 1.6 mmol/mol, and that Sr is incorporated with a partition coefficient of about 0.16. An 80 My record of shell Sr suggests that oceanic Sr concentrations have changed significantly (Graham *et al.,* 1982; Delaney and Boyle, 1986), and a published late Quaternary

record (Cronblad and Malmgren, 1981) suggests that shell Sr variations correlate with climate change.

Recent studies, focused on benthic Foraminifera (Fig. 15.4c) (McCorkle *et al.,* 1995; Elderfield *et al.,* 1996; Rathburn and Deckker. 1997; Rosenthal *et al.,* 1997b), have demonstrated that there is a systematic decrease in benthic shell Sr with water depth throughout the oceans. Temperature, pressure and calcite saturation have all been suggested as potential controls. However, the linearity of the Sr decrease with depth and the uniformity of this relationship in the oceans suggest that pressure is the most likely cause of the change.

Foraminifer shells record small but systematic shifts of about 5% in Sr/Ca over the last 250 kyrs (Martin *et al.,* 1997). These shifts are clearly correlated with climate episodes, and provide tantalizing evidence that oceanic Sr concentrations might have oscillated in response to changes in the partitioning of shelf carbonates (high in Sr) and pelagic carbonates (depleted in Sr) (Stoll and Schrag, 1998). However, confidently ascribing secular shifts in shell Sr to corresponding shifts in seawater Sr/Ca requires eliminating all other potential influences, including physical properties such as temperature, and secondary influences such as dissolution, which also change synchronously with climate.

15.7.4   Fluorine

Fluorine is a conservative element in seawater with a residence time of 0.5 My. Fluoride is one of the few anions that has been studied in carbonates (others include borate and sulphate), partly because anion incorporation is much less understood than cation incorporation. Theoretical considerations suggest that the proportion of F to Ca might reflect salinity variations (Rosenthal and Boyle, 1993). Recent studies do not demonstrate consistent relationships between shell F/Ca and temperature and salinity (Opdyke *et al*., 1993; Rosenthal and Boyle, 1993; Rosenthal *et al*., 1997b). A decrease in F/Ca of planktonic shells with increasing water depth demonstrates that post-depositional dissolution

modifies the fluorine of deposited shells (Rosenthal and Boyle, 1993).

15.7.5 Boron isotopes

The ratio of ^{10}B to ^{11}B (denoted $\delta^{11}B$) does not vary within the ocean. There is, however, a large isotopic fractionation between the two aqueous species – 'boric acid, $B(OH)_3$, and borate, $B(OH)_4^-$ (Spivack *et al.,* 1993). The ratio between boric acid and borate is a strong function of pH. If the charged borate species is the only one that is incorporated into foraminifer shells, the $\delta^{11}B$ composition of shells serves as a proxy of pH, a relationship demonstrated by both core-top and culturing studies (Spivack *et al.,* 1993; Sanyal *et al.,* 1995, 1996). Studies of ancient sediments suggest that shell $\delta^{11}B$ records substantial oceanic shifts in pH between glacial and interglacial episodes. However, the implied pH shifts are less homogeneous than might be expected, suggesting that oceanic pH changes in complex ways, or alternatively, there are other undocumented influences on shell $\delta^{11}B$.

15.8 CHEMICAL PROXIES: Li, U, V, $^{87}Sr/^{86}Sr$, AND $^{143}Nd/^{144}Nd$

15.8.1

Chemical proxies record secular changes in ocean chemistry. Like the physical proxies, chemical proxies are generally conservative in seawater. They differ from the physical proxies because variability in shell content over time is thought to be primarily mediated by changes in seawater composition. Seawater composition of these elements is controlled by inputs and outputs that are sensitive to climate change or tectonic reorganization. The chemical proxies include the isotope systems of Sr and Nd. Secular variations in the Sr isotopic composition of seawater are well established over geological time and have proven to be an important stratigraphic and geochemical tool.

15.8.2 Lithium

Li is a conservative element in seawater with a long residence time (> 1 My). One of its major oceanic sources is the hydrothermal interaction of seafloor basalt and seawater (von Damm *et al.*, 1985). Therefore, on long time scales, seawater Li might vary with shifts in the extent of seafloor spreading (Delaney and Boyle, 1986). Delaney attempted to document such shifts, and concluded that the limited variation in shell Li/Ca over the last 100 My constrains potential long term changes in hydrothermal venting of Li (and by implication production of seafloor basalt) to ± 30%.

15.8.3 Uranium and Vanadium

Both U and V, nearly conservative in seawater, have major oceanic sinks in suboxic (little or no oxygen) sediments, where reduction of U and V leads to their incorporation into insoluble phases. Thus, it is hypothesized that shifts in the areal extent of suboxic sediments would decrease the seawater concentrations of U and V, and this change would be recorded in foraminifer shells (Russell *et al.*, 1994, 1996; Hastings *et al.,* 1996a,b). Uranium and V occur as oxyanions in seawater and therefore would not be expected to substitute into shell calcite in any simple way. Russell *et al.* (1996) and Hastings *et al.* (1996a,b) used planktonic culturing to demonstrate the U and V are incorporated into shell calcite in proportion to their seawater concentration, both with partition coefficients of about 0.01. Down-core records of these elements are somewhat equivocal as to the extent of seawater shifts in U and V, partly because foraminifer U/Ca and V/Ca are subject to postdepositional change.

15.8.4 Strontium isotopes

The $^{87}Sr/^{86}Sr$ ratio of seawater is constant throughout the ocean because of the 5 My residence time of Sr (Faure, 1986). But on long time scales, seawater $^{87}Sr/^{86}Sr$ changes, because it reflects shifting balances between the various

source and sinks of dissolved Sr. Over the last 24 My (since the late Oligocene), the $^{87}Sr/^{86}Sr$ ratio of the oceans, as recorded in foraminifer shells and bulk deep-sea carbonates, has risen quite dramatically from about 0.7082 to the present value of over 0.7091 (Fig. 15.5). The nearly monotonic rise over the period serves as a useful stratigraphic tool (DePaolo and Ingram, 1985; Hodell *et al.*, 1991). The cause of this increase is hypothesized to be changes in the isotopic composition and flux of Sr from rivers draining uplifted continental areas such as the Himalayas, which include rocks enriched in radiogenic Sr (high $^{87}Sr/^{86}Sr$) (Raymo *et al.,* 1988; Edmond, 1992; Raymo and Ruddiman, 1992).

Foraminifer shells contain about 1.4mmol/ mol Sr/Ca (Fig. 15.1). Some researchers have used them exclusively for Sr isotopic work, and others argue that the same results can be achieved using bulk carbonate (Richter and DePaolo, 1988). Because all of the Sr in foraminifer shells is precipitated from seawater, and because these shells are likely to be less prone to diagenesis than the finer carbonate fraction,

it seems prudent to use foraminifer shells for Sr isotopic work.

15.8.5   Neodymium isotopes

In contrast to Sr, Nd is particle reactive and has a low seawater concentration ($< 25 \times 10^{-12}$ mol/kg) and a relatively short residence time (Bruland, 1983). The $^{143}Nd/^{144}Nd$ ratio of seawater varies from about 0.5120 in the Atlantic Ocean to 0.5125 in the Pacific Ocean (Faure, 1986). This difference arises because average continental rocks are depleted, whereas oceanic-basalts are enriched, in $^{143}Nd/^{144}Nd$. The Atlantic Ocean derives its Nd from the many rivers draining a dominantly continental terrain (for example the Amazon, Congo, and Mississippi). The Pacific derives its Nd from far fewer major rivers, which drain a dominantly basalt terrain, and from interaction with the great ridges of young basalt that characterize the Pacific basin.

Nd might be incorporated into Foraminifera via solid solution, although $NdCO_3$ is isomorphous with aragonite rather than calcite (Speer,
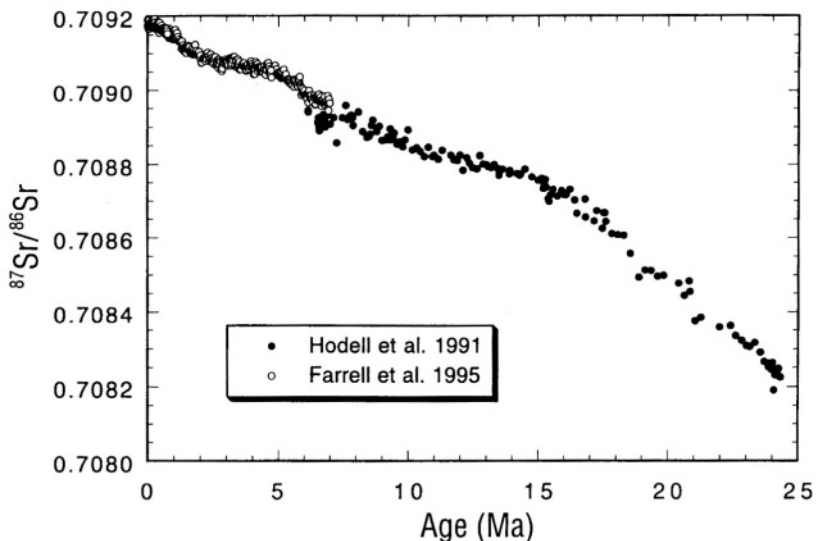
Figure 15.5 High resolution strontium isotope stratigraphy for the last 24 My, based on analyses of planktonic foraminifer shells; data from DSDP Hole 588 (Hodell *et al.*, 1991) and ODP Site 758 (Farrell *et al.*, 1995). The data indicate a rapid rise in seawater $^{87}Sr/^{86}Sr$ over this time period, presumably in response to an increase in the weathering of uplifted radiogenic rocks. The rise is sufficiently systematic that it can be used as a stratigraphic and chronological tool. Modified from Hodell *et al.*, 1991.

1983). There have been a number of efforts to use the isotopic composition of foraminiferal Nd as a recorder of shifts in weathering patterns (Palmer and Elderfield, 1986). Because Nd has a strong affinity for the Mn and Fe oxide phases that coat shells, it is very difficult to be certain that the measured Nd actually comes from shell calcite (Palmer, 1985; Palmer and Elderfield, 1986).

15.9 DIAGENETIC PROXIES

15.9.1

These are proxies that reveal information about the post-depositional history of foraminifer shells. Although diagenetic proxies do not provide primary information about past environments, they are a critical source of information about the long-term integrity of the primary chemical signal encoded in shells. Mn is the most important of the diagenetic proxies, because in most environments its presence above background levels indicates that Mn has been added to the shells by secondary precipitation. The physical proxies Mg, Sr, and F also appear to reflect aspects of the diagenetic history of foraminifer shells. In the context of using these elements as recorders of physical parameters, it is imperative that researchers separate the influence of primary and secondary factors on shell composition.

15.9.2 Manganese

A major issue in the study of any chemical proxy in marine sediments is the extent to which the primary chemical signature might be altered by post-depositional processes. One way in which this might happen is the precipitation of secondary coatings on shells. An example of such coatings is Mn-carbonate, a mineral that forms in the reducing conditions typical of ocean-floor sediments. Under the suboxic conditions that typically underlie productive oceanic regions, solid phase Mn is mobilized and released into pore waters by reduction to Mn^{2+}, which is

followed by precipitation of $MnCO_3$ (Boyle, 1983). Mn-carbonate is less soluble than calcite, and therefore the coatings cannot be easily separated from primary shell material. Mn-carbonate coatings are distinct from the Mn-oxide coatings which are far more common but can be removed by chemical reduction during sample preparation (Boyle, 1981). Mn-carbonate coatings either contain or trap high levels of certain trace elements such as Cd and Ba. An additional complication is that infaunal benthic Foraminifera incorporate pore water Mn into their shells, and pore water levels can vary by two orders of magnitude (Martin et al., 1996).

$MnCO_3$ precipitates appear to be ubiquitous in deep-sea cores, and in some oceanic regions it is difficult to find a site in which shells are not coated by precipitates. Researchers disagree in their definition of what is considered an acceptable level of shell Mn/Ca, from as low as 50 μmol/mol to as high as > 150 μmol/mol (Boyle, 1983; Boyle and Keigwin, 1985/1986; Delaney, 1990; Ohkouchi et al., 1994). With the exception of infaunal benthic Foraminifera, primary shell material has <1 μmol/mol Mn/Ca. Because Mn-carbonate shell coatings are a critical limiting factor for foraminiferal trace element proxies like Cd, investigations of how Mn-carbonate forms, why it appears to be precipitated heterogeneously between various foraminifer species, and how coatings might be removed from primary shell material will all further foraminiferal trace element research.

15.10 NEW FRONTIERS IN TRACE ELEMENT PALEOCEANOGRAPHY

Geochemists undoubtedly will continue to search for new foraminiferal trace element proxies. Most of the trace elements that would be expected to substitute in foraminifer shells at measurable concentrations have already been studied (Table 15.1). The prime remaining candidate is the transition metal Zn. Seawater Zn is a nutrient proxy somewhat intermediate between Cd and Ba, and it shows a strong oceanic association with silicic acid (Bruland, 1983).

This association suggests that Zn might be a unique candidate for the reconstruction of silicic acid concentrations in past surface waters. Zn also forms a solid solution in the calcite series (Reeder, 1983). The biggest potential drawback to utilizing foraminiferal Zn is that it is highly contamination prone (Boyle, 1981). Other trace elements that might be worthy of investigation in Foraminifera include:

(1) Na and K, and possibly Rb and Cs, which are conservative alkali metals that could possibly serve as physical proxies. Levels of Na in foraminifer shells are about 5 mmol/mol, but a specific control has not been demonstrated (Bender *et al.,* 1975; Delaney *et al*., 1985).

(2) Fe, Co, Ni, Cu, and Ag are all transition metals which are possible nutrient and/or particle-reactivity proxies (Bruland, 1983; Martin *et al*., 1983; Martin and Gordon, 1988). Shell-bound Fe will be extremely difficult to determine, because of contamination from Fe bearing oxides and clays (Boyle, 1981). Both Co and Ag are present at $< 50 \times 10^{-12}$ mol/kg in seawater and will be consequently very low in foraminifer shells.

(3) REE, the rare earth elements including La, Ce, Nd, Sm, Eu, and Yb, might be useful as seawater chemistry and particle-reactivity proxies (Elderfield and Greaves, 1982; de Baar *et al*., 1985).Preliminary researchsuggests that it is difficult to separate shell bound REE from oxide-bound REE (Palmer, 1985).

Much of the research on nutrient proxies like Ba and Cd has focused on deep-water benthic Foraminifera, because of the interest in establishing changes in abyssal flow. The application of trace elements to the study of thermocline and upper intermediate waters is a relatively new, uncharted area (Rosenthal *et al.,* 1997b; Marchitto *et al.,* 1998). There are other important questions that might be answered using nutrient proxies in planktonic Foraminifera. Cd, in particular, appears to be a promising tool to characterize changes in nutrient supply and utilization in surface waters. Ba might be a sensitive tracer of riverine and melt water discharge.

Another frontier is the application of trace elements to studies of anthropogenic perturbation. It has already been demonstrated that Holocene shallow-water benthic Foraminifera record changing seawater Cd due to upwelling and pollution (van Geen *et al.,* 1992; van Geen and Husby, 1996). It should be possible to use this technique to demonstrate changes in coastal waters in response to pollution.

Finally, the application of foraminiferal trace elements to longer, million year time scales has so far been limited to only a handful of records (Graham *et al.,* 1982; Delaney and Boyle, 1986, 1987; Delaney, 1990). Elements present at truly trace concentrations, such as Cd, will be necessarily more difficult to study on these time scales, because the potential for diagenetic addition is high. But minor elements such as Mg and Sr, which might be less prone to diagenetic alteration, offer the potential to investigate some important problems, including the evolution of seawater temperatures and chemistry in the Tertiary.

15.11   SUMMARY AND CONCLUSIONS

Trace elements in foraminifer shells are controlled by seawater composition and the physical and biological conditions during calcification. Because it is possible to calibrate shell composition against the controlling factors, foraminiferal trace elements provide researchers with a toolbox of powerful proxies to investigate the chemical, physical, and biological evolution of the oceans. Some of the most important challenges faced by trace element researchers are to (1) establish precise relationships among shell chemistry, seawater composition, and physical and biological factors; (2) to apply elemental tracers to the past and take into account the range of potential complications that affect proxy interpretation; and (3) to establish which secondary factors such as diagenesis may affect post-depositional shell chemistry. With a precise knowledge of the factors that control shell composition, and in conjunction with stable isotopes, foraminiferal trace elements should provide a very powerful tool to study ocean and climate evolution.

15.12 ACKNOWLEDGMENTS

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**PART IV:
PRESERVATION
OF RECORD**

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16

Taphonomy and temporal resolution of foraminiferal assemblages

Ronald E. Martin

16.1 INTRODUCTION

The surface mixed layer of sediment, which ranges in thickness from a few centimeters to as much as a meter, acts as a low-pass filter that damps high frequency signals before their incorporation into the historical record. This damping mechanism is referred to as time-averaging, which is the process by which fossils of different ages are mixed into a single assemblage. Because of time-averaging, a fossil assemblage represents a *minimal* duration of (at best) a few decades, and more likely hundreds to thousands of years, unless the assemblage is rapidly preserved by unusual conditions (Lagerstätten). Time-averaging occurs because the generation times of organisms are inherently much shorter than net rates of sediment accumulation and burial (Kidwell, 1993). The mixed layer is also a taphonomically active zone (Davies *et al.,* 1989) in which stratigraphic signals are damped by biological mixing (bioturbation) and dissolution.

This chapter reviews what little is really known about the taphonomy and temporal resolution of foraminiferal assemblages in major depositional settings. Although post-mortem transportation of tests has been demonstrated to vary with respect to such factors as test size, shape, and density (e.g. Kontrovitz *et al.,* 1978, 1979; Zhang *et al.,* 1993), studies of assemblages suggest that little post-mortem transport of Foraminifera normally occurs (e.g. Snyder *et al.,* 1990a,b). Therefore, the effects of bioturbation and dissolution on the formation of foraminiferal assemblages are emphasized.

16.2 BIOTURBATION: TEMPORAL RESOLUTION AND PORE WATER CHEMISTRY

The most popular bioturbation models are based on the concept of diffusion (see Matisoff, 1982; Cutler, 1993; Martin, 1993, for reviews). Diffusion-based models assume that mixing is a random redistribution of sediment particles by large numbers of organisms over many individual transport events, and that, taken collectively, small transport events move particles over large distances (Martin, 1998, derives the

relevant equations using a random walk model). The Guinasso-Schink (1975) model, in particular, may be reduced to a dimensionless parameter (G) that represents the ratio of bioturbation ('biodiffusion') rate (D), sedimentation rate (v), and mixed layer thickness (m):

$$G = D/mv \qquad (1)$$

Reported biodiffusion coefficients vary by about six orders of magnitude and decrease from shallow water ($D \simeq 10^{-6} \, cm^2 \, sec^{-1}$) to the deep sea ($D \simeq 10^{-8} \, cm^2 \, sec^{-1}$; Matisoff, 1982; biodiffusion coefficients are also often stated in terms of thousands of years). Biodiffusion coefficients also typically decrease with depth, even within the same environment (Fig. 16.1; Aller and Cochran, 1976; Benninger *et al.,* 1979; Benoit *et al.,* 1979; Cochran and Aller, 1979).

Equation (1) has been criticized on a number of grounds. For example, according to the equation, a thick mixed layer should result in a better-preserved signal than a smeared one (Wheatcroft, 1990; Wheatcroft *et al.,* 1990; see Martin, 1998, for review of other criticisms). Nevertheless, G is heuristically useful in understanding the interplay of bioturbation and sedimentation rates and mixed layer thickness in generating a stratigraphic signal. When G is small ($\leqslant 0.1$; rapid v or slow mixing), an impulse tracer (such as a microtektite or volcanic ash layer) is transferred through the mixed layer before it can be extensively re-worked, and its concentration profile is bell-shaped or 'Gaussian' (Fig. 16.2). When G is large ($\geqslant 1$; slow v or rapid mixing), the tracer exhibits an exponential decrease upward and a nearly uniform distribution in the mixed layer (Fig. 16.2).

Under conditions of a thin mixed layer ($m \simeq 5$–$10 \, cm$) and rapid bioturbation, equation (1) reduces to a box model, in which tracers are assumed to be rapidly and homogeneously distributed in the mixed layer (Figures 16.1, 16.2), an assumption that is often unjustified (Berger *et al.,* 1979). The most frequently cited box model is that of Berger and Heath (1968):

$$\frac{-dP}{P} = \frac{-dL}{m} \qquad (2)$$

where P = probability of finding a particle in the mixed layer, L = thickness of sediment deposited on the layer, and m = mixed layer thickness.

Integrating (2) results in a decay formula:

$$P = P_0 e^{(-S/m)} \qquad (3)$$

Thus, if species z becomes extinct, the distribution of the species is given by:

$$P_z = P_{sz} e^{[-(S_e + m)/m]} \qquad (4)$$

where P_{sz} = original concentration of z at a distance of m below the level of extinction, and S_e = sediment thickness above (after) the extinction.

According to (4), the concentration of an
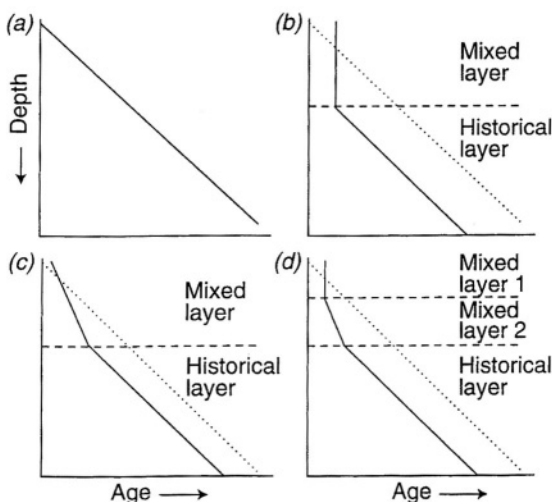
Figure 16.1 Hypothetical plots of mean tracer age versus depth in sediment. (A) No bioturbation. Slope of line is constant and determined by sediment accumulation rate only. (B) Completely bioturbated mixed layer. Within mixed layer, mean tracer age (solid line) is the same at all depths because of homogeneous mixing, and tracer age profile is shifted toward somewhat older ages because of upward reworking of older remains from historical layer. By contrast, age profile of tracer in *historical* layer is displaced toward younger mean age relative to unmixed profile (dotted line) because of downward reworking of younger material from mixed layer. (C) Gradual decrease of bioturbation rate with depth in mixed layer. Slope of age profile within mixed layer is proportional to D. Case C is intermediate between cases A and B. (D) Mixed layer consists of two layers. Mixed layers 1 and 2 have values like those for cases B and C, respectively; thus, mixed layer 1 is homogeneously mixed, whereas mixed layer 2 is not. (Modified from Cutler, 1993).
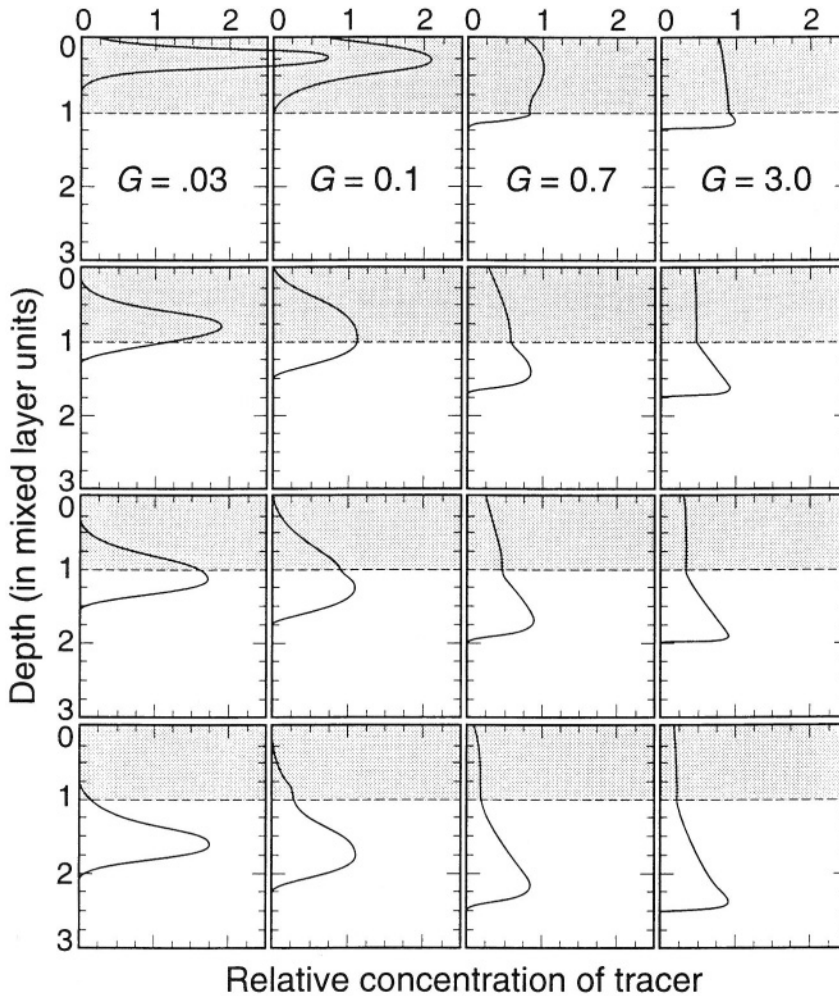
Figure 16.2 Time series showing the downward transmission of an impulse signal in relation to the mixing parameter G (equation (1)). Mixed layer indicated by stippling. Depth in mixed layer units; time normalized to time required for one mixed layer thickness to accumulate. When G is small (rapid sedimentation, slow mixing), an impulse tracer is buried below the mixed layer before it can be extensively reworked (bell-shaped profile). If G is large (slow sedimentation, rapid reworking), the concentration of tracer decreases upward exponentially, and its concentration in the mixed layer is relatively uniform. Modified from Guinasso and Schink (1975) after Martin (1993).

extinct species above its true level of extinction decreases upward exponentially according to the thickness of sediment deposited after its extinction. Based on equation (4), Berger and Heath (1968) calculated the proportion of the original concentration of a species z at a distance S_e above its disappearance. By specifying acceptable levels of reworking (contamination), the level of stratigraphic resolution was calculated. In their example, if $m = 4$ cm and contaminant level (due to reworking) is 10% of the original concentration of the species, then the original extinction level may be as much as 9 cm deeper in the section (Fig. 16.3; see also Fig. 16.4). For a sedimentation rate of 1 cm kyr^{-1}, this means a resolution of 9000 years; for a rate of 4 cm kyr^{-1}, a resolution of 2250 years is obtained. According to the model, the exact level of extinction is indicated when the concentration of the species is $1/e$ or 0.37 times its maximum
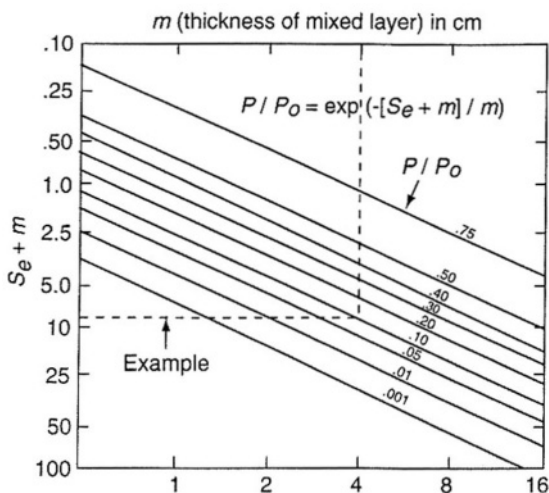
Figure 16.3 Proportion of the original concentration of a species (P/P_0) found in sediment at a distance S_e above its level of disappearance. See text for further discussion (modified from Berger and Heath, 1968).

concentration below, and is independent of the mixed layer thickness (Berger and Heath, 1968). Similar models were developed by these authors for species appearances: first appearance datums (FADs) tend to be smeared downward much less than last appearance datums (LADs) are smeared upward, because bioturbators are largely confined to the mixed layer, and tend to remain near the sediment-water interface (SWI) as sediment is deposited at the SWI from the water column (see also Glass, 1969).

Reworking of substantially older (ca. hundreds-of-thousands to millions-of-years) or younger microfossils into younger (or older) sediments by 'leaking' or 'piping' (remanié) is not usually a serious problem, and is all but ignored by biostratigraphers. In most cases, microfossil-based biostratigraphic zonations are sufficiently precise at such time scales that reworked specimens are typically recognized by their anomalous stratigraphic occurrence and qualitative state of preservation (surface degradation, breakage, infilling with foreign sediment). Berger and Heath (1968) concluded that bioturbation would not normally be responsible for such reworking, as the concentration of the reworked marker would probably be on the order of 10^{-6} of its original concentration when, in their example, the thickness of

sediment separating Recent from older material was as little as 1 m. They suggested that erosion is the dominant process mixing older assemblages into younger pelagic sediments. Cutler and Flessa (1990) came to a similar conclusion for shallow-water assemblages: bioturbation is a relatively inefficient means of producing stratigraphic disorder, but physical reworking disorders sequences rapidly.

In the case of ecostratigraphic studies. Berger and Heath (1968) concluded that serious stratigraphic errors may occur if the stratigraphic range of a species is similar in thickness to the mixed layer; this is likely to occur in the deep-sea during times of climatic fluctuations, when species may alternately appear and disappear relatively rapidly, leaving sufficient time for substantial biological reworking (cf. Fig.16.4d). Such signals are more easily deciphered under regimes of higher sediment accumulation rates (e.g. Martin *et al.,* 1993; Martin and Fletcher, 1995, for shallow continental slope of the northeast Gulf of Mexico). On even shorter time scales, size-selective transport of sediment particles (e.g. Foraminifera versus coccolithophorids, microtektites) back to the SWI by bioturbators may produce artifactual peaks (McIntyre *et al.,* 1967; Glass, 1969; Robbins, 1986; Wheatcroft and Jumars, 1987; Wheatcroft, 1992; cf. Ruddiman and Glover, 1972; Ruddiman *et al.,* 1980).

Besides smearing stratigraphic signals, bioturbation also affects pore water chemistry and hardpart preservation. Typically, beneath a surficial oxidized zone, bioturbation oxidizes organic matter and sulfides to produce carbonic and sulfuric acids, respectively (Walter and Burton, 1990):

$$CH_2O + O_2 \rightarrow H_2CO_3 \qquad (5)$$

$$2O_2 + HS^- \rightarrow SO_4^= + H^+ \qquad (6)$$
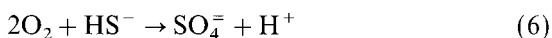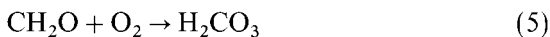
Conversely, bacterial sulfate reduction increases pore water alkalinity (total dissolved bicarbonate and carbonate ion, and smaller contributions of other ions such as borate), thereby enhancing shell ($CaCO_3$) preservation (Walter and Burton. 1990):
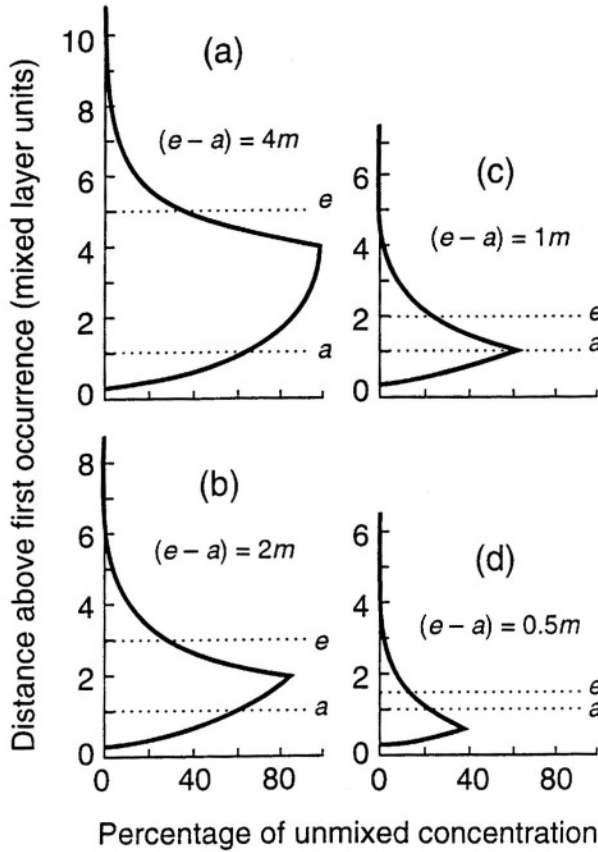
Figure 16.4 Biostratigraphic distribution of a taxon after vertical mixing. a and e denote levels of appearance and extinction, respectively, in each of four examples (a–d) of decreasing stratigraphic duration; thicknesses are measured in multiples of mixed layer thickness (*m*). Thin (short) intervals are more likely to be obscured by bioturbation (see text for further discussion). Modified from Berger and Heath (1968).

$2CH_2O + SO_4^=$

$$\rightarrow HS^- + HCO_3^- + H_2CO_3 \qquad (7)$$
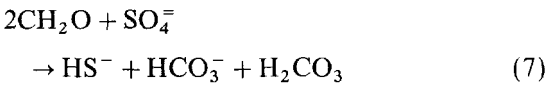
Alkalinity may also increase deeper in the sediment column as a result of other oxidation-reduction reactions involving organic carbon that use different electron acceptors (see Canfield and Raiswell, 1991, for review).

16.3 PRESERVATION AND TEMPORAL RESOLUTION IN MARINE SETTINGS

16.3.1 Carbonate shelves

Large reef-dwelling Foraminifera, such as *Amphistegina gibbosa* and *Archaias angulatus*,

often form highly-abraded, current-winnowed lags in shallow-water carbonate environments (Martin, 1986; Martin and Wright, 1988) that may dominate assemblages to the point of obscuring reef zonations (Martin and Liddell, 1988, 1989, 1991). These and other species would therefore be expected to persist in sediment for relatively long periods of time and to be mixed extensively both upward and downward in the mixed layer, which may be up to ~ 1 m thick in carbonate sediments (Walter and Burton, 1990).

Kotler *et al.* (1991, 1992) and Martin and Liddell (1991) conducted laboratory and field experiments that simulated abrasion, dissolution, and bioerosion of common reef foramini-

feral species based on energy conditions and depositional setting ('taphofacies') under which assemblages form (Liddell *et al.,* 1987; Liddell and Martin, 1989). With the exception of fragile species such as *Planorbulina acervalis,* the Foraminifera examined were resistant to abrasion. Abrasion-resistant forms varied substantially in susceptibility to dissolution, however: *Archaias angulatus,* which is prevalent in back-reef environments, dissolved rapidly, whereas *Amphistegina gibbosa,* which characterizes the reef crest and shallow fore reef, dissolved much more slowly. Differences in dissolution rate probably resulted from differences in both test architecture and mineralogy; tests of *Amphistegina gibbosa* and *Archaias angulatus* are, for example, characterized by 4–5% and 14–16% Mg-calcite, respectively.

Although Kotler *et al.* (1991, 1992) experimentally reproduced some natural abrasion and dissolution-related test surface features, surface features obtained in bioerosion experiments did not resemble natural features. This is not to say that bioerosion does not occur in carbonate sediments, as the process has been documented in a number of cases. Biological destruction of foraminiferal tests is caused by microbes (e.g. fungi), especially in quiet-water environments, and from selective or indiscriminate ingestion of tests by invertebrates and vertebrates, although the intensity of destruction varies considerably (see Martin and Liddell, 1991, for discussion and references). Nevertheless, in studies to date, shells of large taxa, such as bivalves, appear to be destroyed primarily by bioerosion (Aller, 1995; Cutler, 1995), whereas foraminiferal tests are lost primarily to dissolution (Buzas, 1965; Green *et al.,* 1992, 1993b; Martin *et al.,* 1995, 1996; Powell *et al.,* 1984 noted similar behavior for juvenile molluscs).

Based on the slow rates of experimental test degradation versus the highly degraded nature of many natural tests, Kotler *et al.* (1991, 1992) and Martin and Liddell (1991) concluded that test degradation is inhibited in carbonate sediments. Indeed, subsequent radiocarbon dating demonstrated that pristine to highly degraded tests of *Amphistegina* and *Archaias* from natural

assemblages range from modern to > 2,000 calendar yrs (ages corrected for reservoir and vital effects; Martin *et al.,* 1995, 1996). Mixing of older material with younger sediment appears to be extensive in carbonate-rich environments because high sedimentary $CaCO_3$ levels buffer dissolution and promote time-averaging. Indeed, based on amino acid racemization techniques, Murray-Wallace and Belperio (1995) found that the large reef-dwelling foraminifer *Marginopora vertebralis* was reworked from late Pleistocene (ca. 125,000 ka) into modern carbonate tidal flat sediments, and that reworked specimens (remanié) were indistinguishable from modern ones.

Kotler *et al.*'s (1992) results are in marked contrast to the results of Waller and Burton (1990), who found that red algal (18 mol% Mg-calcite), echinoid (12 mol% Mg), and coral (aragonite) substrates dissolved relatively rapidly in field experiments. The carbonate substrates utilized by Walter and Burton (1990) would appear to be far more reactive, however, than Foraminifera (Kotler *et al.,* 1992). Thus, differential solubility of carbonate particles in carbonate environments probably results not only from differences in mineralogy, but also from differences in (1) substrate size, shape, and surface area (surface/volume ratio; relatively high in red algae, low in Foraminifera), (2) organic matter content, and (3) microstructure ('Sorby Principle'; Folk and Robles, 1964).

16.3.2   Siliciclastic tidal flats

It is almost axiomatic in taphonomy that, in general, the bigger the shell, the longer it lasts (depending on mineralogy, microstructure. etc.). One deduction from this tenet is that big shells should be older, and should appear older, than small shells from the same horizon. Macrofossil assemblages should therefore exhibit much greater variation in the durations of time-averaging than microfossil assemblages from the same deposit (Martin and Liddell, 1991; Martin, 1993; Kowalewski, 1997). Comparison of time-averaging of hardparts belonging to different taxa bears on such crucial topics as distinguish-

ing reworking from survivorship across extinction horizons (Signor-Lipps effect; Signor and Lipps, 1982; Flessa, 1990; Meldahl, 1990; Mac-Leod and Huber, 1996), and biostratigraphic zonations based on different taxa that are used to assess the rates and mechanisms of extinction.

Martin *et al.* (1995, 1996) tested the above hypotheses by comparing the state of preservation (taphonomic grade) and age of *Chione* (bivalve) and foraminiferal tests from Holocene tidal flats of Bahia la Choya, Mexico (northern Gulf of California). They found that hardpart size and taphonomic grade are not infallible indicators of shell age, preservability, or temporal resolution of fossil assemblages, as did Flessa *et al.* (1993; contrary to Brett and Baird, 1986; Brandt, 1989). Disarticulated *Chione* collected from the SWI exhibited an age range of several hundred years to ~80–125 Ka based on Accelerator Mass Spectrometer (AMS) ^{14}C dates and amino acid racemization (D-Alloisoleucine/L-Isoleucine) values, and old (or young) valves ranged from highly altered to virtually pristine. Their age range is much greater than that reported by Flessa *et al.* (1993) from the same area (see also Wehmiller *et al.,* 1995; Flessa and Kowalewski, 1994).

Foraminiferal tests at Choya Bay were surprisingly old (up to ~2,000 calendar years), despite their pristine appearance, which suggested a young age (Martin *et al.,* 1995, 1996; dated tests consisted of *Buccella mansfieldi* and *Elphidium* cf. *E. crispum*). The substantial age differences between bivalves and Foraminifera hinted that the means of test preservation differed from that of bivalves. Foraminifera reproduced in discrete (~a few weeks) seasonal pulses, which were followed by periods of intense dissolution of several months duration related to low sediment accumulation rates (~ 0.038 cm yr^{-1}; Flessa *et al.,* 1993) and intensive bioturbation (oxidation of organic matter and sulfides to produce carbonic and sulfuric acids, respectively; equations 5 and 6). After each seasonal reproductive pulse of $CaCO_3$, some tests are apparently rapidly incorporated into a subsurface shell layer (up to ~ 1 m below the SWI) by Conveyor Belt Deposit Feeders

(CDFs; van Straaten, 1952; Rhoads and Stanley, 1965; Meldahl, 1987) and preserved there, as the rest of the pulse quickly dissolves. Ultimately, some of these older tests, as well as bivalves, are exhumed by CDFs and storms, which biases assemblages toward ages older than those predicted (cf. Shroba, 1993). Indeed, Meldahl *et al.* (1997) found that durations of time-averaging of bivalve assemblages decreased to a few hundred years in settings of apparently higher sediment accumulation rates elsewhere in the Gulf of California.

At Choya Bay, however, foraminiferal abundance tends to increase to the north across the flat, indicating that conditions suitable for test preservation can vary dramatically over relatively short distances. The depth to the subsurface shell layer shallows northward from > 60 cm on the southern flat to ~10 cm in some places over a Pleistocene outcrop. Burrow densities (estimated visually) also tend to decrease to the north, especially when sediment thickness is $\leqslant 20$–25 cm. The shallowness of the Pleistocene platform on the northern margin of the bay apparently inhibits the intensity of bioturbation (i.e. bioturbators cannot burrow to their preferred habitat depth), and this allows alkalinity to build-up via sulfate reduction, especially in the summer (see seasonal geochemical data in Martin *et al.,* 1995).

16.3.3   Marshes

Not surprisingly, marshes and other coastal environments have received considerable scrutiny from sedimentologists, stratigraphers, and geomorphologists because of their accessibility, their ecological and economic importance, and their sensitivity to sea-level change, especially in light of natural Holocene sea-level rise that is confounded with apparent anthropogenic global warming. Foraminifera have been used to reconstruct high-frequency (decadal to millenial), low amplitude (< 10 m) changes of Holocene sea level to ±5–10 cm (Scott, 1976a; Scott and Medioli, 1978, 1980a, 1986; Williams, 1989, 1994; Thomas and Varekamp, 1991; Varekamp *et al.,* 1992; Gehrels, 1994; Nydick *et al.,* 1995;

Varekamp and Thomas, 1998; see also chapter 9). This resolution surpasses that of (1) marsh plants (e.g. *Spartina alterniflora*; Goldstein, 1988b; Gehrels, 1994), which exhibit coarser zonations and may decay beyond recognition; (2) the Holocene portion of the marine oxygen isotope curve; and (3) coral reef terraces (e.g. Wheeler and Aharon, 1991).

Marshes would appear to exhibit intrinsically high temporal resolution. Bioturbation in salt marshes 'does not constantly churn sediments as is commonly the case in shallow subtidal settings' (Goldstein *et al.*, 1996, p. 11) because, although dense halophyte roots pump oxygen into surficial sediment (which would ordinarily promote bioturbation), they also impede bioturbation by crabs, insects, and polychaetes (Basan and Frey, 1977; Frey and Basan, 1981; Howard and Frey, 1985; Sharma *et al.*, 1987; Nydick *et al.*, 1995). Bioturbation in marshes is also counteracted by high rates of sedimentation (e.g. Sharma *et al.*, 1987; Fletcher *et al.*, 1992; Nydick *et al.*, 1995), which should decrease attentuation of stratigraphic signals by rapidly transmitting signals through the mixed layer (Fig. 16.2). For example, assuming $v \cong 0.3\text{--}0.5 \text{ cm yr}^{-1}$ (cf. equation (1); e.g. Church *et al.*, 1981, 1987; Krishnaswami *et al.*, 1980; Sharma *et al.*, 1987; Luther *et al.*, 1991), the transit time through the mixed layer (T_m) is only ~40–60 years, which surpasses the T_m of ~2,000–5,000 years for many deep-sea cores ($m \cong 5\text{--}10 \text{ cm}$; $v \cong 2\text{--}5 \text{ cm kyr}^{-1}$) used in 'high-resolution' paleoclimate studies (Schiffelbein, 1985, 1986). Rates of bioturbation in marshes and mixed layer thickness tend to increase into the lower marsh, however, as subtidal settings are approached.

Hippensteel and Martin (1999) conducted a study of temporal resolution in South Carolina (Folly Beach) marshes and back-barrier overwash fans based on the Guinasso-Schink (1975) model (equation (1)). Using deep-sea microtektite (tracer) concentration profiles. Officer and Lynch (1983) solved for *G*:

$$G = \frac{\beta_2 + \sqrt{\beta_2^2 + \pi^2 \beta_1 (\beta_2 - \beta_1)}}{2\pi^2 \beta_1} \qquad (8)$$

where β_1 and β_2 are the slopes (fitted by least squares) of the base and upwardly-smeared portions of the tracer layer, respectively (cf. Figures 16.2, 16.4); i.e. the vertical concentration gradient. Hippensteel and Martin (1999) calculated β_1 and β_2 from the slopes of the base and upwardly bioturbated portions of washovers fans (~25 cm in thickness); these fans were enriched in Oligo-Miocene Foraminifera (tracers) that had been eroded from subtidal offshore outcrops by storms and redeposited in back-barrier marshes. Using equation (1), and assuming $m = 20 \text{ cm}$ and $v = 0.2 \text{ cm yr}^{-1}$ (Sharma *et al.*, 1987), Hippensteel (1995) calculated an average D of $1.0 \times 10^{-7} \text{ cm}^2 \text{ sec}^{-1}$ ($\pm 0.14 \times 10^{-7} \text{ cm}^2 \text{ sec}^{-1}$; 95% Confidence Interval) for a high marsh site ($n = 2$ washovers). At two sites located at the high marsh-low marsh boundary, average D was $3.45 \times 10^{-7} \text{ cm}^2 \text{ sec}^{-1}$ and $5.94 \times 10^{-7} \text{ cm}^2 \text{ sec}^{-1}$ (± 0.39 and $0.79 \times 10^{-7} \text{ cm}^2 \text{ sec}^{-1}$; respectively; ($n = 3$) for each site). For a streamside site, D was $7.88 \times 10^{-7} \text{ cm}^2 \text{ sec}^{-1} \pm 0.863 \times 10^{-7} \text{ cm}^2 \text{ sec}^{-1}$ ($n = 3$). These rates correspond to observed burrow densities in the marsh. Low and intermediate marsh bioturbation rates fall at the low end of the range for intertidal-shallow subtidal environments such as Long Island Sound ($\sim 10^{-7}\text{--}10^{-4} \text{ cm}^2 \text{ sec}^{-1}$; Matisoff, 1982). whereas high marsh values approach low deep-sea rates ($10^{-8}\text{--}10^{-9} \text{ cm}^2 \text{ sec}^{-1}$; Matisoff, 1982), which argues for excellent temporal resolution (low signal attenuation) in marsh sediments.

Hippensteel (1995) also restored washover events to their presumed original levels. The original datum (x_0) can be restored from the observed tracer (Oligo-Miocene Foraminifera) peak x_m by

$$x_0 = x_m - \left[1 - \frac{\ln \dfrac{8\pi^2 G^2 + 2}{4G + 1}}{\pi^2 G - 1} \right] m \qquad (9)$$

(Officer and Lynch, 1983; see also Officer, 1982; Officer and Lynch. 1982). Using equations (8) and (9). Hippensteel (1995) calculated displacements and corresponding temporal offsets of washovers that generally agree with the trend

of increasing bioturbation from high to low marsh. For a high marsh site, he calculated a displacement of 5–13 cm and a temporal offset of 28–65 years for $n = 2$ washovers. For two sites at the high–low marsh boundary, displacements and temporal offsets were 7–34 cm and ~40–170 years, respectively (total $n = 6$), but for a stream-side site only 0.4–14 cm and 2–68 years (n = 3). These values again indicate resolution that potentially surpasses that of deep-sea cores.

Much of the dynamics of formation of marsh foraminiferal assemblages has been overlooked, however (Jonasson and Patterson. 1992; Goldstein and Harben, 1993; Hoge, 1994, 1995; Goldstein et al., 1996). Differential preservation of foraminiferal assemblages can, for example, mimic the magnitude and frequency of sea-level change determined from foraminiferal assemblages (Fig. 16.5). As van de Plassche (1991,

p. 176) warns, 'until … higher age and depth resolution is obtained, the precise relation between the nature and magnitude of … low-amplitude sea-level movements … and causes and effects of climate change … remains unknown.' Alteration of surface assemblages is critical because marsh zonations, and corresponding inferences about sea level, are recognized downcore primarily using either relative (%) or absolute (number of tests gram^{-1} sediment) abundances of key species. In low marshes, fragile agglutinated (e.g. *Ammotium salsum, Miliammina fusca*) and calcareous (e.g. *Ammonia beccarii*) Foraminifera are often lost via oxidation of organic test cements and dissolution, respectively, so that the fossil assemblage may be dominated by typical high marsh, robust agglutinated species (such as *Jadammina macrescens* and *Trochaminna inflata*) that comprised much smaller proportions of the original
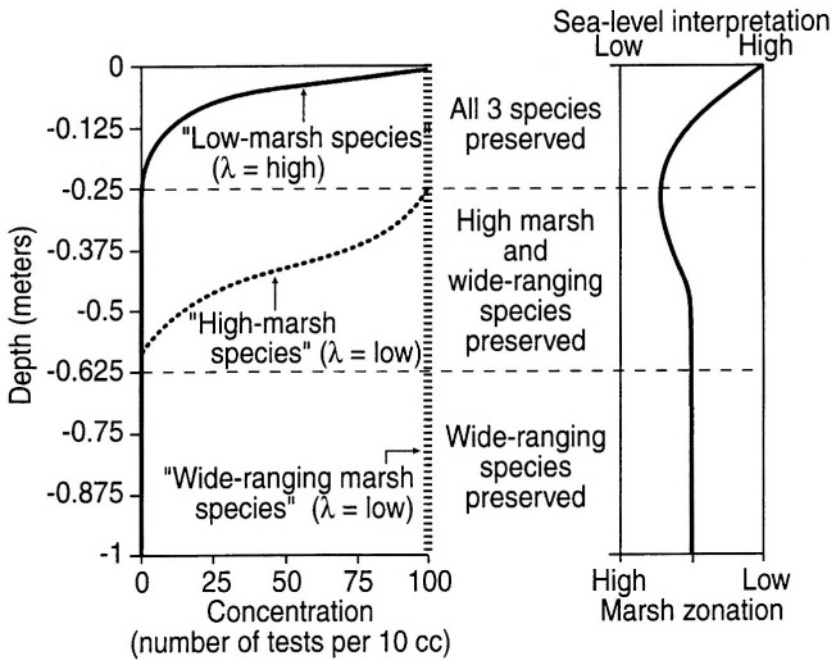
Figure 16.5 Hypothetical effects of differential preservation of marsh foraminiferal assemblages on sea-level interpretation. Left column shows hypothetical assemblages: solid curved line = *Ammotium salsum* (epifaunal-shallow infaunal, mainly inhabiting low marsh, and exhibiting high rate of decay or high 'λ'); dotted line = *Jadammina macrescens* (epifaunal-infaunal, mainly higher marsh, low λ); dashed vertical line = *Arenoparrella mexicana* (wide-ranging epifaunal to deep infaunal, low λ). Biodiffusion coefficient (D) and sedimentation rate (v) held constant. Concentrations are absolute, not relative. Right column: sea-level interpretation. Differential preservation of robust species mimics sea-level rise and fall when none has occurred.

living assemblage at the SWI (Jonasson and Patterson, 1992; Goldstein and Harben, 1993; Patterson *et al.*, 1994; Goldstein *et al.*, 1996; Fig. 16.5; cf. Scott and Medioli, 1980b). A number of sea-level curves are in fact based on abundance changes of *J. macrescens* and other robust species. The lack of Foraminifera in highest high marsh and non-marine sediments has also been widely employed as a sea level indicator, but this condition does not necessarily imply a non-marine origin. Test loss in the high marsh no doubt also occurs during early diagenesis, just as in the low marsh. Although not yet investigated for Foraminifera, differential preservation of marsh assemblages may also vary according to latitude because of differences in metabolizability of organic matter (Reaves, 1986).

Differential preservation of infaunal species may also affect the formation of marsh assemblages and, potentially, sea-level interpretations. Goldstein and Harben (1993; see also Goldstein, 1988b; Goldstein *et al.*, 1996) found that the abundance of the common marsh species *Arenoparrella mexicana* changed from ~5% at the surface to ~50% within the top 3–5 cm of sediment because of large infaunal populations. This species, which may live to depths of ~30 cm and 'bypass' the mixed layer, is resistant to degradation and may dominate high marsh death assemblages despite small living populations.

16.3.4   Offshore shelf and slope environments

Gradients in water energy and surface productivity ($CaCO_3$ and organic carbon) and oxygen availability occur across the shelf and into slope environments (Fig. 16.6; Berger and Killingley, 1982; Ekdale *et al.*, 1984). Nevertheless, just as in shallow-water settings, sedimentation rate, which decreases with water depth, may be the overriding factor in the formation and time-averaging of microfossil assemblages in shelf and slope settings. Lin and Morse (1991) concluded that off the Mississippi Delta and Texas–Louisiana shelf, for example, rates of sulfate reduction (and alkalinity generation; cf. equation (7)) and

pyrite concentration generally decrease exponentially with increasing water depth, all of which reflect decreasing sedimentation rates (Lin and Morse, 1991; Loubere *et al.,* 1993a,b; Middleburg *et al.,* 1997). Sulfate reduction rates in this region are intermediate between those of shallow nearshore organic carbon-rich sediments and carbon-poor deep-sea sediments (Canfield, 1991; euxinic basins are an exception; e.g. Berger and Soutar, 1970; see also Canfield and Raiswell, 1991). At high sedimentation rates, labile organic matter undergoes a shorter period of oxic and suboxic degradation before it is incorporated into subsurface layers where it can support sulfate reduction (Canfield, 1991; Lin and Morse, 1991). The decline in sulfate reduction rates across the shelf and slope, and especially beyond the shelf-slope break, may be related not only to a decline in sedimentation rates in deeper settings (Nozaki *et al.,* 1977; Carpenter *et al.,* 1982; Smith and Schafer, 1984) but also to decreased surface water productivity, as a commonly-observed peak in foraminiferal (benthic and planktonic) abundance occurs near the continental shelf edge (e.g. Bandy, 1953). As rates of sulfate reduction decline across the shelf and slope (Lin and Morse, 1991), rates of bioturbation must either decline or be counteracted by increased input of $CaCO_3$ or sediment for good preservation to occur.

In the case of microfossils, the exact relationships between sedimentation, shell input, sulfate reduction, etc., and the formation of foraminiferal assemblages on the deeper shelf have only recently begun to be explored in detail. Douglas *et al.* (1980) concluded that life and death assemblages of the upper slope (100–400m) of the southern California borderland are strongly similar (based on surface samples), but Loubere and Gary (1990; see also Loubere *et al.*, 1993a,b) concluded that there was substantial specimen loss in the upper 10 cm of boxcores from off the Mississippi Delta and the western Gulf of Mexico continental slope. Denne and Sen Gupta (1989) came to similar conclusions for Texas–Louisiana slope assemblages: they found that bathyal calcareous species could be grouped into those that are well-preserved (increasing

1. Decreasing bioturbation

2. Decreasing sedimentation rate (α productivity in surface ocean)

3. Decreasing C_{org} preservation (α sed. rate and bioturbation)

4. Decreasing sulfate reduction (α sed. rate)
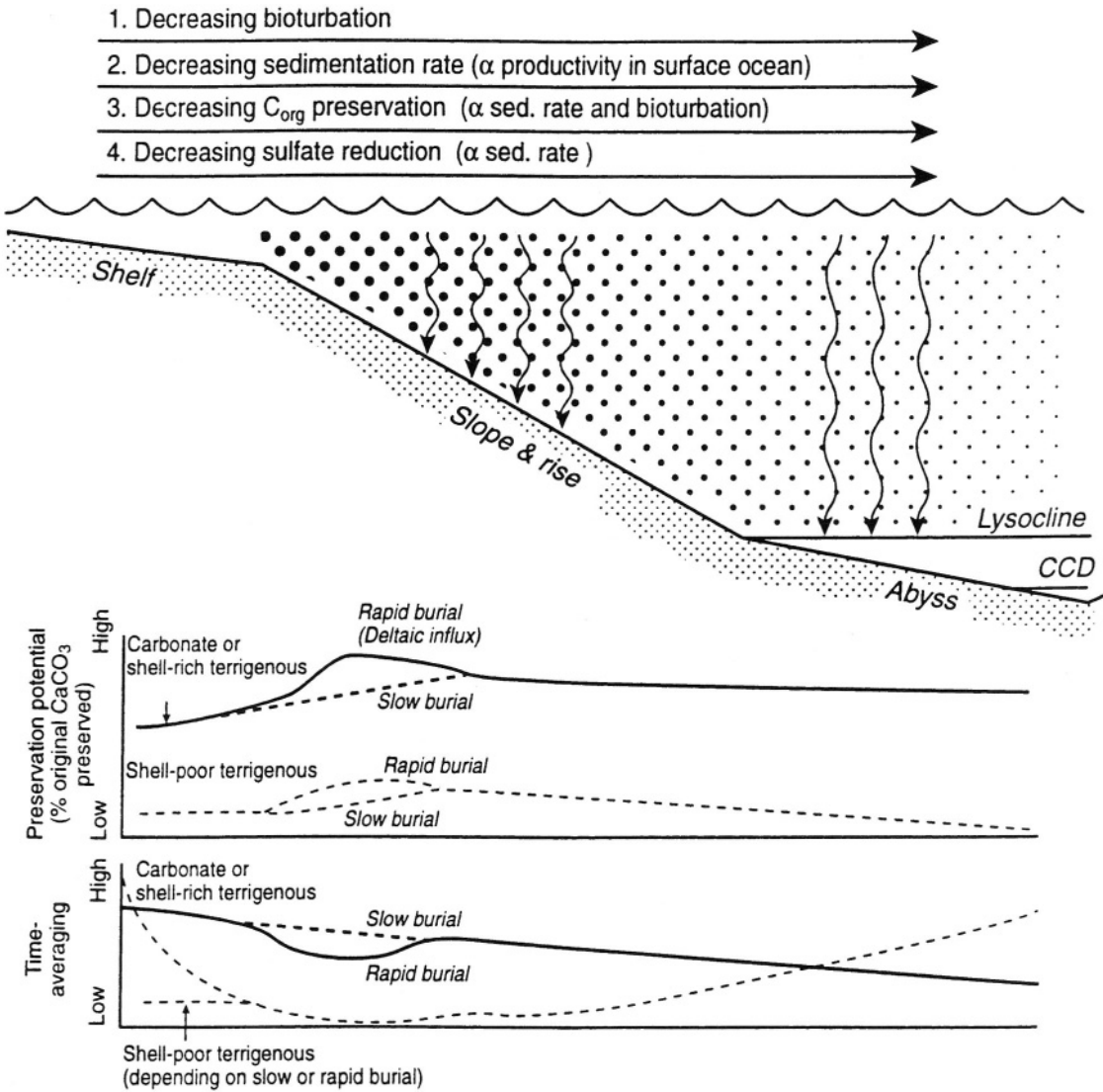
Figure 16.6 Speculative gradients in preservation and time-averaging across a passive continental margin. Gradients are based primarily on decreasing rates of bioturbation with water depth (decreasing values of D), and, in descending order, on decreasing rates of sedimentation, organic matter burial, and sulfate reduction. 'Preservation potential' is defined as the percent original shell ($CaCO_3$) material preserved. In carbonate environments, high rates of bioturbation are probably counteracted by high shell concentrations and sulfate reduction, thereby promoting preservation and time-averaging. In shell-poor shallow-water terrigenous sediments, assemblages may be either more or less time-averaged than carbonate-rich assemblages, depending on sedimentation and bioturbation rates. In deltaic environments (shelf and slope), rapid burial should inhibit time-averaging, but sediment starvation (via delta lobe-switching) probably promotes it. Time-averaging is expected to increase on the continental rise, but low rates of bioturbation keep time-averaging at a minimum above the lysocline. Below the lysocline, and especially the CCD, extensive dissolution and reworking may accentuate time-averaging depending upon corrosiveness of bottom waters. See text for further discussion. (Modified from Martin, 1993).

downcore), moderately preserved (no trend), and poorly preserved (decreasing downcore). Agglutinated species were either resistant to disaggregation (no trend) or disaggregation-prone (decreasing downcore; see also Smith, 1987; Murray, 1989).

Benthic Foraminifera in slope and deep-sea environments also frequently exhibit depth stratification and microhabitat preferences that reflect changes in surface productivity, organic carbon influx, and pore water oxygen content (Corliss, 1985; Loubere *et al.,* 1993a,b; Rathburn and Miao, 1995). Depth stratification may represent a situation analogous to infaunal macroinvertebrates mixing with long dead epifaunal species (K. Flessa, 1993, personal communication); changes in pore water chemistry with depth in sediment may also affect stable isotope ratios of tests of foraminifers living infaunally (McCorkle *et al.,* 1990). Corliss and Emerson (1990) concluded that habitat depth in sediment is related to organic carbon input (which decreases with water depth) and dissolved oxygen in the pore waters (based on dissolved Mn^{2+} profiles). Shelf species tend to be epifaunal (shallow oxic layer), whereas on the continental slope and rise, the oxidized surface layer is relatively thick and Foraminifera are primarily deep infaunal species (see also Loubere *et al.,* 1993a).

Unfortunately, because of a paucity of dates, durations of time-averaging of shelf and slope foraminiferal assemblages must for the present be based on the accumulation of macroinvertebrate hardparts (cf. results for Choya Bay). Flessa and Kowalewski (1994; see also Flessa, 1993(compiled 734 published radiocarbon dates (many conventional and uncalibrated) from modern nearshore (< 10m) and shelf (> 10m) habitats, assuming that the maximum age of a shell serves as an estimate of time-averaging. Deep shelf shells (n = 126 localities total) exhibited a bimodal distribution: slightly more than 25% (33 localities) fell into the 0 3,000 year class, whereas ~25% (31 localities) fell into the 9,000–12,000 age class, with a median of 9,435 years. Nearly 70% (42 localities) of nearshore shells (66 localities total) fell into the

0–500 year class. The median age of all shells was ~1,255 years. For both deep and shallow shelves, the number of shells in greater age classes declined rapidly toward the maximum age class of 36,000–39.000 years, which is near the upper limit of radiocarbon dating.

Flessa (1993) suggested a number of explanations for the general increase in duration of time-averaging away from shore (see also Flessa and Kowalewski, 1994). Shells may tend to be younger in nearshore settings because of faster rates of destruction (especially via bioerosion but also because of abrasion and fragmentation, and predation); greater sediment accumulation rates, which ought to leave younger shells nearer the SWI barring other processes; higher rates of shell production, which would bias assemblages toward younger ages; the possible counteraction of increased sedimentation on bioturbation; and the Holocene rise in sea level: very old shells may not have been able to accumulate in many nearshore settings because sea level reached within ~ 10 m of its present position only ~ 7,000 years ago. Thus, the relatively recent rise in sea level may have restricted the potential duration of time-averaging in nearshore sediments, while shells continued to accumulate further offshore.

16.3.5 Deep sea

The onset of $CaCO_3$ dissolution in the deep-sea begins ~0.5–1 km above the lysocline (Emerson and Bender, 1981); the lysocline tends to shallow toward the continental margins because of oxidation of greater amounts of organic matter of both marine and terrigenous origin (Bé, 1977; Berger, 1977). In the sediment itself, dissolution is concentrated in the mixed layer (Archer *et al.,* 1989), which is normally on the order of 5–10 cm thick.

Much of the work on dissolution of calcareous hardparts has been on planktonic Foraminifera because of their use in biostratigraphic and paleoceanographic interpretation. Douglas (1971) developed a dissolution-susceptible scale for planktonic Foraminifera (later modified by Malmgren, 1987). Planktonic species that have

somewhat higher Mg test concentrations are more susceptible to dissolution (Savin and Douglas, 1973; Bender *et al.*, 1975); also, species that are most susceptible to test dissolution tend to settle the most slowly (e.g. Berger, 1967, 1968, 1970a, 1971; Parker and Berger, 1971; see Bé, 1977, for review). This is because most shallow-dwelling species harbor symbiotic dinoflagellates and typically have small thin-walled porous tests in order to remain afloat in the photic zone (e.g. *Globigerinoides ruber*), whereas deeper-dwelling species often have dissolution-resistant features such as thick test walls and rope-like keels that decrease their buoyancy (e.g. *Globorotalia menardii*). Preferential settling of certain species may also affect their dissolution behavior: in the case of *Globorotalia truncatulinoides,* for example, the exposed cone of the test was more severely affected by dissolution than the flat (spiral surface) in experiments (Bé *et al.,* 1977b). Morphological features may also differ in their mineralogy and dissolution susceptibility (Brown and Elderfield, 1996), and sediment infilling tends to confine dissolution to the outer surfaces of tests (Hecht *et al.,* 1975; Keir and Hurd, 1983).

Although planktonic tests are typically not transported far as they settle through the water column, they begin to dissolve, especially after they have reached the ocean bottom, as a result of the oxidation of organic matter and sulfides (equations (5) and (6); Adelseck and Berger, 1977). Consequently, the number of 'assemblages' present in the plankton may be reduced in number in sediment: Bé and Hutson (1977) found that in the tropical and subtropical Indian Ocean six 'life assemblages' were reduced to two thanatocoenoses in sediment and that the number of species in the sediment assemblages was greater than in the planktonic assemblages. The apparent sea surface temperature (SST) reflected by the thanatocoenosis may therefore be inaccurate (e.g. Bé and Hutson, 1977). Le and Thunell (1996) developed a method which filters out the effect of differential dissolution on the calculation of SSTs.

Broecker *et al.* (1991) developed a radiocarbon-based age (mixing) model for deep-sea assemblages based on the Berger-Heath (1968) approach. This model is based on the assumption that dissolution within the mixed layer is proportional to the residence (replacement) time of biogenic grains within the mixed layer, and that the age and thickness of the mixed layer reflect the extent of dissolution. Broecker *et al.* (1991) hypothesized that there are three basic forms of dissolution in the deep sea: (1) homogeneous dissolution, in which each grain loses a constant fraction of its mass per unit time (irrespective of grain type): homogeneous dissolution should shift the mass distribution of assemblages toward younger grains because the replacement time of grains in the mixed layer by new grains from the pelagic rain will be reduced; therefore, the greater the extent of homogeneous dissolution, the younger the age (based on ^{14}C dates) of core top assemblages; (2) sequential dissolution, in which grain type A dissolves completely before grain type B begins to dissolve, and so on: in this case, core top ages should increase with the extent of dissolution; and (3) interface dissolution of all sediment grains at the SWI before burial: like sequential dissolution, interface dissolution increases the replacement time of grains in the mixed layer and thus increases the radiocarbon age of the core top.

To determine where in the spectrum dissolution actually occurs, Broecker *et al.* (1991) employed two approaches. One was to compare mixed layer depths calculated from downcore radiocarbon dates on bulk $CaCO_3$ with those calculated from (a) actual core-top ages and (b) Holocene accumulation rates, assuming a steady-state system (based on the Berger-Heath model) with no dissolution. In this model, calculated mixed layer thicknesses are proportional to radiocarbon age. Therefore, to the extent that homogeneous dissolution has occurred, the calculated mixed layer thickness will be smaller than the measured thickness. The second approach was to compare radiocarbon dates on core tops from a range of water depths (and therefore range of dissolution), but all collected within a relatively small area so as to minimize variation in pelagic rain rates of biogenic particles (planktonic Foraminifera, etc.). In the first

test, measured mixed layer thicknesses were less than thicknesses calculated from the model (i.e. homogeneous dissolution does not occur). In the second test, ages approximate those for sequential or interface dissolution (i.e. ages are older than those predicted by the model).

Broecker *et al.* (1991) concluded, however, that neither interface or sequential dissolution could be occurring. They ruled out interface dissolution because dissolution appears to occur within the sediment (Archer *et al.,* 1989), and not exclusively at the SWI. Sequential dissolution was also ruled out because in the deepest cores (near or below CCD), planktonics are absent and benthics nearly so (Broecker *et al.,* 1991, table 3); i.e. microfossil components appear to be degraded at nearly equal rates. Since homogeneous dissolution also does not appear to occur, these authors sought an explanation for core top assemblage ages based on changes in deep-water $CO_3^=$ ion concentration through time. They suggested that Pacific waters became more corrosive, and Atlantic waters less so, during the last glacial–interglacial transition. Under such conditions, Holocene accumulation rates would have been reduced by chemical erosion in the Pacific, thereby increasing the likelihood of reworking older (glacial) sediments into the mixing zone (cf. Berger and Heath model; see also Murray-Wallace and Belperio, 1995). Broecker *et al.* (1991) determined that radiocarbon ages for Pacific deep-sea core tops were 8,000–10,000 years greater than those for Atlantic core tops from comparable depths below the lysocline.

Differential preservation in deep-sea sediments may be more complicated than Broecker *et al.* (1991) concluded, however. Dissolution is neither purely homogeneous or sequential: benthic Foraminifera tend to be more resistant than planktonics (Berger, 1968; Corliss and Honjo, 1981; Bé, 1977). The benthic/planktonic ratio, for example, has often been used as an index of post-mortem alteration of deep-sea assemblages (Thunell, 1976) and even planktonic tests may show differential resistance (Berger, 1968). Benthic Foraminifera also differ in their resistance to dissolution, but the relationship between fora-

miniferal ecology, microstucture, habitat, and preservation is unclear. Corliss and Honjo (1981), for example, found that the reef-dwelling *Amphistegina* was much less resistant to dissolution than characteristic bathyal and abyssal species, such as *Nuttallides umbonifera,* which prefers waters beneath the CCD (Bremer and Lohmann, 1982).

Thus, like differential preservation of Foraminifera on shallow shelves, dissolution-resistant benthic (or planktonic) Foraminifera may erroneously increase deep-sea core-top age estimates (cf. Rathburn and Miao, 1995). Indeed, all forms that co-occurred in sediment of Broecker *et al.*'s (1991) study showed evidence of partial dissolution. Moreover, DuBois and Prell (1988) found that in the tropical Atlantic, mixed layer ages of sublysocline (>4400m) cores decreased (by ca. 500–1,000 years) relative to core tops from above the lysocline. They found that increased weight percent fragmentation and percent resistant planktonics coincided with changes in age at this depth. Therefore, in sediments below the lysocline, the radiocarbon age structure of the mixed layer in the Atlantic is opposite to that of the Pacific (see also Broecker *et al.,* 1991). Decreased corrosiveness (relative to the Pacific) of overlying waters and higher carbonate content of sediments have apparently allowed a type of sequential dissolution to proceed in Atlantic sublysocline environments that produces younger (not older) core top ages; i.e. old skeletons are removed faster than young ones so that mixed layer ages decrease (DuBois and Prell, 1988). In terms of mixed layer age, this is just the opposite of sequential dissolution as defined by Broecker *et al.* (1991). DuBois and Prell (1988) concluded that in the case of dissolution, the steady-state model is inappropriate for calculating temporal resolution and that *^{14}C stratigraphies from different preservational settings cannot be strictly compared*: although sediment may have the same radiocarbon age, the proportions of the components producing that age may not be the same if the particles have different preservational histories.

To complicate matters further, Loubere

(1989) found that, based on the Berger-Heath (1968) model, significant variation in species abundances occur in the mixed layer as a result of taxon depth stratification. Infaunal taxa increase non-linearly in abundance with depth to the level of their true habitat, below which taxon abundance remains constant, whereas epifaunal assemblages may be significantly modified. He concluded that the best representation of total taxon abundance occurs at the base of the bioturbated zone (see also Denne and Sen Gupta, 1989; cf. Rathburn and Miao, 1995).

Loubere (1991; see also Loubere, 1997) also found that certain deep-sea (East Pacific Rise) Foraminifera respond to surface productivity (organic carbon) gradients. Significantly, some species appear to be highly adaptable (in terms of microhabitat preference and depth stratification) to changes in food availability and environmental conditions (Linke and Lutze, 1993). At great depths, deep-water epifaunal species predominate because organic carbon (food) becomes limiting.

16.4 DECONVOLUTION: THE RECONSTRUCTION OF SIGNAL INPUTS

In theory it is possible to reconstruct any input to the stratigraphic record. Unfortunately, such approaches have so far met with only limited success. A number of attempts have been made at direct deconvolution (unmixing or 'unfiltering') of sedimentary signals (e.g. $^{18}\delta O$) based on the Berger-Heath and Guinasso-Schink mixing models (Berger *et al.,* 1977; Schiffelbein, 1985, 1986), but the deconvolution overestimated mixing intensity and produced artificial overshoots and offsets, including artificial meltwater spikes (Jones and Ruddiman, 1982). Christensen (1986) and co-workers (Christensen and Bhunia, 1986; Christensen and Goetz, 1987; Christensen and Osuna, 1989; Christensen and Klein, 1991; see also Robbins, 1982) were more successful in reconstructing fluxes of pollutants and radiotracers in lake sediments using both the Guinasso-Schink (1975) and Berger-Heath (1968) mixing models; they assumed that bioturbation

and sedimentation rates are constant and they treated sediment compaction effects by assuming particular porosity profiles. Although these assumptions appear valid for the thin mixed layer of lacustrine environments (~5–10 cm) where Christensen *et al.* worked, they do not appear to hold for most marine environments, with the exception of the deep-sea, which is also typified by a thin mixed layer.

In response to these difficulties, Bard *et al.* (1987) developed a technique based on a discretized version of the Laplace transform. They first deconvolved abundance curves of species of planktonic Foraminifera and then the isotopic signals stored in their shells. Other workers have noted that even at an abrupt lithologic or paleoclimatic boundary, abundant species above and below the boundary that are indicative of climate change are worked upward and downward across the boundary (Berger and Heath, 1968; Hutson, 1980; see also Andree *et al.,* 1984; Broecker *et al.,* 1984; Peng and Broecker, 1984; Andree, 1987). In Bard *et al.*'s (1987) technique, comparison of actual data with unmixed curves enabled recognition of bioturbation. Nevertheless, restored signals may be erroneous when species abundances approach zero; the technique also assumes that bioturbation and sedimentation rates remain constant (box model of Berger and Heath, 1968).

Peng *et al.* (1977, 1979) developed numerical models of *continuous* inputs (as opposed to impulse signals like those discussed above). In such models, the Guinasso-Schink or Berger-Heath models (or modifications thereof) are solved 'in reverse' by specifying various sedimentary parameters (e.g. *m, v, D*) and solving for the unknown (e.g. test inputs). Given the spatio-temporal variation in test inputs, however ((Buzas, 1965, 1968, 1969, 1970; Green *et al.,* 1993b; Martin *et al.,* 1995, 1996; see Murray, 1991b, for brief review), it is probably best to use averaged inputs (determined from seasonal studies) in an attempt to smooth data and prevent artificial overshoots. Actual test inputs can then presumably be determined by varying test inputs into the model (while holding other parameters constant) until preserved concen-

trations predicted by the model are similar to those sampled in cores.

Although numerical models have the advantage of removing amplification of noise, like analytical models, they have the disadvantage of not providing unique solutions. In theory, different equations or values of sedimentary parameters may produce the same result (Boudreau, 1986a,b, 1997; Bard *et al.,* 1987) and small errors in measurement may swamp the system (Simon, 1986). Considering the difficulties of analytical solutions, however, if estimates of sedimentary parameters (D, m, v) can be reasonably constrained, numerical models may provide the greatest promise for reconstructing stratigraphic signals. For example, Pizzuto and Schwendt (1997) modeled six thousand years of sediment accumulation and autocompaction in a Delaware (U.S.A.) marsh using a FORTRAN program (SQUISH3) based on finite-consolidation strain theory:

$$\frac{\partial^2 e}{\partial z^2} - \lambda(\gamma_s - \gamma)\frac{\partial e}{\partial z} = \frac{1}{G}\frac{\partial e}{\partial t}, \qquad (10)$$

where $(\gamma_s - \gamma)$ is the submerged unit weight of sediment, G is a finite strain consolidation coefficient, and z is the volume of solids per unit area above an arbitrary datum, and

$$e = (e_i - e_f)e^{-\gamma\sigma} + e_f, \qquad (11)$$

in which e_i and e_f are the void ratios at the beginning and end of primary consolidation, respectively, and σ is the effective stress. The model was applied to an accumulating column of sediment consisting of sediment layers of specified void ratios deposited at specified time intervals. Material properties of the sediment were determined initially from laboratory and field studies and rates constrained by radiocarbon dates. The model was then used to reproduce the distribution of void ratios within a vibracore, the actual thicknesses of sedimentary units, and the history of elevation changes of the SWI that was consistent with both a previously-determined sea-level curve for the Delaware coast and the downcore sequence of paleoenvironments. According to the model, horizons have been lowered as much as 2.3 m

by autocompaction alone, the rate of which has ranged from one-half to one-third of the rate of sea-level rise!

16.5 THE CIRCUMVENTION OF TIME-AVERAGING

Methods of minimizing time-averaging are of critical importance in the study of paleoclimate signals preserved in deep-sea cores. Schiffelbein (1984; see also Schiffelbein. 1985, 1986) concluded that in deep-sea cores with sedimentation rates of up to 7 cm/ka, high frequency (ca. 3,000 yr) signals show severe attenuation. One way to accentuate signal-to-noise ratios is to 'slack' records from different sites (e.g. Imbrie *et al.,* 1984a).

By contrast, methods of circumventing time-averaging have received much less attention in shallow-shelf settings. McKinney and Frederick (1992; see also McKinney and Allmon. 1995; McKinney, 1996; McKinney *et al.,* 1996) examined patterns of local extinction using the abundances of 25 species of benthic Foraminifera collected at 1 m intervals from a single section of the Eo-Oligocene Ocala Limestone of northern Florida. They analyzed the population abundance fluctuations through time (upsection) using a fractal-based technique called rescaled-range analysis (Sugihara and May, 1990). This method appears to minimize the effects of time-averaging and potential hiatuses (Sadler and Strauss, 1990) because it is fractal-based (independent of scale). Let $n(t)$ equal the abundance of a species during a particular time interval t, and let $x'(t)$ represent the normalized deviations of abundance $[n'(t) = \bar{n}(t) - n(t)$ for each t between 0 and T or the entire time interval]. The rescaled range is then

$$R(T) = \max n'(t) - \min n'(t) \qquad (12)$$

where $0 \leqslant t \leqslant T$. Variations in $R(T)$ through time are then analyzed with a fractal model

$$R(T) = cT^H, \qquad (13)$$

where c is a proportionality constant $[R(T) \propto T^H]$ and $H = 1/F$, where $F =$ the fractal

dimension. $F = 1$ for a straight line and $F = 2$ for a plane; if $F = 2$, then $H = 0.5$, which means that the plane is 'filled' by the curve and represents a random walk (Sugihara and May, 1990). For $H = 0.5$, the time series (the collection of n's over the entire time interval T) of rescaled abundance variations R represents a random walk (Brownian motion) no matter what the scale of Δt (duration of observation); abundance fluctuations show no 'persistent' trend in a particular direction (increase or decrease). As F decreases from 2 to 1, H increases above 0.5, and R becomes less-and-less plane-filling (tending toward a line). In this case, there is a persistent trend of increasing variation in abundance at every scale of Δt. There will be 'higher highs' and 'lower lows' because as Δt increases, variation also increases. If, on the other hand, H decreases to <0.5, variation decreases ('antipersistent'). McKinney and Frederick (1992) found a significant negative correlation ($r = -0.60$; $p < 0.05$) between H of a species and its stratigraphic range, and concluded that populations with greater abundance fluctuations go extinct sooner than those that maintain relatively stable populations.

16.6   CONCLUSIONS

Shells of different taxa may be degraded by different pathways in the same depositional setting because of differences in size, mineralogy, microstructure, sedimentation rate, and pore water chemistry. Thus, intuitively obvious generalizations about taphonomy may be false (e.g. Martin *et al.,* 1996; Martin, 1998). Moreover, most actualistic studies of foraminiferal taphonomy have concentrated on shallow-water environments, no doubt because of their accessibility and perhaps also funding, whereas much of the fossil record formed in deeper shelf and slope environments. Generalizations based on shallow-water settings may prove to be inapplicable to deep-water settings.

Some depositional settings are better-suited for particular types of investigations than others, depending on the desired scale of temporal resolution (Kowalewski, 1997). Realistically, the best temporal resolution that can probably be attained in most cases is in the deep sea. where relatively continuous cores normally provide adequate temporal resolution. But even in this setting, signals may be damped (Schiffelbein, 1984) and the effects of bioturbation and erosion underestimated (Berger *et al.,* 1979; Martin *et al.,* 1993; Martin and Fletcher, 1995). On the other hand, sites of rapid burial, such as deltas, may be suitable for paleobiologic investigations on ecologic scales, although on longer (evolutionary-biostratigraphic) scales, the continuity of section may become an impediment because of delta lobe-switching or sea-level change, and must be evaluated (e.g. Martin *et al.,* 1993; Martin and Fletcher. 1995).

Although it is viewed negatively by most workers, time-averaging is often an advantage, since short-term noise is damped (Behrensmeyer and Kidwell, 1985). For example, modern macroinvertebrate death assemblages from soft-bottom habitats are comparable to repeated (and expensive!) biological surveys in assessing the 'long-term' dynamics (hundreds of years) of biological communities (Kidwell and Flessa, 1995). Given the sensitivity of Foraminifera to environmental change (e.g. Alve, 1995a), micropaleontology is well-suited to contribute to the paradigm shift in the earth sciences from resource exploitation to resource conservation. But, micropaleontologists must begin to accentuate what can be regained from the fossil record rather than what is lost (Behrensmeyer and Kidwell, 1985; Martin, 1991, 1995). They must seek more quantitative models of the distribution and preservation of microfossils, the reconstruction of the shell original inputs (signals), and the implications for community homeostasis. This will be no small feat, given the difficulties encountered so far. but we can only learn by trying.

16.7   ACKNOWLEDGMENTS

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