1 Introduction

Planktic foraminifers are marine protozoans with calcareous shells and chambered tests (Plate 1.1), first appearing in the mid-Jurassic approximately 170 million years ago, and populating the global ocean since the mid-Cretaceous (cf. Frerichs et al. 1972; Caron and Homewood 1983). The scientific and economic value of planktic foraminifers is based on their global marine abundance since the Lower Cretaceous ~110 Million years ago. Owing to the high preservation potential of their calcareous shell, planktic foraminifers provide information on the past environment and climate. Physical conditions and chemical composition of ambient seawater are reconstructed from faunal assemblages, i.e. the presence or absence of foraminifer species, as well as through the chemical composition of their test calcite, including crystallinity of the test wall, and changes in stable isotope and element ratios.

Test: The foraminifer shell is called a test. Shell and test are often used synonymously. Shell may be used for part(s) of the test, and for fragments of the test.

Planktic—planktonic: Planktic and planktonic may be used synonymously. In the strict Greek meaning the word planktic is possibly correct (Burckhardt 1920; Rodhe 1974). In the international literature both planktic and planktonic are used to the same degree, and either term may be applied based on personal preference. In benthic foraminifers, the term benthic has largely been used over the past decades, and benthonic has been out of fashion for some time.

Modern planktic foraminifers evolved from the earliest Tertiary including the first spinose species in Earth history soon after the Cretaceous-Paleogene (K/Pg) boundary (Olsson et al. 1999). Most modern species live in the surface to thermocline layer of the open ocean, and in deep marginal seas as the Mediterranean, Caribbean, South China Sea, and Red Sea. Some species descend to waters as deep as several thousand meters in the tropical to temperate ocean. Planktic foraminifers are largely absent from shallow marginal seas, for example the North Sea where reproduction is impeded. The presence and absence of planktic foraminifer species at the regional scale is related to the quality and quantity of food, physical and chemical properties of ambient seawater, and displays an overall latitudinal pattern at the global scale.

Species abundance varies according to seasons as well as on an interannual scale, and on longer time-scales depending on environmental conditions, and affected by climate change. Symbiont-bearing species depend on light and are restricted to the euphotic zone of the surface ocean. Symbiont-barren species may dwell as

R. Schiebel and C. Hemleben, *Planktic Foraminifers in the Modern Ocean*,
DOI 10.1007/978-3-662-50297-6_1

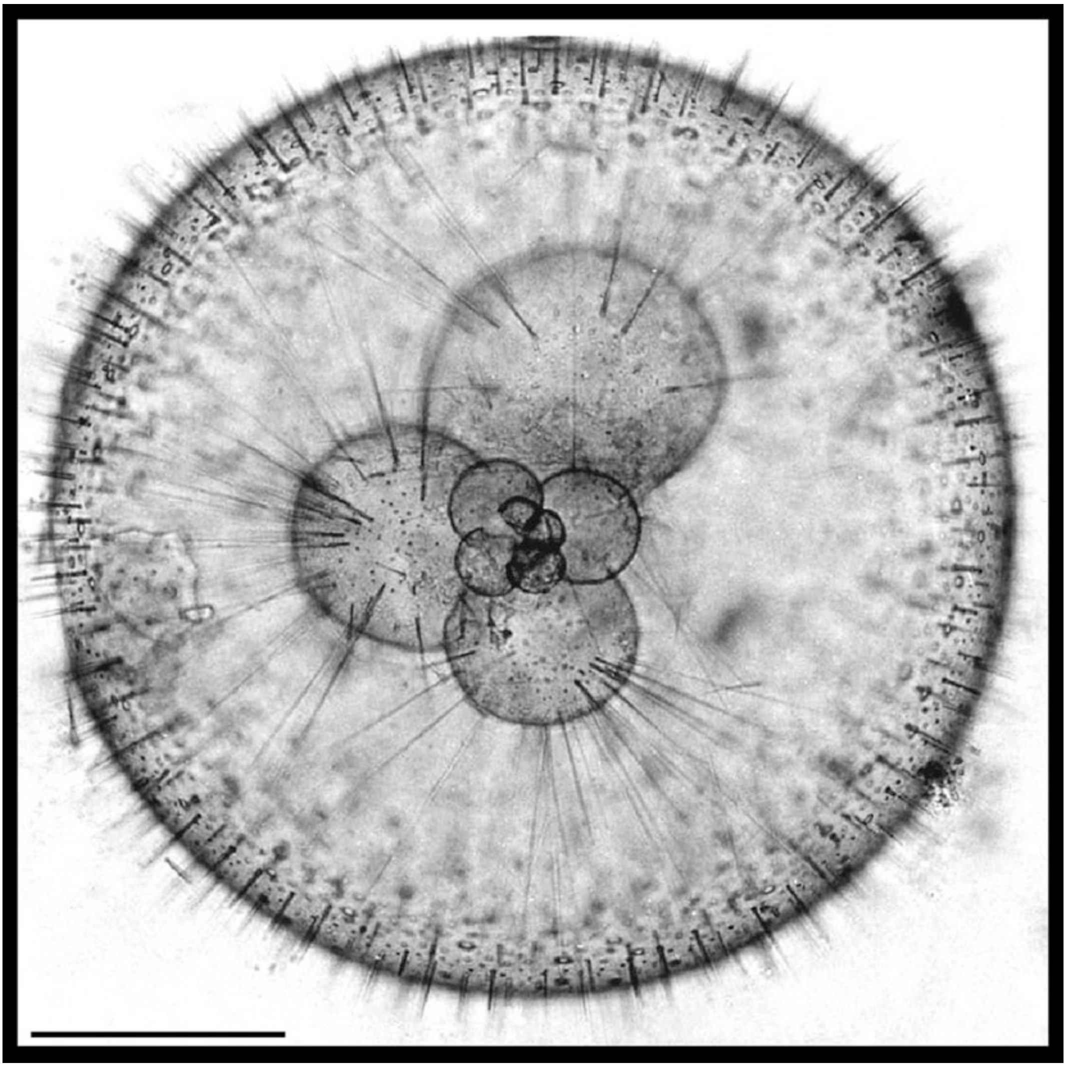

Plate 1.1 The modern planktic foraminifer species *Orbulina universa* seen in transmitted light. The inner trochospiral test of the pre-adult individual is surrounded by the spherical adult test. Spines are protruding from both inner trochospiral and outer spherical test. Pores are visible as tiny dark spots on the inner and outer test. Multiple small *circles* on the outer test wall are the apertures of the adult individual. The opening at the inner trochospiral test is caused by dissolution. Scale bar 200 μm

deep as the abyssal ocean, and have been sampled from below 4000 m water depth. Planktic foraminifers are rather marginal to marine biological research including modern biogeochemistry (Sarmiento and Gruber 2006), although they are major producers of marine calcareous particles (i.e. their tests) deposited on the ocean floor forming the globigerina ooze (e.g., Vincent and Berger 1981). Data compilation of a large variety of marine Plankton Functional Types (see text box below) have shown that planktic foraminifers possibly constitute a minor but ubiquitous component of marine planktic biomass (Buitenhuis et al. 2013). In addition, modeling approaches on the planktic foraminifer population dynamics from the 1990s have contributed to a better understanding of planktic foraminifer ecology and application in paleoceanography (e.g., Signes et al. 1993; Žarić et al. 2006; Fraile et al. 2009; Lombard et al. 2011; Roy et al. 2015).

Plankton functional type (PFT): The expression plankton functional type (PFT) is used in modeling, and includes different conceptual categories of organisms as, for example, organisms of similar ecology, and serving similar roles within an ecosystem (Anderson 2005). The PFTs included in the MAREDAT initiative on the ecology and biomass of marine plankton are picophytoplankton, diazotrophs, coccolithophores, Phaeocystis, diatoms, picoheterotrophs, microzooplankton, planktic foraminifers (which range between micro- and mesozooplankton), mesozooplankton, pteropods, and macrozooplankton (Buitenhuis et al. 2013).

By contributing substantially to the fossil record of marine sediments, planktic foraminifers provide indispensable ecologic information used in paleoecologic, paleoceanographic, and stratigraphic research from the Lower Cretaceous (~110 millions years, Ma). Faunistic and biogeochemical (e.g., stable isotopes) information from the calcareous (calcite, $CaCO_3$) planktic foraminifer tests is used to reconstruct, for example, temperature and salinity of the past surface ocean. Radiocarbon (^{14}C) gives an absolute age of test formation of late Pleistocene and Holocene sediments. Factors determining the modern faunal composition are applied to the interpretation of the fossil assemblages, for example, by multiple regression techniques (i.e. transfer functions), yielding information (proxy data) on ancient environmental parameters. The chemical composition, i.e. stable isotope and element ratios of the calcareous test (calcite, $CaCO_3$) provides an assessment of the chemical and physical state of ambient seawater, and is applied to the reconstruction of temperature, and biological productivity of the past marine environment.

Proxy (*pl.* proxies): A proxy is a measurable feature from which another not directly measurable characteristic can be derived. For example, the test of a planktic foraminifer bears certain stable isotope ratios (e.g., $^{18/16}O$), measurable with a mass spectrometer, from which temperature and other parameters of ambient seawater can be reconstructed by applying empirically derived formulae (see, e.g., Fischer and Wefer 1999).

1.1 A Brief History of Planktic Foraminifer Research

Technological improvement of binocular microscopes allowed the French naturalist Alcide d'Orbigny (1826) to describe the first planktic foraminifer species *Globigerina bulloides* from beach sands of Cuba, but erroneously classifying it with the cephalopods. Alcide d'Orbigny's family lived in the village of Esnandes at the Baie d'Aiguillon north of La Rochelle (France), where Alcide's father Charles Marie d'Orbigny was a renowned 'naturaliste'. Young d'Orbigny was fortunate enough to look at the sediments of the bay, and to find at a rich benthic foraminifer fauna using the first good binocular microscopes available in the 1820s (Vénec-Peyré 2005). D'Orbigny's French contemporary Félix Dujardin (1835), then, correctly described planktic foraminifers as unicellular organisms. Some 30 years later, Owen (1867) suspected the planktic life habit of these organisms. Following the Challenger Expedition from 1872 to 1876, the surface-dwelling habitat of planktic foraminifers was generally recognized thanks to observations provided by John Murray in the Challenger Reports (Brady 1884). Foraminifer biology was described first by Rhumbler (1911). In the first half of the 20th century, foraminifers were widely used for stratigraphic purposes in the search for hydrocarbon reservoirs, and Joseph

Cushman published a plethora of catalogues on foraminifers of all major ocean basins, and from various time-slices (e.g., Cushman 1911; Cushman and Todd 1949).

Distribution and ecology of different living planktic foraminifer species were first studied on plankton samples by Schott (1935). From the 1960s, planktic foraminifers have been used in biostratigraphy to date marine sediments sampled, for example, within the Deep Sea Drilling Programme (DSDP) from 1964 to 1983, followed by the Ocean Drilling Programme (ODP), and the Integrated Ocean Drilling Programme (IODP) from 2003 onward. The taxonomy of modern planktic foraminifers was largely improved by the seminal publication of Frances Parker (1962).

Distribution, ecology, and biology of the live fauna mostly of the western North Atlantic were extensively studied by Bé, Hemleben, Anderson, and co-workers, including graduate students and post-doctoral appointees, between the late 1950s and 1980s. Among these participants were David Caron and Howard Spero who became significant researchers in the field. Other major contributors included Peter Wiebe, Sharon Smith, Susumu Honjo, and Richard Fairbanks at Woods Hole Oceanographic Institution. At about the same time, Esteban Boltovskoy developed new sampling methods, and conducted projects on the production and sedimentation of planktic foraminifers in the South Atlantic. Ecological significance of modern species was applied to paleoecological and paleoceanographic settings to obtain new information on the ancient ocean and Earths' climate. Since the late 1960s, Wolfgang Berger and co-workers supplied ample information in many papers on planktic foraminifer carbonate chemistry and application of proxies to paleoceanography, starting in the eastern north Pacific, and later focusing on the South Atlantic (e.g., Berger 1981; Berger et al. 1989; Kemle-von-Mücke and Hemleben 1999; see also Fischer and Wefer 1999). Population dynamics and carbon turnover of modern planktic foraminifers mostly of the eastern North Atlantic and Indian Ocean including adjacent regions were studied by Christoph Hemleben and co-workers since the late 1960s (e.g., Hemleben 1969; Hemleben and Spindler 1983; Hemleben et al. 1989; Bijma and Hemleben 1994; Schiebel et al. 1995; Schiebel 2002).

In the early 1970s, a joint group guided by O. Roger Anderson, Allan Bé (both Lamont-Doherty Earth Observatory), Christoph Hemleben, and Michael Spindler (both Tübingen University), came together at the Bermuda Biological Station (BBS) in order to culture planktic foraminifers (e.g., Bé et al. 1977; Hemleben et al. 1989). The BBS is close to blue water locations and thus exceptionally suited to experiment with planktic foraminifers. Living foraminifers were sampled by means of SCUBA collection and net tow sampling, and a sophisticated experimental set up in order to maintain viable planktic foraminifers from early ontogenetic stages to maturity was developed. Almost the entire range of all basic planktic foraminifer behavior was observed and recorded. Analyses of planktic foraminifers from laboratory culture have been substantially advanced by Howard Spero and co-workers at the University of California (e.g., Spero 1986; Spero et al. 2015). Culturing of planktic foraminifers also has been conducted at the Bellairs Research Institute at Barbados (e.g., Caron et al. 1982; Spindler et al. 1984), the Caribbean Marine Research Center on Lee Stocking Island, Bahamas (e.g., Spero and Williams 1988; Spero and Lea 1993), the H. Steinitz Marine Biology Laboratory at Eilat, Gulf of Aquaba (e.g., Erez et al. 1991, and references therein), the Caribbean Marine Biological Institute (CARAMBI) at Curacao (e.g., Bijma et al. 1992), the Isla Magueyes Marine Laboratory at Puerto Rico (e.g., Hönisch et al. 2011; Allen et al. 2011, 2012). However, a second generation of any planktic foraminifer species has never been successfully achieved in laboratory culture, which remains one of the major issues to be solved in the future.

Recent work focuses on planktic foraminifer taxonomy, stratigraphy, evolution, ecology, carbonate chemistry, paleoceanography, population dynamics, and biology. Stratigraphy and paleoceanography were among the original scientific interests in planktic foraminifers, due to their economic and scientific value, respectively.

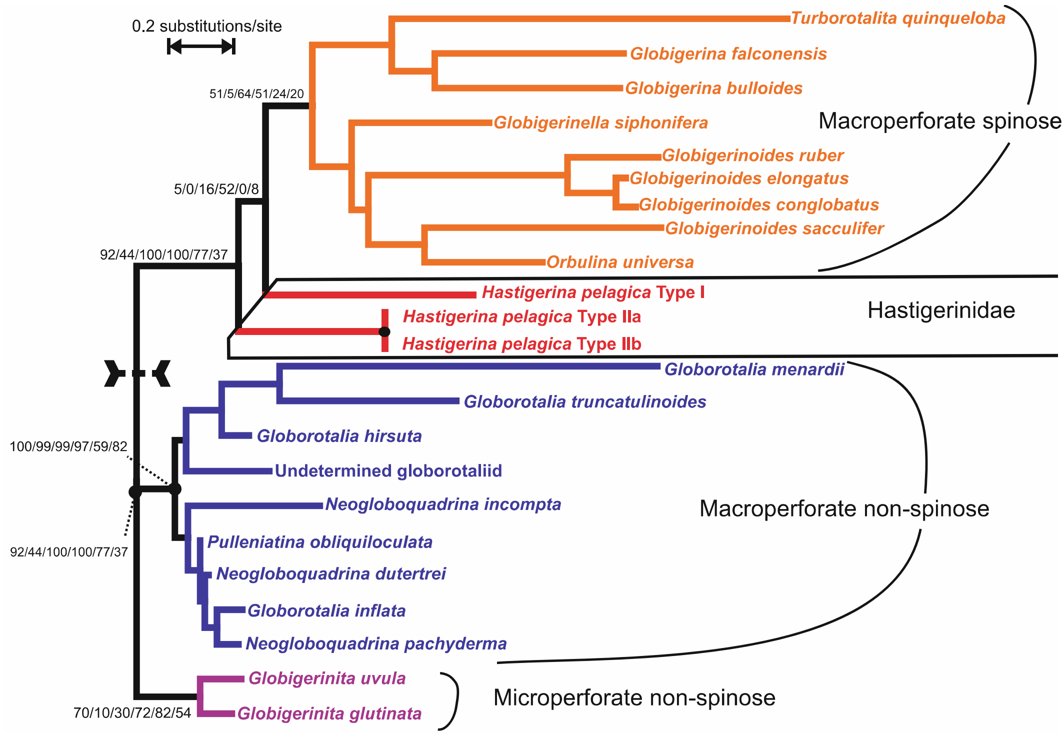

Fig. 1.1 Phylogenetic relationships of the four major groups of modern planktic foraminifers, macroperforate spinose, macroperforate non-spinose, microperforate spinose, and Hastigerinidae, based on a maximum likelihood reconstruction from SSU rDNA. Modified after Aurahs et al. (2009), from Weiner et al. (2012)

Modern techniques of molecular genetics (i.e. DNA sequencing) are currently applied to reveal the taxonomic and phylogenetic relations (Fig. 1.1) of the earlier established morphospecies (Table 1.1) distinguished by their test architecture (e.g., Darling et al. 1997; de Vargas et al. 1999; André et al. 2014). The relation to morphological features of the tests of modern species is reviewed in the fossil species (e.g., Hemleben et al. 1999; Hemleben and Olsson 2006).

Technological development of mass spectrometry analytical systems provides ever more precise measurements of rare elements, stable isotope ratios and 'clumped isotopes'. Based on these advances, new proxies have been developed in paleoceanography (see the review of Katz et al. 2010). Laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) and secondary ion mass spectrometry (NanoSIMS) allow analyses of single chambers of tests, and hence better interpretation of ontogenetic changes in planktic foraminifer ecology. Outer and inner shell architecture is analyzed and visualized at high-resolution using X-ray micro-tomography (e.g., Johnstone et al. 2010). Using refined technology, new knowledge has been gained from planktic foraminifer research, and the field has been substantially advanced, but simultaneously a number of intriguing new questions have been raised. Planktic foraminifer assemblages and test properties have become increasingly valuable proxies, and are applied in monitoring climate and environmental change including the position and strength of marine currents and fronts, oxygenation of the water column, and ocean acidification, among others. In 2010, SCOR (Scientific Committee on Oceanic Research) Working Group 138 was formed to synthesize the current knowledge on 'Modern Planktic Foraminifera and Ocean Changes'.

Investigation of modern and geologically ancient planktic foraminifers have diversified

Table 1.1 Modern planktic foraminifer morphospecies sorted by genus, including author and year of first description, and page of detailed description given in Chap. 2

Genus	Species	Author	Year
Beella	*digitata*	(Brady)	1879
Berggrenia	*pumilio*	(Parker)	1962
Bolliella	*adamsi*	Banner and Blow	1959
Candeina	*nitida*	d'Orbigny	1839
Dentigloborotalia	*anfracta*	(Parker)	1967
Gallitellia	*vivans*	(Cushman)	1934
Globigerina	*bulloides*	d'Orbigny	1826
	falconensis	Blow	1959
Globigerinella	*calida*	(Parker)	1962
	siphonifera	(d'Orbigny)	1839
Globigerinita	*glutinata*	(Egger)	1895
	minuta	(Natland)	1938
	uvula	(Ehrenberg)	1861
Globigerinoides	*conglobatus*	(Brady)	1879
	ruber	(d'Orbigny)	1839
	sacculifer	(Brady)	1877
Globoquadrina	*conglomerata*	(Schwager)	1866
Globorotalia	*cavernula*	Bé	1967
	crassaformis	(Galloway and Wissler)	1927
	hirsuta	(d'Orbigny)	1839
	inflata	(d'Orbigny)	1839
	menardii	(d'Orbigny)	1865
	scitula	(Brady)	1882
	theyeri	Fleisher	1974
	truncatulinoides	(d'Orbigny)	1839
	tumida	(Brady)	1877
	ungulata	Bermudez	1960
Globorotaloides	*hexagonus*	(Natland)	1938
Globoturborotalita	*rubescens*	Hofker	1956
	tenella	(Parker)	1958
Hastigerina	*digitata*	(Rhumbler)	1911
	pelagica	(d'Orbigny)	1839
Neogloboquadrina	*dutertrei*	(d'Orbigny)	1839
	incompta	(Cifelli)	1961
	pachyderma	(Ehrenberg)	1861
Orbulina	*universa*	d'Orbigny	1839
Orcadia	*riedeli*	(Rögl and Bolli)	1973
Pulleniatina	*obliquiloculata*	(Parker and Jones)	1865
Sphaeroidinella	*dehiscens*	(Parker and Jones)	1865
Streptochilus	*globigerus*	(Schwager)	1866

(continued)

Table 1.1 (continued)

Genus	Species	Author	Year
Tenuitella	*compressa*	(Fordham)	1986
	fleisheri	Li	1987
	iota	(Parker)	1962
	parkerae	(Brönnimann and Resig)	1972
Turborotalita	*clarkei*	(Rögl and Bolli)	1973
	humilis/cristata	(Brady)/Heron-Allen and Earland 1929	1884
	quinqueloba	(Natland)	1938

substantially since the first discoveries (see, e.g. the reviews and books of Vincent and Berger 1981; Hemleben et al. 1989; Murray 1991; Schiebel and Hemleben 2005; Kucera 2007). An enormous wealth of information is available from textbooks, printed papers, online publications, and various Internet sites (e.g., www.species-identification.org, www.EMIDAS.org, www.eforams.org). Many more researchers and working groups, beyond those referred to above, have added an enormous wealth of knowledge, which is presented in the following topical Chaps. 2–10.

References

Allen KA, Hönisch B, Eggins SM, Rosenthal Y (2012) Environmental controls on B/Ca in calcite tests of the tropical planktic foraminifer species *Globigerinoides ruber* and *Globigerinoides sacculifer*. Earth Planet Sci Lett 351–352:270–280. doi:10.1016/j.epsl.2012.07.004

Allen KA, Hönisch B, Eggins SM, Yu J, Spero HJ, Elderfield H (2011) Controls on boron incorporation in cultured tests of the planktic foraminifer *Orbulina universa*. Earth Planet Sci Lett 309:291–301. doi:10.1016/j.epsl.2011.07.010

Anderson TR (2005) Plankton functional type modelling: running before we can walk? J Plankton Res. doi:10.1093/plankt/fbi076

André A, Quillévéré F, Morard R, Ujiié Y, Escarguel G, de Vargas C, de Garidel-Thoron T, Douady CJ (2014) SSU rDNA divergence in planktonic Foraminifera: molecular taxonomy and biogeographic implications. PLoS ONE. doi:10.1371/journal.pone.0104641

Aurahs R, Göker M, Grimm GW, Hemleben V, Hemleben C, Schiebel R, Kučera M (2009) Using the multiple analysis approach to reconstruct phylogenetic relationships among planktonic Foraminifera from highly divergent and length-polymorphic SSU rDNA sequences. Bioinforma Biol Insights 3:155–177

Bé AWH, Hemleben C, Anderson OR, Spindler M, Hacunda J, Tuntivate-Choy S (1977) Laboratory and field observations of living planktonic Foraminifera. Micropaleontology 23:155–179

Berger WH (1981) Paleoceanography: the deep-sea record. In: Emiliani C (ed) The oceanic lithosphere. The sea. pp 1437–1519

Berger WH, Smetacek V, Wefer G (1989) Productivity of the ocean: present and past. John Wiley & Sons, Chichester

Bijma J, Hemleben C (1994) Population dynamics of the planktic foraminifer *Globigerinoides sacculifer* (Brady) from the central Red Sea. Deep-Sea Res I 41:485–510. doi:10.1016/0967-0637(94)90092-2

Bijma J, Hemleben C, Oberhänsli H, Spindler M (1992) The effects of increased water fertility on tropical spinose planktonic foraminifers in laboratory cultures. J Foraminifer Res 22:242–256

Brady HB (1884) Report on the Foraminifera dredged by the H.M.S. "Challenger" during the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–1876. Zoology 9:1–814

Buitenhuis ET, Vogt M, Moriarty R, Bednaršek N, Doney SC, Leblanc K, Le Quéré C, Luo YW, O'Brien C, O'Brien T, Peloquin J, Schiebel R, Swan C (2013) MAREDAT: towards a world atlas of marine ecosystem data. Earth Syst Sci Data 5:227–239. doi:10.5194/essd-5-227-2013

Burckhardt G (1920) Zum Worte Plankton. Schweiz Z Hydrol 1:190–192

Caron DA, Bé AWH, Anderson OR (1982) Effects of variations in light intensity on life processes of the planktonic foraminifer *Globigerinoides sacculifer* in laboratory culture. J Mar Biol Assoc U K 62:435–451

Caron M, Homewood P (1983) Evolution of early planktic foraminifers. Mar Micropaleontol 7:453–462. doi:10.1016/0377-8398(83)90010-5

Cushman JA (1911) A monograph of the Foraminifera of the North Pacific Ocean Part II Textulariidae. Smithsonian Institution, United States National Museum

Cushman JA, Todd R (1949) Species of the genus *Chilostomella* and related genera. Contrib Cushman Lab Foraminifer Res 25:84–99

Darling KF, Wade CM, Kroon D, Brown AJL (1997) Planktic foraminiferal molecular evolution and their polyphyletic origins from benthic taxa. Mar Micropaleontol 30:251–266

De Vargas C, Norris R, Zaninetti L, Gibb SW, Pawlowski J (1999) Molecular evidence of cryptic speciation in planktonic foraminifers and their relation to oceanic provinces. Proc Natl Acad Sci 96:2864–2868

D'Orbigny AD (1826) Tableau méthodique de la classe des Céphalopodes. Ann Sci Nat 1:245–314

Dujardin F (1835) Recherches sur les organismes inférieurs. Ann Sci Nat-Zool Biol Anim 2:343–377

Erez J, Almogi-Labin A, Avraham S (1991) On the life history of planktonic Foraminifera: lunar reproduction cycle in *Globigerinoides sacculifer* (Brady). Paleoceanography 6:295–306

Fischer G, Wefer G (1999) Use of proxies in paleoceanography: examples from the South Atlantic. Springer, Berlin, Heidelberg

Fraile I, Schulz M, Mulitza S, Merkel U, Prange M, Paul A (2009) Modeling the seasonal distribution of planktonic Foraminifera during the last glacial maximum. Paleoceanography. doi:10.1029/2008PA001686

Frerichs WE, Heiman ME, Borgman LE, Bé AWH (1972) Latitudal variations in planktonic foraminiferal test porosity: Part 1. Optical studies. J Foraminifer Res 2:6–13

Hemleben C (1969) Ultramicroscopic shell and spine structure of some spinose planktonic Foraminifera. In: Brönniman P, Renz HH (eds) Proceedings of 1st International Conference, Plankt Microfoss. Leiden, pp 254–256

Hemleben C, Olsson RK (2006) Wall textures of Eocene planktonic Foraminifera. In: Pearson PN, Olsson RK, Huber BT, Hemleben C, Berggren WA (eds) Atlas of Eocene planktonic Foraminifera. Cushman Found Spec Publ 41:47–66

Hemleben C, Olsson RK, Berggren WA, Norris RD (1999) Wall texture, classification, and phylogeny. In: Olsson RK, Hemleben C, Berggren WA, Huber BT (eds) Atlas of Paleocene planktonic Foraminifera. Smithonian Contrib Paleobiology 85:10–19

Hemleben C, Spindler M (1983) Recent advances in research on living planktonic Foraminifera. Utrecht Micropaleontol Bull 30:141–170

Hemleben C, Spindler M, Anderson OR (1989) Modern planktonic Foraminifera. Springer, Berlin

Hönisch B, Allen KA, Russell AD, Eggins SM, Bijma J, Spero HJ, Lea DW, Yu J (2011) Planktic foraminifers as recorders of seawater Ba/Ca. Mar Micropaleontol 79:52–57

Johnstone HJH, Schulz M, Barker S, Elderfield H (2010) Inside story: an X-ray computed tomography method for assessing dissolution in the tests of planktonic Foraminifera. Mar Micropaleontol 77:58–70. doi:10.1016/j.marmicro.2010.07.004

Katz ME, Cramer BS, Franzese A, Hönisch B, Miller KG, Rosenthal Y, Wright JD (2010) Traditional and emerging geochemical proxies in Foraminifera. J Foraminifer Res 40:165–192

Kemle-von-Mücke S, Hemleben C (1999) Planktic Foraminifera. In: Boltovskoy E (ed) South Atlantic zooplankton. Backhuys Publishers, Leiden

Kucera M (2007) Chapter six: planktonic Foraminifera as tracers of past oceanic environments. In: Developments in marine geology. Elsevier, pp 213–262

Lombard F, Labeyrie L, Michel E, Bopp L, Cortijo E, Retailleau S, Howa H, Jorissen F (2011) Modelling planktic foraminifer growth and distribution using an ecophysiological multi-species approach. Biogeosciences 8:853–873. doi:10.5194/bg-8-853-2011

Murray JW (1991) Ecology and distribution of planktonic Foraminifera. In: Lee JJ, Anderson OR (eds) Biology of Foraminifera. Academic Press, London, pp 255–285

Olsson RK, Hemleben C, Berggren WA, Huber BT (1999) Atlas of Paleocene planktonic Foraminifera. Smithonian Contrib Paleobiology 85, pp 252

Owen SRI (1867) On the surface-fauna of mid-ocean. J Linn Soc Lond Zool 9:147–157

Parker FL (1962) Planktonic foraminiferal species in Pacific sediments. Micropaleontology 8:219–254

Rhumbler L (1911) Die Foraminiferen (Thalamorphoren) der Plankton-Expedition. Die allgemeinen Organisations-Verhältnisse der Foraminiferen, Erster Teil

Rodhe W (1974) Plankton, planktic, planktonic. Limnol Oceanogr 19:360

Roy T, Lombard F, Bopp L, Gehlen M (2015) Projected impacts of climate change and ocean acidification on the global biogeography of planktonic Foraminifera. Biogeosciences 12:2873–2889. doi:10.5194/bg-12-2873-2015

Sarmiento JL, Gruber N (2006) Ocean biogeochemical dynamics. Princeton University Press, Princeton and Oxford

Schiebel R (2002) Planktic foraminiferal sedimentation and the marine calcite budget. Glob Biogeochem Cycles 16(4), 1065. doi:10.1029/2001GB001459

Schiebel R, Hemleben C (2005) Modern planktic Foraminifera. Paläontol Z 79:135–148

Schiebel R, Hiller B, Hemleben C (1995) Impacts of storms on Recent planktic foraminiferal test production and $CaCO_3$ flux in the North Atlantic at 47°N, 20°W (JGOFS). Mar Micropaleontol 26:115–129

Schott W (1935) Die Foraminiferen des äquatorialen Teil des Atlantischen Ozeans: Deutsche Atlantische Expeditionen Meteor 1925–1927. Wiss Ergeb, 43–134

Signes M, Bijma J, Hemleben C, Ott R (1993) A model for planktic foraminiferal shell growth. Paleobiology 19:71–91

Spero HJ (1986) Symbiosis, chamber formation and stable isotope incorporation in the planktonic foraminifer *Orbulina universa*. PhD Thesis, University of California

Spero HJ, Eggins SM, Russell AD, Vetter L, Kilburn MR, Hönisch B (2015) Timing and mechanism for intratest Mg/Ca variability in a living planktic foraminifer. Earth Planet Sci Lett 409:32–42. doi:10.1016/j.epsl.2014.10.030

Spero HJ, Lea DW (1993) Intraspecific stable isotope variability in the planktic Foraminifera

Globigerinoides sacculifer: results from laboratory experiments. Mar Micropaleontol 22:221–234

Spero HJ, Williams DF (1988) Extracting environmental information from planktonic foraminiferal $\delta^{13}C$ data. Nature 335:717–719

Spindler M, Hemleben C, Salomons JB, Smit LP (1984) Feeding behavior of some planktonic foraminifers in laboratory cultures. J Foraminifer Res 14:237–249

Vénec-Peyré MT (2005) Les Planches inédites de foraminifères d'Alcide d'Orbigny. Publ Scient Mus Paris, MNHN pp 302

Vincent E, Berger WH (1981) Planktonic Foraminifera and their use in paleoceanography. Ocean Lithosphere Sea 7:1025–1119

Weiner A, Aurahs R, Kurasawa A, Kitazato H, Kucera M (2012) Vertical niche partitioning between cryptic sibling species of a cosmopolitan marine planktonic protist. Mol Ecol 21:4063–4073. doi:10.1111/j.1365-294X.2012.05686.x

Žarić S, Schulz M, Mulitza S (2006) Global prediction of planktic foraminiferal fluxes from hydrographic and productivity data. Biogeosciences 3:187–207