

Atlas of Benthic Foraminifera

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Ann Holbourn, Andrew S. Henderson and Norman MacLeod

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Introduction

Benthic foraminifera inhabit all marine environments, living either above, at, or below the sediment water interface in water depths ranging from the intertidal zone to the deep ocean (Corliss, 1980; Jorissen, 1999; Pawlowski and Holzmann, 2008). In the deep sea, they represent the most important contributors to the meio-faunal biomass and their distribution is intricately linked to the flux of particulate organic matter from the upper ocean to the sea floor (Gooday et al., 1992; Altenbach and Struck, 2001; Gooday, 2003). Benthic foraminifera comprise the oldest group of deep-sea organisms, tracking back to 1150–690 million years according to molecular data and possibly 716–635 million years according to the fossil record (Culver, 1991; Pawlowski et al., 2003; Bosak et al., 2011), although they exhibit relatively slow evolution rates in comparison to planktonic foraminifera (Pawlowski et al., 1997; Kucera and Schönfeld, 2007). Thus, on account of their geographic ubiquity, their abundance in Mesozoic and Cenozoic deep-sea sediments and in Phanerozoic sediments overall, and their utility as indicators of past environmental conditions, benthic foraminifera continue to play a pivotal role in paleoceanographic and paleoclimatic research.

1. Test Morphology and Classification

Taxonomy

Benthic foraminifera belong to a large group of marine “amoeboid” protists, recently classified as a stand-alone phylum within the eukaryote Supergroup Rhizaria in the Protist Kingdom (Adl et al., 2005). Foraminifera have granulo-reticular anastomosing pseudopodia and a single- or multi-chambered test, although naked or soft-shelled forms have been included at the higher taxonomic level (Lee, 1990; Pawlowski et al., 2003). These forms

are traditionally poorly known, but recently have been shown to be both taxonomically diverse and abundant in many oceanic environments (Gooday et al., 2008). The classical definition of foraminifera is based on possession of three main diagnostic characters: (1) a test composed of calcite secreted by the cell or consisting of mineral grains embedded in the organic test, (2) a unique reproductive cycle with alternation of a uninucleate haploid generation and a diploid generation that can be multinucleate, and (3) the presence of streaming granulo-reticular (granular, branching, network-like) pseudopodia, generally called rhizopodia (Lee, 1990; Tendal, 1990; Bowser and Travis, 2002).

The suprageneric morphological classification of benthic foraminifera remains a matter of intense debate. Three main morphological characters are given priority in classification schemes: (1) the wall structure of the test (essentially agglutinated, porcelaneous, or hyaline), (2) the number of chambers (monothalamous versus polythalamous), and (3) the test morphology including mode of coiling, chamber arrangement, and apertural system. A comprehensive description of morphological features, which are used in foraminiferal classification, is provided in Hottinger (2006). While most of the recent classification schemes give priority to the composition and structure of the test wall (Wood, 1949; Loeblich and Tappan, 1984, 1987, 1989, 1992; Sen Gupta, 1999), alternative classification schemes view the test architecture as an equally or higher ranking criterion for the suprageneric classification of foraminifera (Mikhalevich, 2004; Tyszka, 2006; Kaminski et al., 2011). Molecular-genetic analyses support the notion that some species with different wall structures are phylogenetically closely related but indicate that monothalamous and polythalamous forms are distinct and may have separated in an early stage of the evolution of foraminiferids (Pawlowski et al., 2003).

Wall structure

Benthic foraminifera (except for soft-bodied allogromids) possess three main types of wall structure: hyaline perforate calcitic or aragonitic, imperforate porcelaneous, and agglutinated with either calcareous or organic cement (Wood, 1949). The different wall structures of hyaline and porcelaneous foraminifera arise from different biomineralization processes ranging from extracellular crystal nucleation on a preformed organic template (hyaline tests) to intracellularly formed crystals released to the cell periphery (high Mg calcite of porcelaneous tests) (Hemleben et al., 1986; Debenay et al., 2000; Erez, 2003; de Nooijer et al., 2009). These different modes of calcification have major implications for the uptake of trace elements and the resulting geochemical signature of foraminiferal calcite in relation to ambient seawater. In general, hyaline benthic foraminifera have lower Mg/Ca than porcelaneous foraminifera, but their Mg/Ca ranges from lower to much higher values than in calcite precipitated inorganically from seawater (Bentov and Erez, 2006). Controlled calcification within a space of biologically regulated ion concentration has the advantage that the concentration of ions in the calcifying solution (including pH) is mainly controlled by the organism, although the energy cost to concentrate the essential ions is high (Erez, 2003; Bentov and Erez, 2005; de Nooijer et al., 2009). Ongoing research gradually provides new insights into the complex species-dependent and environment-dependent process of calcification and incorporation of various trace elements in living foraminifera (e.g., de Nooijer et al., 2007; Dissard et al., 2010; Raitzsch et al., 2010).

2. Biology

The living cell consists of two types of cytoplasm: cell-body cytoplasm and reticulopodia (or rhizopodia), which constantly exchange smaller organelles through cytoplasmic streaming (Lee and Anderson, 1991; Bowser and Travis, 2002). The most distinctive character of the living foraminifer is the reticulate network of branched pseudopodia or reticulopodia, which extends from a single aperture or multiple apertures in the test and plays a key role in most life processes, including food acquisition, digestion, test construction, signal transmission, locomotion, and anchoring to hard substrates (Travis and Bowser, 1991; Bowser and Travis, 2002; Murray, 2006). The network of pseudopodia constantly changes its form, producing dynamically branching and joining strands that exhibit bidirectional flow and transport granules (commonly mitochondria) both toward and away from the aperture. Detailed biological descriptions of living foraminifera are provided by Lee and Anderson (1991), Goldstein and Bernhard (1997), Sen Gupta (1999), Lee and Hallock (2000), Cedhagen et al. (2002) and Gooday et al. (2008).

There is still only limited understanding about the nutrition, lifespan, reproduction cycles, and test biomineralization processes of most deep-water benthic foraminifera. The scant information that is available points to a huge heterogeneity of life histories, growth patterns, and reproduction strategies ranging from extremely fast reproduction and short lifespans for opportunist taxa exploiting phytodetritus pulses (Gooday, 1988) to lifespans of several years with slow growth and extremely low reproduction rates for

deep-water agglutinated foraminifera (Ohga and Kitazato, 1997; Hess et al., 2000; Kuhnt et al., 2005).

The feeding strategies of bathyal and abyssal foraminifera appear similarly diverse (Lee, 1980; Lipps, 1983; Gooday, 1990, 1993, 2003), including suspension, detritus feeding (particularly on diatoms, Suhr et al., 2003), and bacterial scavenging (Langezaal et al., 2005). In organic-rich sediments, detritus feeding takes place both at the surface of the sea floor and infaunally within the top few decimeters of the sediment, which become increasingly depleted in oxygen with depth. In oxygen-poor environments foraminifera may live symbiotically with prokaryotes (Buck and Bernhard, 2001). However, oxygen is also brought down to levels that would otherwise remain anoxic by the burrowing macrofauna, locally expanding the depth habitat of infaunal taxa (Murray, 1991; Loubere et al., 1995). In oligotrophic areas, where the organic export flux is low, surface dwellers consist mainly of epifaunal suspension feeders, while infaunal detritivores are scarce. Dissolved organic matter may additionally provide an important source of food for some species of benthic foraminifera (DeLaca et al., 1981; Nomaki et al., 2011), whereas carnivory (e.g., Dupuy et al., 2010) and parasitism (e.g., Sigwart, 2009) constitute less common modes of feeding (Murray, 1991).

3. Ecology

Microhabitat

The life position and depth distribution of deep-water benthic foraminifera at the sediment–water interface has been a major field of ecological research since the importance of epifaunal and infaunal habitats and species-specific microhabitat preferences for isotope and trace element studies and paleoenvironmental reconstructions were recognized (Corliss, 1985; Jones and Charnock, 1985; Altenbach and Sarnthein, 1989). The initial concept related benthic foraminiferal morphology and pore distribution on the surface of the test to depth habitat at the sea floor (“morphotype”-concept, Corliss and Chen, 1988; Corliss, 1991). This was later modified to account for the capability of motile benthic deep-water foraminifera to rapidly adapt their microhabitat to changes in food availability and oxygenation (Linke and Lutze, 1993; Loubere, 1996; Ohga and Kitazato, 1997; Jorissen, 1999). This dynamic adaptation is also reflected in the so-called TROX model (TROX = TRophic OXYgen model, Jorissen et al. 1995, 2007), which explains that the depth of the foraminiferal microhabitat is controlled by food availability in oligotrophic ecosystems and by oxygen concentration in eutrophic ecosystems. In oligotrophic environments, the microhabitat depth is limited by the low amount of food available within the sediment, whereas in eutrophic systems, the penetration depth of most taxa depends on the level of oxygen present in the sediment (Jorissen et al., 1995).

Biogeography

Deep-water benthic foraminifera are generally cosmopolitan and their distribution within ocean basins is primarily controlled by environmental parameters such as flux rate of particulate organic matter from the upper ocean to the sea floor and carbonate dissolution, rather than by physical barriers or the physico-chemical

properties of deep-water masses (Altenbach et al., 1999; Jorissen et al., 2007; Pawlowski and Holzmann, 2008; Gooday and Jorissen, 2012). One reason for the cosmopolitan distribution pattern of deep-water foraminifera is their capability for fast dispersal and recolonization of new substrates at the sea floor, which is unusual for other benthic organisms (Hess and Kuhnt, 1996; Alve, 1999; Murray, 2006). This rapid dispersal has been shown to be due to the occurrence of propagules (Alve and Goldstein, 2003; Goldstein and Alve, 2011). Living deep-sea benthic foraminifera, in contrast to shallow-water forms, show high genetic as well as morphological similarity over large distances in the world's oceans (e.g., from Arctic to Antarctic, Pawlowski et al., 2007). Deep-water benthic foraminiferal populations of the geological past were similarly cosmopolitan. Late Cretaceous abyssal agglutinated assemblages living below the calcite compensation depth (CCD) were first documented from Deep Sea Drilling Project (DSDP) sites in the Indian and West Pacific Oceans (Krasheninnikov, 1973, 1974) and later from Ocean Drilling Program (ODP) sites in the Central West and East Atlantic Ocean (Moullade et al., 1988; Kuhnt and Moullade, 1991; Kuhnt et al., 1996a).

Population dynamics

Observational and experimental studies provided evidence for a close benthic–pelagic coupling linking deep-sea benthic foraminiferal population dynamics and changes in surface ocean productivity on various temporal scales (Gooday, 1988, 2002; Smart et al., 1994; Heinz et al., 2001). While eutrophic surface ocean conditions favor low diversity with blooms of opportunistic species in the deep sea (e.g., Ohga and Kitazato, 1997), oligotrophic environments sustain low population density, promoting high diversity with complex trophic relationships, morphological innovations, and full exploitation of ecological niches (Gooday, 1999). On longer timescales, changes in surface productivity during major climatic and paleoceanographic events influence the population structure of deep-sea communities, but probably also lead to speciation and long-term evolutionary turnover within small and geographically isolated communities (e.g., Hallock et al., 1991; Groves and Yue, 2009). It has, for instance, been argued that the latitudinal gradient in diversity in deep-sea benthic foraminifera is linked to seasonality of productivity at high latitudes (e.g., Corliss et al., 2009) and evolved with the establishment of continental ice-sheets on the Antarctic continent (Thomas and Gooday, 1996).

4. Evolution

From the Late Mesozoic to Cenozoic, three large-scale steps can be recognized in the evolution of deep-water benthic foraminifera.

- (1) A stepwise middle Cretaceous evolutionary turnover from the early Aptian to early Turonian appears related to the development of oceanic anoxic events. Increases in organic export flux from the upper ocean triggering deep-sea anoxia may have enabled allopatric speciation within isolated small populations and led to the occupation of vacant niches. The middle Cretaceous turnover resulted in a major radiation

with the emergence of several modern lineages including buliminids, cassidulinids, and rotalids (Brasier, 1980; Tappan and Loeblich, 1988) as well as the appearance of most “modern” genera of agglutinated deep-water foraminifera (Kuhnt et al., 1996b). Surprisingly, the Cretaceous–Paleogene boundary event, which had major repercussions on the marine plankton, had little evolutionary impact on deep-water benthic foraminifera (Culver, 2003; Thomas, 2007; Alegret et al., 2012).

- (2) The most rapid and severe extinction in deep-water benthic foraminifera (30%–50% of species) occurred at the end of the Paleocene (Thomas and Shackleton, 1996; Thomas, 1998). Interestingly, this event did not concur with a major extinction event in the marine plankton, nor with global deep-water anoxia, nor a substantial change in organic export flux or carbonate dissolution (Thomas, 2003, 2007). However, the extinction appears related to a period of rapid deep ocean warming at the Paleocene–Eocene boundary affecting all major oceans. This deep ocean warming was possibly associated with ocean acidification and increased ocean stratification resulting in decreased upwelling and open-ocean productivity together with extension of oxygen minimum zones (Winguth et al., 2012).
- (3) Following the early Eocene recovery, three smaller-scale episodes of accelerated turnover coincided with intervals of pronounced global cooling and cryosphere expansion (Thomas et al., 2000; Zachos et al., 2001), which occurred across the Eocene–Oligocene boundary, in the middle Miocene (Berggren, 1972; van Morkhoven et al., 1986; Berggren and Miller, 1989; Miller et al., 1992; Thomas et al., 2000; Zachos et al., 2001; Thomas, 2007) and in the middle Pleistocene (“*Stilostomella* extinction”, Weinholz and Lutze, 1989; Schönfeld, 1996; Hayward, 2001; Hayward et al., 2010). Many long-lived genera of benthic foraminifera, which had decreased in abundance during earlier periods of cooling, finally became extinct during episodes of more intense global cooling.

5. Applications

Biostratigraphy

The utility of benthic deep-water foraminifera as biostratigraphic index fossils is limited by their slow evolution rates, strong environmental dependency, and inconsistent taxonomy (Boltovskoy, 1980; Kucera and Schönfeld, 2007; Hayward et al., 2010). However, the availability of more complete DSDP and ODP sedimentary successions containing well-preserved benthic assemblages allowed development of bathyal and abyssal benthic foraminiferal zonations for the Cenozoic (Berggren and Miller, 1989) and Cretaceous (Geroch and Nowak, 1984; Moullade, 1984; Kuhnt et al., 1992). The latter zonations are mainly applied in high latitudes and sub-CCD abyssal environments, where planktonic foraminiferal zonations cannot be used.

Paleobathymetry and sea-level reconstructions

Benthic foraminifera were recognized as paleobathymetric indicators after distribution studies along slope transects off California and

in the Gulf of Mexico indicated meaningful changes in assemblage composition with water depth (Bandy, 1953, 1961; Bandy and Arnal, 1957; Pflum and Frerichs, 1976). Van Morkhoven et al. (1986) compiled globally applicable charts of paleobathymetric distributions for 125 Cenozoic cosmopolitan deep water benthic foraminifera, which were subsequently widely used in subsidence and sea-level history reconstructions (e.g., Kaiho, 1992; Katz and Miller, 1993, 1996). However, modern ecological investigations revealed that oxygenation and food availability (which generally diminishes with increasing water depth) rather than water depth per se were primary controls on benthic foraminiferal distribution (Jorissen et al., 1995, 2007; Van der Zwaan et al., 1999; Murray, 2001). It has also been found that some deep-dwelling species are only able to reproduce under high hydraulic pressure (Tiedemann et al., 2012).

Paleoceanography and paleoclimate research

The reconstruction of past climates and ocean conditions relies heavily on geochemical analyses of the carbonate tests produced by benthic foraminifera. In particular, stable isotope and trace element analyses provide unique information on past variations in the carbon cycle, ocean pH, ventilation and circulation, productivity, temperature, salinity, ice volume, and seawater chemistry. Some challenging issues with the use of deep-sea benthic foraminifera in geochemical analysis are their relative scarcity, as compared to planktonic foraminifera, and the need to use monospecific specimens for analysis in order to avoid “vital effects” problems. Some recent studies, however, have perfected techniques, which only use very small quantities of calcite, (e.g., laser ablation). The development of geochemical proxies has progressed enormously in recent decades and an overview of potential applications for paleoclimatic and paleoceanographic reconstructions through time is presented below. A comprehensive review of traditional and emerging geochemical proxies in foraminifera by Katz et al. (2010) provides many details beyond the brief overview presented here.

Stable oxygen and carbon isotopes

Benthic foraminiferal $\delta^{18}\text{O}$ generally reflects a mixed signal, which varies as a function of global ice volume, the source of deep-water formation, and bottom water temperature (Shackleton and Opdyke, 1973). Thus benthic $\delta^{18}\text{O}$ can be used to reconstruct past variations in global ice volume and water mass temperature and to identify the source regions of water masses. Benthic foraminiferal $\delta^{18}\text{O}$ has also proven to be a powerful stratigraphic tool, allowing the development of high-resolution timescales for the Pleistocene and Pliocene (Imbrie et al., 1984; Lisiecki and Raymo, 2005) and for older intervals of the Cenozoic (Holbourn et al., 2005, 2007; Pälike et al., 2006) through the correlation of glacial cycles to computed changes in the geometry of Earth’s orbit (Laskar et al., 2004, 2011).

The $\delta^{13}\text{C}$ of epibenthic foraminiferal species is primarily a function of the dissolved inorganic carbon $\delta^{13}\text{C}$ in bottom water (Duplessy et al., 1984; Curry et al., 1988) and as such co-varies with the ventilation and nutrient content of deep-water masses. As water masses move away from their source areas, they progressively become enriched in nutrients and CO_2 with low $\delta^{13}\text{C}$ values as a result of organic matter oxidation through the water

column. Epibenthic species of the genera *Cibicidoides*, *Nuttalides*, and *Planulina* and the infaunal sediment-dwelling genus *Uvigerina* ($\delta^{18}\text{O}$ only) are most commonly used for stable isotope analysis. The $\delta^{13}\text{C}$ of infaunal benthic foraminifera is mainly related to the $\delta^{13}\text{C}$ of pore water, thus carrying a signal influenced by decomposing organic matter at the ocean floor (Mackensen et al., 1993, 2000; Mackensen and Licari, 2004). On a global scale, carbon isotope values of benthic foraminifera may indicate changes in the carbon cycle such as release of isotopically light carbon into the ocean–atmosphere system, as documented for the Paleocene–Eocene maximum (e.g., Thomas and Shackleton, 1996; Zachos et al., 2001). In such instances, benthic foraminiferal $\delta^{13}\text{C}$ can additionally be used as a stratigraphic tool for detailed correlation of sedimentary successions (Saltzman and Thomas, 2012).

Minor and trace elements

The variable uptake of minor and trace elements in the crystal lattice of calcareous foraminiferal tests reflects ambient environmental conditions at the sea-floor depth, either in bottom waters or pore waters, where the tests were formed. Thus, analysis of various minor and trace elements in foraminiferal tests can provide powerful tools to reconstruct past hydrographic and circulation changes.

Analysis of Mg/Ca in benthic foraminiferal calcite tests makes it possible in principle to independently reconstruct bottom water temperatures and in conjunction with $\delta^{18}\text{O}$ to separate the temperature and global $\delta^{18}\text{O}$ seawater (related to ice volume) signals in the $\delta^{18}\text{O}$ measured in tests. Studies have focused on a few taxa (*Cibicidoides pachyderma*, *Planulina wuellerstorfi*, *Oridorsalis umbonatus*, *Hoeglundina elegans*, and *Melonis* spp.), which showed relatively high temperature sensitivity (Lear et al., 2002, 2010; Martin et al., 2002; Rosenthal et al., 2006). However, uncertainty concerning the accuracy of calibration equations (Bryan and Marchitto, 2008) and the carbonate saturation effects altering the Mg/Ca relationship (Erez, 2003; Elderfield et al., 2006; Rosenthal et al., 2006; Yu and Elderfield, 2008) suggests that benthic foraminiferal paleothermometry especially at depth, where saturation may be of major importance, is not as straightforward as originally envisaged.

The distribution of the trace metals cadmium (Cd), barium (Ba), and zinc (Zn) follows the cycling of organic matter and varies as a function of water depth and deep-water circulation. Thus, the elemental ratios of Cd/Ca, Ba/Ca, and Zn/Ca in foraminiferal calcite can be used as tracers of water masses and circulation change (Boyle, 1988, 1992; Lea and Boyle, 1989, 1990; Marchitto et al., 2000). Benthic foraminiferal Cd/Ca varies proportionally to seawater Cd (which parallels the nutrient element phosphorus) and has proven useful for reconstructing glacial–interglacial variability in deep ocean circulation (Boyle and Keigwin, 1985; Rickaby et al., 2000; Zahn and Stüber, 2002; Marchitto and Broecker, 2006). Zn/Ca is a sensitive tracer of past ocean carbonate chemistry, as the partition coefficient in benthic foraminifera closely depends on the carbonate saturation state of the deep ocean (Marchitto et al., 2000, 2005). Benthic foraminiferal Ba/Ca has also been used to reconstruct glacial–interglacial changes in water mass distribution. However, its most promising application appears to be in planktonic foraminifera for the

reconstruction of past variations in fluvial inputs to the ocean (Weldeab et al., 2007).

Boron isotope ($\delta^{11}\text{B}$) and B/Ca

The use of boron isotopes in benthic foraminiferal tests to reconstruct bottom water pH is still in an early stage, as initial measurements of large numbers of mixed benthic species produced unrealistic and highly scattered data. However, recent attempts to measure $\delta^{11}\text{B}$ in the epibenthic species *Planulina wuellerstorfi*, which has a high boron concentration, appeared more promising (Yu and Elderfield, 2007; Hönisch et al., 2008). Recent measurements of $\delta^{11}\text{B}$ in individual *Cibicidoides* species to reconstruct past changes in the ocean carbonate system were also encouraging (Rae et al., 2011). Analysis of B/Ca in calcitic benthic foraminiferal tests has been used as an alternative approach to reconstruct paleo-pH (Yu and Elderfield, 2007). Initial studies indicated that the uptake of boron in benthic foraminifera in the deep ocean was closely related to carbonate saturation in the deep ocean (Yu et al., 2007; Foster, 2008; Brown et al., 2011). However, some recent results indicated considerable scatter in the B/Ca of at least some co-occurring morphotype species, suggesting potential complications arising with the application of this proxy (Rae et al., 2011).

6. Impact of Deep Sea Drilling

During the first phase of ocean drilling, 72 papers on deep-water benthic foraminifera were published in the Initial Reports of the Deep Sea Drilling Project between 1969 and 1987 (Table 1). A large proportion of these papers were dedicated to Jurassic and Cretaceous records, since deep-sea drilling provided the first opportunity to study “deep-time” deep-water assemblages in a much better preserved state than in most land outcrops. Entirely new assemblages of Late Jurassic to Cretaceous abyssal agglutinated foraminifera from sub-CCD environments were described in particular, shedding new light on the ecology and evolution of this hitherto poorly known group (Krasheninnikov, 1973, 1974). Cenozoic calcareous deep-sea species were previously known from some land sections (e.g., Velasco Formation, Mexico; Oceanic Formation, Barbados (van Morkhoven et al., 1986), but the realization that many species are cosmopolitan and have long stratigraphic ranges came with the analysis of samples recovered by the DSDP. Benthic assemblages also were commonly much better preserved in the deep-sea material than in land outcrops.

The expanded and more complete sedimentary successions obtained during the follow-on phases of ocean drilling with the ODP and Integrated Ocean Drilling Program (IODP) offered, in particular, the opportunity to develop high-resolution, astronomically calibrated time series over extended intervals of the Cenozoic. These continuous records provided fresh insights into the evolution of deep-water benthic foraminifera, as speciation and extinction events could be more precisely constrained and correlated across different oceans. Furthermore, these records allowed development and testing of new hypotheses concerning global radiation and mass extinction events in the deep sea and

their relations to ocean chemistry and climate change. A total of 51 papers on deep-water benthic foraminifera were published in ODP volumes between 1988 and 2004 (Table 2). In the later stages of ODP and IODP, the papers directly linked to specific drilling legs were commonly no longer published in the Scientific Results volumes, but in the general literature, thus being more difficult to trace.

7. Approach of this Atlas

A voluminous literature concerns the taxonomy of foraminifera, as more than 60,000 species have been described, the majority of which are benthic species (Culver, 1993). The standard of published illustrations and descriptions of type specimens, which form the basis of the taxonomy, varies enormously. This mainly reflects the lack of taxonomic standardization and the dispersion of descriptions and illustrations in a wide range of publications that have strong historical or regional associations. Thus, benthic foraminiferal taxonomy remains highly unwieldy, which severely compromises the application of benthic foraminifera for paleoceanographic and paleoclimatic research. It is especially difficult for geochemical paleoceanographers, who cannot consult benthic foraminiferal specialists, to exert quality control on specimens picked for analysis, as these are subsequently dissolved, prohibiting any further taxonomic check.

We have compiled a database of 300 deepwater benthic foraminifera, which comprises sets of fully focused, composite images and standardized taxonomic descriptions that consolidate previous taxonomic efforts. We illustrate whenever possible type specimens, mainly deposited in collections of the Smithsonian Institution, The Natural History Museum, London, and the Jagiellonian University, Kraków, for which only drawings or black and white illustrations were previously available. We additionally illustrate well-preserved material, mainly topotypic, from deep-sea cores, commercial wells, and land sections. For selected species, SEM micrographs are given for comparison and documentation of smaller specimens. The digital imaging techniques that we used involve taking a number of images per specimen. This image set constitutes a series of ‘slices’ taken sequentially at different focal plane depths such that all aspects of the specimens’ morphology are captured within an in-focus slice. A composite image is then built up by combining the areas in each image slice that are in focus. The resulting composite image provides a true-color image of the specimen viewed with full focus throughout the field of view. These images, which are the most realistic view of what the micropaleontologist actually ‘sees’ through the microscope tube, are particularly useful for illustrating type specimens that were previously poorly illustrated. The technique additionally has the benefit of not altering the original specimens, and thus is particularly suitable for type specimens. We used a Kontron Electronic ProgRes 3012 camera scanner, attached to a Leica Diaplan Microscope or an Allen Compact Video Microscope, or a Zeiss Axiocam camera, attached to a Leica MZ16 stereoscopic microscope, to produce digital images. A fully in-focus composite image was generated with the help of an image manipulation application (Adobe Photoshop) or with the help of automated imaging software (Syncroscopy Automontage). By

Table 1

Morphographic studies of deep-water benthic foraminifera published in the Initial Reports of the Deep Sea Drilling Project. Time slices are coded as: ju = Late Jurassic, ku = early Cretaceous, ko = late Cretaceous, pal = Paleogene, neo = Neogene, quart = Quaternary. Access to listed publications is available through the Integrated Ocean Drilling Program website (<http://www.iodp.org>).

Author	Year	Leg	Chapter	Age
Luterbacher	1972	11	dsdp11_18	ju-ku
Berggren	1972	12	dsdp12_14	pal-neo
Douglas	1973	17	dsdp17_21	ko-neo
Krasheninnikov	1973	20	dsdp20_11	ku-ko
Maync	1973	13	dsdp13pt2_41_1	ku
Bartenstein	1974	27	dsdp27_35	ju-ku
Krasheninnikov	1974	27	dsdp27_32	ko
Kuznetsova	1974	27	dsdp27_34	ju-ku
Scheibnerova	1974	27	dsdp27_36	ku
Vincent et al.	1974	24	dsdp24_21	pal
Luterbacher	1975	32	dsdp32_25	ku
Webb	1975	29	dsdp29_22	pal
McNulty	1976	33	dsdp33_08	ku-ko
Resig	1976	34	dsdp34_63	pal-neo
Rögl	1976	35	dsdp35_33	ko-neo
Boersma	1977	39	dsdp39_29	pal-neo
Sliter	1977	36	dsdp36_10	ku-ko
Sliter	1977	39	dsdp39_30	ku-ko
Beckmann	1978	40	dsdp40_18	ko
Cameron	1978	40	dsdp40_20	neo
Gradstein	1978	44	dsdp44_32	ku
Krasheninnikov & Pflaumann	1978	41	dsdp41_10	ku-ko
Kuznetsova & Seibold	1978	41	dsdp41_08	ju-ku
Lutze	1978	41	dsdp41_13	neo
Proto Decima & Bolli	1978	40	dsdp40_19	pal
Scheibnerova	1978	40	dsdp40_17	ku
Wright	1978	41	dsdp41pt1_31	neo
Bock	1979	48	dsdp48_14	ku
Butt	1979	47	dsdp47pt1_04	ku
Dupeuple	1979	48	dsdp48_18	ku-ko
Lutze	1979	47	dsdp47pt1_11	quart
Murray	1979	48	dsdp48_16	pal-neo
Schnitker	1979	48	dsdp48_15	pal-neo
Sigal	1979	47	dsdp27pt2_05	ku-ko
Butt	1980	55	dsdp55_08	pal-neo
Keller	1980	56	dsdp56_57p2_24	pal-neo
Sliter	1980	50	dsdp50_09	ju-ko
Thompson	1980	56	dsdp56_57pt2_22	pal-neo
Matoba & Yamaguchi	1982	64	dsdp64pt2_45	neo-quart
Basov & Krasheninnikov	1983	71	dsdp71pt2_28	ku-quart
Blanc-Vernet	1983	76	dsdp76_18	neo-quart
Dailey	1983	72	dsdp72_34	ku-pal
Gradstein	1983	76	dsdp76_20	ju

Table 1
(Continued)

Author	Year	Leg	Chapter	Age
Tjalsma	1983	72	dsdp72_33	pal–neo
Boersma	1984	75	dsdp75_13	neo
Clark & Wright	1984	73	dsdp73_13	pal
Hemleben & Tröster	1984	78	dsdp78a_26	ko
McNulty	1984	75	dsdp75_10	ku–ko
Murray	1984	81	dsdp81_09	pal–neo
Riegraf et al.	1984	79	dsdp79_26	ju
Schnitker	1984	81	dsdp81_17	neo
Boersma	1985	82	dsdp82_37	pal
Caralp	1985	80	dsdp80pt2_26	quart
McDougalll	1985	84	dsdp84_09	neo–quart
Magniez & Sigal	1985	80	dsdp80pt1_18	ku
Miller et al.	1985	80	dsdp80pt1_13	pal
Poag & Low	1985	80	dsdp80pt1_12	neo
Thomas	1985	85	dsdp85_17	pal–quart
Boersma	1986	90	dsdp90pt2_20	pal–neo
Kurihara & Kennett	1986	90	dsdp90pt2_21	neo
Lago	1986	87	dsdp87_10	neo–quart
Leckie & Webb	1986	90	dsdp90pt2_24	pal–neo
Schröder	1986	96	dsdp96_33	quart
Sliter	1986	89	dsdp89_09	ku–ko
Blanc-Vernet & Moullade	1987	93	dsdp93_06	neo–quart
Hart	1987	95	dsdp95_05	ko
Hulsbos	1987	93	dsdp93_10	pal
Katz & Miller	1987	95	dsdp95_08	pal
Miller & Katz	1987	95	dsdp95_07	ku–ko
Saint-Marc	1987	93	dsdp93_11	pal
Scott	1987	95	dsdp95_09	quart
Thomas	1987	94	dsdp94pt2_33	pal–quart

applying further standard digital processing techniques (e.g., sharpening, color and level balance, brightness/contrast, and the addition of a uniform background color), the final image was completed.

Our selection of deep-water benthic foraminifera focused on calcareous groups that are of stratigraphic or paleoecological significance for IODP studies and/or are increasingly being used for geochemical analyses. Many of these groups have a particularly confused taxonomic history, including the genera *Bolivina*, *Bulimina*, *Cibicides*, *Globobulimina*, *Planulina*, *Stilostomella*, and *Uvigerina*. We have additionally targeted agglutinated taxa to highlight morphologic features such as wall texture, grain and cement composition, test color and opacity, chamber arrangement, shape of sutures, and inner structure including early

ontogenic stages, as these represent important taxonomic criteria that are not detectable in SEM illustrations. We present systematic data (descriptions, synonymies, biogeographic, paleoecologic, and stratigraphic ranges) that were assembled from primary research, from the literature and from consultation with specialists. The generic taxonomic classification follows Loeblich and Tappan (1987) with a few exceptions, which mainly reflect taxonomic updates published subsequently. We used the revised timescale of Gradstein et al. (2004) and biostratigraphic zonation therein. Our hope is that these new illustrations and revised descriptions of selected deep-water benthic foraminifera will contribute to the clarification of their taxonomy and will support efforts to develop reliable proxies for paleontological and geochemical research.

Table 2

Monographic studies of deep-water benthic foraminifera published in the Scientific Results of the Ocean Drilling Program. Time slices are coded as: ju = Late Jurassic, ku = early Cretaceous, ko = late Cretaceous, pal = Paleogene, neo = Neogene, quart = Quaternary. Access to listed publications is available through the Integrated Ocean Drilling Program website (<http://www.iodp.org>).

Author	Year	Leg	Chapter	Age
Moullade et al.	1988	103	sr103_21	ko
Osterman & Qvale	1989	104	sr104_37	pal-neo
Cotalongo et al.	1990	107	sr107_30	neo-quart
Hasegawa et al.	1990	107	sr107_29	neo-quart
Sprovieri & Hasegawa	1990	107	sr107_28	neo-quart
Weinholz & Lutze	1990	108	sr108_07	quart
Clark	1990	110	sr110_10	neo-quart
Resig	1990	112	sr112_16	neo-quart
Thomas	1990	113	sr113_35	ko-neo
Boersma	1990	115	sr115_20	pal-neo
Iaccarino & Proto Decima	1990	116	sr116_18	neo
Scott & Leger	1990	116	sr116_16	neo-quart
Hermelin	1991	117	sr117_03	quart
Schröder-Adams	1991	119	sr119_31	pal-quart
Nomura	1991	121	sr121_01	ko-pal
Nomura	1991	121	sr121_02	pal-quart
Kaminski & Huang	1991	124	sr124_12	pal
Mackensen & Berggren	1992	120	sr120_34	pal
Mackensen	1992	120	sr120_36	neo
Quilty	1992	120	sr120_23	ko
Jones & Wonders	1992	122	sr122_33	ku
Zaninetti et al.	1992	122	sr122_24	trias
Haig	1992	123	sr123_14	ku
Kaminski et al.	1992	123	sr123_13	jur-ku
Milner	1992	125	sr125_04	pal
Kaiho & Nishimura	1992	126	sr126_20	quart
Kaiho	1992	126	sr126_19	pal-quart
Brunner	1992	127	sr127-128_12	neo-quart
Kato	1992	127	sr127-128_22	neo-quart
Nomura	1992	127	sr127-128_29	neo
Wightman & Kuhnt	1992	129	sr129_13	ko
Katz & Miller	1993	133	sr133_06	neo
Akimoto	1994	134	sr134_12	pal-neo
Schönfeld & Spiegler	1995	141	sr141_15	neo-quart
Dowsett & Ishman	1995	145	sr145_08	neo
Zellers	1995	146	sr146pt1_05	neo-quart
Collins et al.	1996	149	sr149_07	ju
Collins et al.	1996	149	sr149_09	neo-quart
Kuhnt & Collins	1996	149	sr149_08	ko-pal
Katz & Miller	1996	150	sr150_05	pal-neo
Osterman & Spiegler	1996	151	sr151_09	pal-neo
Osterman	1996	151	sr151_10	neo-quart
Bignot	1998	159	sr159_33	pal
Kuhnt et al.	1998	159	sr159_31	ko-pal
Holbourn & Kuhnt	1998	159	sr159_30	ko

Table 2
(Continued)

Author	Year	Leg	Chapter	Age
Holbourn & Moullade	1998	159	sr159_28	ku
Kaminski & Austin	1999	162	sr162_11	pal
Eidvin & Nagy	1999	162	sr162_01	neo
Katz	2000	166	sr166_12	neo
Quilty	2002	183	sr183_03	ko
Nomura & Takata	2004	199	sr199_223	pal

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