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Chapter 3

BENTHIC FORAMNIFERAL ASSEMBLAGES FROM COLD-WATER CORAL ECOSYSTEMS

SILVIA SPEZZAFERRI[1], ANDRES RÜGGEBERG[2,3], CLAUDIO STALDER[1], AND STEPHAN MARGRETH[1]

[1]University of Fribourg, Department of Geosciences, Chemin du Musée 6, 1700 Fribourg, Switzerland.
Email: silvia.spezzaferri@unifr.ch, claudio.stalder@unifr.ch

[2]Renard Centre of Marine Geology, Ghent University, Krijgslaan 281, S8, B-9000 Gent, Belgium.
Email: andres.ruggeberg@ugent.be

[3]GEOMAR Helmholtz Centre for Ocean Research Kiel, Wischhofstrasse 1-3, D-24148 Kiel, Germany.
Email: arueggeberg@geomar.de

AUTECOLOGY OF BENTHIC FORAMINIFERA

Deep-sea benthic foraminifera are an important component of the deep-sea biomass in the present oceans. They are adapted to cold, dark and often extremely oligotrophic environments. The benthic foraminiferal fauna is highly diverse and many species have a cosmopolitan distribution. These organisms convey a remarkable amount of information about the present and past ecological conditions at the ocean seafloor and have played an important role to understand the functioning of the marine systems (e.g., Jorissen and others, 2007). Many investigations so far have documented and proved the relationship between foraminiferal species and different ecological and physico-chemical parameters, and to what extent these parameters control spatial and temporal dynamics of foraminiferal communities (e.g., Van der Zwaan and others, 1999; Gooday, 2003; Murray, 2006; Jorissen and others, 2007).

Foraminifera can also be considered as reliable indicators for the origin, quality, quantity, and periodicity of organic matter reaching the seafloor (Lutze and Coulbourn, 1984; Altenbach and Sarnthein, 1989; Herguera and Berger, 1991; Gooday, 1994; Altenbach and others, 1999; Loubere and Fariduddin, 1999). One of the major environmental parameter controlling the distribution of deep-sea benthic foraminiferal faunas is the organic matter flux mainly derived from primary production at the sea surface. In eutrophic environmental settings, the organic particles cannot be consumed directly by benthic organisms, the organic matter can accumulate and thus, sediment pore waters become anoxic. In these cases the limiting variable for benthic foraminiferal distribution becomes the oxygen (Koutsoukos and others, 1990; Hermelin, 1992; Alve, 1995; Jorissen and others, 1995; Bernhard and Sen Gupta, 1999). Water mass properties such as salinity and temperature and bathymetry play only a minor role in their distribution (Jorissen and others, 2007).

Additional limiting environmental parameters for benthic foraminifera are sediment grain size and current velocity (e.g., Miller and Lohmann, 1982; Lutze and Coulbourn, 1984; Mackensen and others, 1990, 1995; Schmiedl and Mackensen, 1997; Schönfeld, 2002a, b). Under high current velocities, some species may live preferentially on elevated substrates like coarse sand grains, dropstones, shell debris, sponges, hydroids, serpulids, and corals. They can live epifaunal on the sediment-water interface. Mackensen and others (1995) recognized that *Trifarina angulosa* correlates with coarse-grained sediments and strong currents. Schönfeld (1997; 2002a, b) documented high abundance of epibenthic species like *Lobatula lobatula* and *Planulina ariminensis* in high-energy environments of the Gulf of Cadiz. These epifaunal species living on elevated substrates are directly exposed to the water

Table 3.1. Autecology of selected species of benthic foraminifera identified in this study (modified after Spezzaferri and others, 2013).

Species	Facies	Preferred substrate	Living strategy	Feeding strategy/ preference
E. exigua	deep mud and pebbly sand facies	mud	infaunal	fresh phytodetritus feeder, seasonal food fluxes
E. vitrea	dead coral facies, shallow mud, pebbly sand facies	mud	infaunal	phytodetritus
C. refulgens	sandwave – dropstone and living coral facies	hard substrates	epifaunal attached	passive suspension feeder, parasitic, predator
C. aravaensis	sandwave – dropstone and living coral facies	hard substrates	epifaunal attached	passive suspension feeder
C. pachyderma	sandwave – dropstone and living coral facies	-	epifaunal, shallow infaunal	passive suspension feeder, ingest fresh diatoms, prefers labile components of organic matter
L. lobatula	living coral facies	hard substrates, coarse sediment	epifaunal, attached	passive suspension feeder
T. angulosa	dead coral facies	sand, coarse sediments	infaunal	-
H. balthica	shallow, deep mud and pebbly sand facies	mud to silt	epifaunal to shallow infaunal	prefers fresh organic matter
M. barleeanum	shallow mud and living coral facies	mud to silt	infaunal	may feed on low and intermediate quality organic matter
C. subglobosum	deep mud facies	-	epifaunal or shallow infaunal	strongly linked to fresh food availability
C. laevigata	living coral facies, off-reef	silt to sand	infaunal	dependent on labile organic matter
G. subglobosa	living coral and dropstone facies	mud	infaunal	phytodetritus feeder, preferentially ingests fresh diatoms
R. scorpiurus	deep mud facies	mud to sand	epifaunal or shallow infaunal	may feed on refractory organic matter and/or degradation products, presence of fresh organic matter flux
O. umbonatus	deep mud facies	mud to sand	-	associated to freshly deposited phytoplankton detritus, but can thrive in nutrient poor waters
C. wuellerstorfi	deep mud facies, off-reef	mud to sand	generally epifaunal, rarely shallow infaunal	suspension feeder, associated to freshly deposited phytoplankton detritus
E. scaber	sandwave facies	fine sand	infaunal detritivor, may be epyphitic on seagrass	detritivor, does not depend on labile organic matter
B. marginata	coral rubble, mud, sediment clogged and living coral facies	mud, silt	deep infaunal in anoxic regions, also shallow infaunal	may feed on low quality organic matter
B. cylindrica	deep mud facies	fine grained sediments	shallow infaunal	prefers high quality organic matter

Table 3.1. Extended.

Oxygen	Energy	Other ecological preferences	References
-	low	opportunistic, large tolerance to varying organic flux	Gooday (1988, 1993); Smart and others (1994); Thomas and others (1995); Thomas and Gooday (1996); Loubere and Fariduddin (1999); Murray (2006)
oxic	low	opportunistic, phytodetritus, low water energy	Jorissen and others (1992); Murray (2006)
oxic	high	stable physico-chemical conditions	Alexander and DeLaca (1987); Van der Zwaan (1982); Kaiho (1994, 1999); Kouwenhoven (2000); Murray (2006)
oxic	high	stable physico-chemical conditions	Margreth and others (2009) Murray (2006)
oxic	high	preferentially oligotrophic environment, stable physico-chemical conditions	Miao and Thunell (1993); Schmiedl and others (2000); Almogi-Labin and others (2000); Murray (2006); Fontanier and others (2002); Margreth and others (2009)
oxic	high	-	Murray (1971); Lutze and Thiel (1989); Schönfeld (2002b); Murray (2006)
-	withstands permanent winnowing	-	Jarke (1960); Murray (1971); Sejrup and others (1981); Hald and Vorren (1984); Mackensen and others (1985); Qvale and Van Weering (1985); Schönfeld (2002a)
suboxic-oxic	-	temperatures 4 -7.5 °C. mean bottom salinities 34.0–35.0 psu	Murray (2006): Kaiho (1994); Elliott and others (1991); Murray (2003); Husum and Hald (2004); Schmiedl and others (2000)
dysoxic	-	$<$10°C, lives in high productivity waters, lives on the redox front	Murray (1973); Corliss (1985); Gooday (1986); Caralp (1989); Loubere (1991); Murray (2006); Koho and others (2008); Fontanier and others (2005; 2008); Morigi and others (2012)
oxic and well ventilated	-	sensitive to changing environment	Murray (2006); Jorissen and others (2009)
can tolerate dysoxia	-	high carbon flux rates	Mackensen and Hald (1988); Murray (2003); Murray (2006); Alve (2010)
-	-	oligotrophic	Corliss (1979); Gooday (1994); Mackensen and others (1995); Fariduddin and Loubere (1997); Suhr and others (2003) Murray (2006)
may stand dysoxia	-	organic matter rich sediments, flux of organic matter 0.8–60 g m^2 yr^{-1}	Althenbach and others (1999); Fontanier and others (2003; 2005); Alve (2010)
prefers well-oxygenated waters		cold water species	Gooday (1988; 1993); Mackensen and others (1985)
oxic	strong currents, well ventilated waters	tolerates temperatures below zero	Gooday (1988; 1993); Wollenburg and Mackensen (1998); Saidova (2011)
-	-	eutrophic environments, tolerates salinity $>$24 per mil for most of the year and temperatures 1–20°C	Debenay (2000); Ernst and others (2002); Fontanier and others (2002); Murray and others (2003); Duijnstee and others (2004); Murray (2006); de Nooijer and others (2008); Alve and Goldstein (2010); Murray and Alve (2011)
may tolerate dysoxia-anoxia	low	in Norway they live in temperatures of 4-13°C, is a high productivity taxa	Jorissen and others (1998); Jorissen and Wittling (1999); Fontanier and others (2002); Husum and Hald (2004); Murray (2006)
dysoxic, limited tolerance for anoxic conditions	-	organic rich sediments in meso- to eutrophic environments	Fontanier and others (2002); Koho and others (2008); Schmiedl and others (2000)

Table 3.1. Continued.

Species	Facies	Preferred substrate	Living strategy	Feeding strategy/ preference
T. earlandi	shallow off- reef, sediment clogged coral facies	mud and sand	free-living, shallow infaunal	-
G. affinis	shallow off- reef	mud	intermediate to deep infaunal	can feed on low and intermediate quality organic matter
D. coronata	sandwave facies, living coral facies	coarse sediments	epifaunal attached	
S. fusiformis	shallow off- reef	mud	deep infaunal	can feed on more refractory organic matter and/or degradation products
Pullenia spp.	living coral facies	mud	infaunal	variable food flux
A. gallowayi	sandwave facies	mud and sand	infaunal	-
N. iridea	off-reef	mud	infaunal	dependent on labile organic matter
U. peregrina	off-mound	mud	shallow infaunal	rich supply of labile organic matter
U. mediterranea	off-mound	mud	shallow infaunal	rich supply of labile organic matter
C. kullenbergi	off-mound	shallow hard substrates and mud	epifaunal, shallow infaunal	passive suspension feeder, oligotrophic environment
N. turgida	off-mound	mud	infaunal	
H. boueana	dead coral facies	hard substrates	epifaunal attached	
P. ariminensis	dead coral facies	hard substrates	epifaunal attached	suspension feeder
S. wrightii	dead coral facies		epifaunal attached	
G. praegeri	living coral facies	hard substrates	epifaunal attached, mobile	suspension feeder
C. carinata	living coral facies, off-mound		shallow infaunal, epifaunal	moderate to high carbon flux rates, preference for high quality food
T. brady	living coral facies		infaunal	
K. bradyi	sandwave facies	mud to silt	epifaunal, attached	
G. soldanii	sandwave facies	mud	epifaunal	
H. sarcophaga	coral rubble, living coral, pebbly sand facies	hard substrates	epifaunal	parasitic, predator
Bulimina spp.	off-mound	mud	infaunal	high carbon flux rates
Bolivina spp.	living coral facies	mud	infaunal	high carbon flux rates
B. difformis	coral rubble and pebbly sand facies	coarse sediments	shallow infaunal	
B. spathulata			shallow infaunal	responding mainly to fluxes of labile organic matter

Table 3.1. Extended. Continued.

Oxygen	Energy	Other ecological preferences	References
well-adapted to dysoxia		cosmopolitan, omnivorous and opportunistic	Murray (2003; 2006); Alve and Goldstein (2010); Alve (2010); Murray and Alve (2011)
zero oxygen level, anoxic, tolerates dysoxia	-	organic matter rich sediments	Fontanier and others (2005; 2008),
oxic	strong bottom currents up to 26–50 cm/s	attached on hydroids and octocorals	Schönfeld (2002b); Hawkes and Scott (2005)
dysoxic, can tolerate anoxia	-	opportunistic	Duchemin and others (2005); Murray (2006); Alve (2003; 2010)
subsoxic	-	high carbon flux rates	Corliss and Chen (1988); Loubere (1998); Gupta and Thomas (1999); Murray (2006)
-	strong bottom currents	-	Wollenburg and Mackensen (1998)
suboxic-dysoxic	-	need pulsed arrivals of phytodetritus to dominate the assemblages	Kaiho (1994); Duchemin and others (2005); Murray (2006); Alve (2010)
tolerant of suboxic conditions		dominantly eutrophic	Altenbach and others (1999); Altenbach and Sarnthein (1989); Fontanier and others (2002; 2003)
oxic, less tolerant to suboxic conditions than *U. peregrina*		dominantly eutrophic	Altenbach and others (1999); De Stiger and others (1998); Fontanier and others (2002; 2003); Murray (2006)
oxic		deep-sea habitat, stable physico-chemical conditions	Fariduddin and Loubere (1997); Jorissen (1988); Morigi and others (2001); Murray (2006); Schmiedl and others (2000); Woodruff and others (1980)
tolerant of suboxic and dysoxic conditions			Kaiho (1994); Murray (2006)
oxic	high energy		Murray (2006); Spezzaferri and Coric (2001)
oxic	high energy		Lutze and Thiel (1989); Schönfeld (1997; 2002a, b), Gross (2000)
well oxygenated waters	high energy	rare in the Oslo Fjord	Murray (2006); Martins and others (2007); Alve and Goldstain (2010)
		opportunistic,	Altenbach and others (1999); Gupta and Thomas (1999); Hess and others (2005); Jorissen and others (2007); Nomura (1983a, b)
facultative anaerob			Gupta (1997)
			Murray (2006)
suboxic, dysoxic			Mullins and others (1985), Murray (2006)
oxic, well oxygenated waters	strong currents linked to the cold-water coral ecosystem		Cedhagen (1994); Freiwald and Schönfeld (1996)
tolerates low oxygen			Brüchert and others (2000); Mackensen and others (1993), Mackensen and others (1990), Mullins and others (1985), Murray (2006), Seidenkrantz and others (2000)
tolerates low oxygen			Loubere (1996); Mackensen and others (1995); Mullins and others (1985); Murray (2006); Seidenkrantz and others (2000)
	can tolerate low oyxgen		Martins and others (2007)
			Fontanier and others (2003)

Table 3.1. Continued.

Species	Facies	Preferred substrate	Living strategy	Feeding strategy/ preference
H. elegans	coral rubble, pebbly sand and off-mound facies	mud and silt	shallow infaunal	preference for high quality resources
S. bulloides	coral rubble, pebbly sand, dropstone facies	mud to silt		seasonal input of organic matter

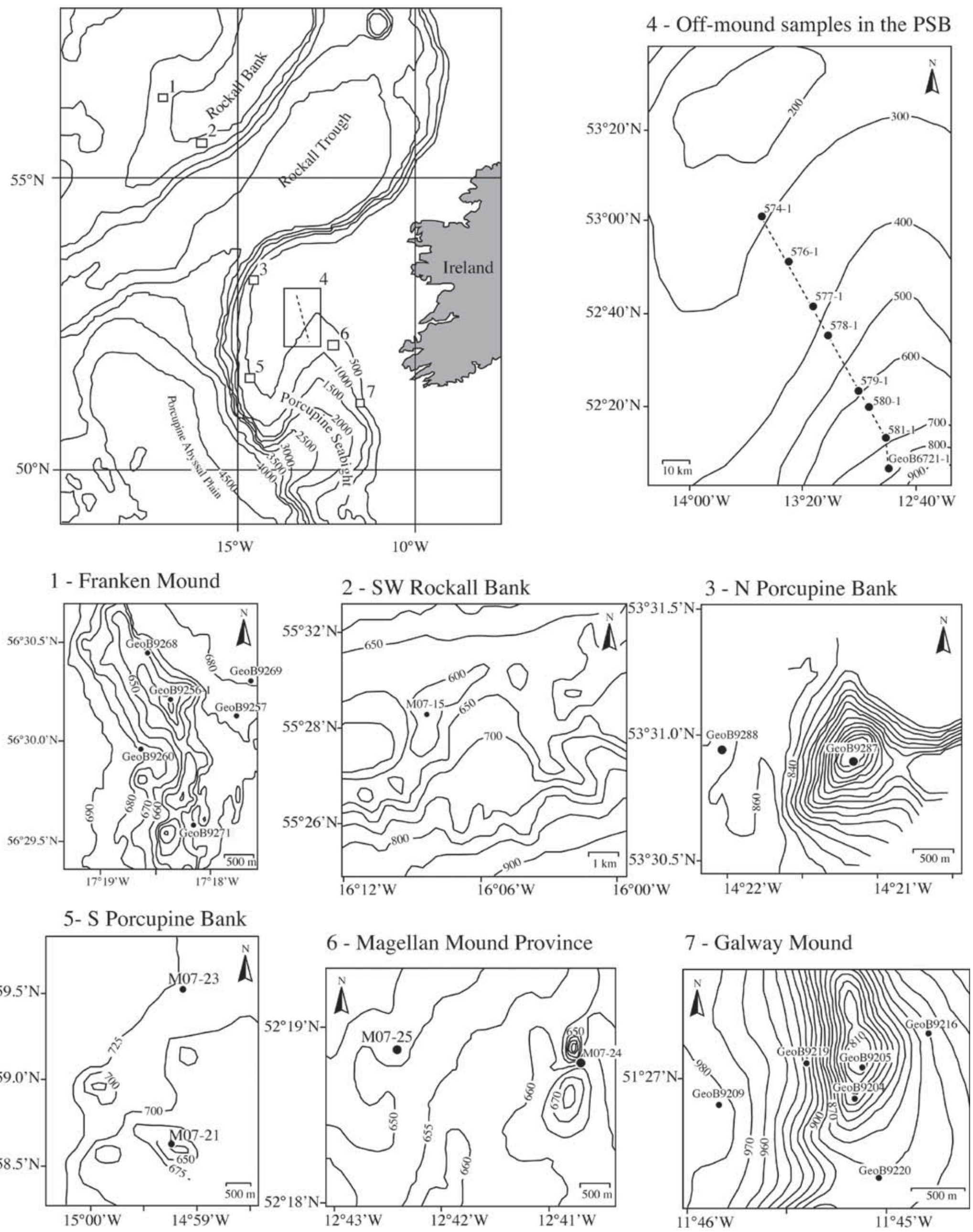


Figure 3.1. Location map of the surface sediment samples from the Porcupine Seabight and Rockall Bank (modified after Margreth and others, 2009). 1 and 2 mark the carbonate mound provinces along the Rockall Bank, 3 and 5 along the Porcupine Bank, and 4, 6 and 7 within the Porcupine Seabight.

Table 3.1. Extended. Continued.

Oxygen	Energy	Other ecological preferences	References
oxic with limited tolerance for low oxygen levels		oligotrophic	Fontanier and others (2002); Geslin and other (2004)
well oxygenated water, may tolerate low oxygen conditions		high productivity	Licari and Mackensen (2005); Hermelin and Shimmield (1990)

masses and flourish, where strong currents mobilize suspended food particles.

There is not sufficient space here to review the huge amount of literature produced for deep-sea benthic foraminiferal assemblages along the Northern European margin and the Eastern Mediterranean. The reader is referred to the list of references reported in Table 3.1 where the autecology of several selected species is presented.

THE PORCUPINE SEABIGHT/ ROCKALL BANK REGION

Only Schönfeld and others (2011), Margreth and others (2009) and Morigi and others (2012) investigated in detail the Recent/Sub-Recent benthic foraminiferal assemblages from these regions. They all document high diversity and population density from cold-water corals.

Table 3.2. Sample number, latitude and longitude, water depth, mound region/mound province and facies of the investigated samples from the Porcupine Seabight (PSB), Porcupine Bank (PB) and Rockall Bank (RB).

Sample	Latitude (N)	Longitude (W)	Depth (m)	Region/Province	Facies
GeoB 9220	51°26.69′	11°45.04′	892	PSB/Belgica	sandwave
GeoB 9209-2	51°26.89′	11°45.81′	982	PSB/Belgica	sandwave
GeoB 9204-1	51°26.94′	11°45.16′	838	PSB/Belgica	living coral
GeoB 9205-1	51°27.04′	11°45.12′	810	PSB/Belgica	living coral
GeoB 9219-1	51°27.05′	11°45.40′	920	PSB/Belgica	living coral
GeoB 9216-1	51°27.09′	11°44.81′	890	PSB/Belgica	living coral
M07-21	51°58.65′	14°59.18′	627	PB/SW PB	dead coral
M07-23	51°59.54′	14°59.05′	721	PB/SW PB	off-mound
GeoB 6721-1	52°09.22′	12°46.31′	696	PB/SW PB	sandwave
P292/581-1	52°13.40′	12°50.24′	736	PSB	off-mound
M07-24	52°18.86′	12°40.78′	663	PSB/Magellan	dead coral
M07-25	52°18.87′	12°42.42′	647	PSB/Magellan	off-mound
P292/580-1	52°20.46′	12°56.72′	630	PSB	off-mound
P292/579-1	52°23.62′	13°01.56′	554	PSB	off-mound
P292/578-1	52°35.67′	13°10.74′	450	PSB	off-mound
P292/577-1	52°41.78′	13°16.43′	356	PSB	off-mound
P292/576-1	52°51.40′	13°25.39′	249	PSB	off-mound
P292/574-1	53°00.80′	13°34.04′	202	PSB	off-mound
GeoB 9287	53°30.91′	14°21.16′	696	PB/N PB	living coral
GeoB 9288	53°31.06′	14°21.77′	870	PB/N PB	dropstones
M07-15	55°29.18′	16°08.24′	552	RB/SE Rockall Trough	living coral
GeoB 9271	56°29.58′	17°18.16′	664	RB/SE Rockall Trough	dropstones
GeoB 9260	56°29.98′	17°18.63′	683	RB/SE Rockall Trough	dropstones
GeoB 9257	56°30.13′	17°17.77′	678	RB/SE Rockall Trough	dropstones
GeoB 9256-1	56°30.20′	17°18.37′	629	RB/SE Rockall Trough	dead coral
GeoB 9269	56°30.28′	17°17.63′	686	RB/SE Rockall Trough	dropstones
GeoB 9268	56°30.44′	17°18.62′	656	RB/SE Rockall Trough	dead coral

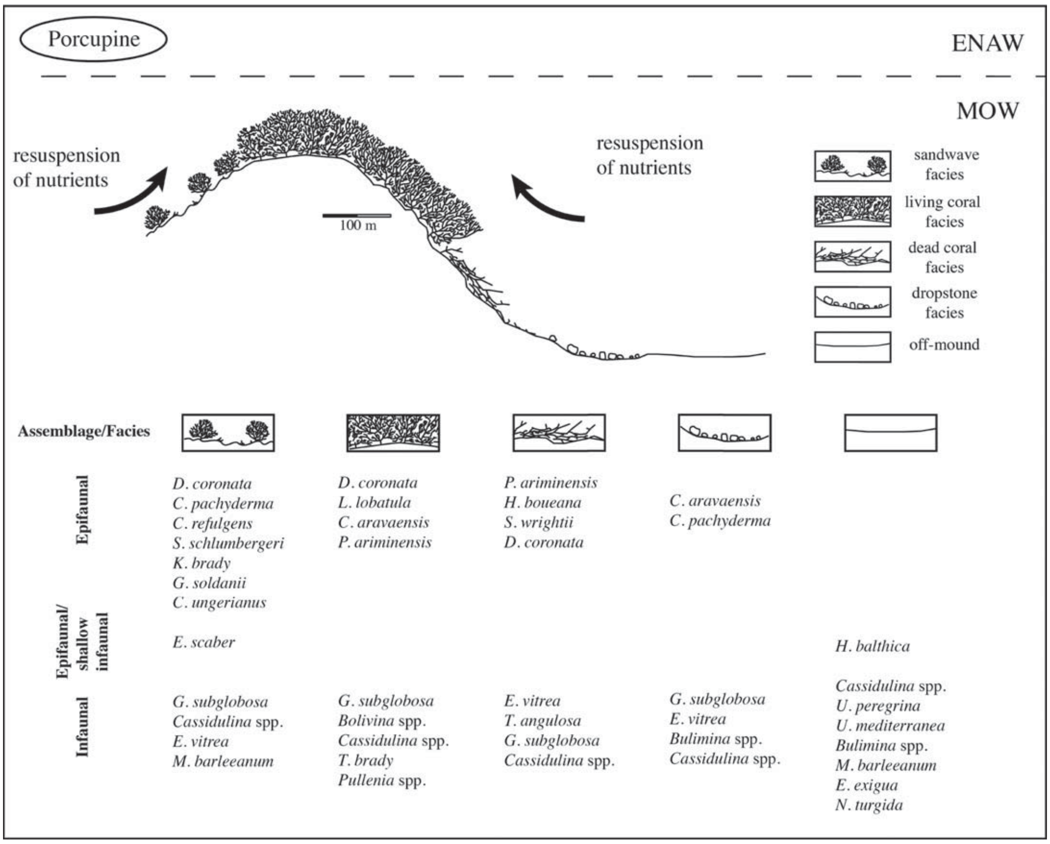


Figure 3.2. A) Model of the distribution of benthic foraminifera microhabitats according to sedimentary facies on a carbonate mound from the Porcupine Seabight, modified from Margreth and others (2009) and Spezzaferri and others (2013). The influence of the Mediterranean Overflow Water (MOW) is also indicated. ENAW = Eastern North Atlantic Water.

Schönfeld and others (2011) showed that epibenthic species are dominant and that *Discanomalina coronata* is associated to coral rubble facies, *Cibicides refulgens* prefers off-mound sand veneer and *Uvigerina mediterranea* dominates in the main depositional area on the southern flank of Galway Mound. They state that nutritional demands, microhabitat preferences, and ecology are the main drivers for species abundance and distribution in the Porcupine Seabight.

Morigi and others (2012) showed that on the Logachev Mound on the Rockall Bank slope dominant species are *Spirillina vivipara*, Allogromiid sp.1, *Globocassidulina subglobosa*, *Adercotryma wrighti*, *Eponides pusillus*, *Ehrenbergina carinata*, *Planulina ariminensis*, *Trochammina inflata*, and *Paratrochammina challengeri*. These authors report absence of foraminifera in adjacent open slope areas characterised by coarse-grained deposits and subject to strong tidal currents. In disagreement with Schönfeld and others (2011) they find that *C. refulgens* is absent in the 'live' assemblages and abundant in the dead assemblages. They attribute this absence to the intense winnowing and reworking of glacial species, although they do not rule out that these attached species were missed in the sampling procedure. During the FP7-Eurofleets cruise CWC Moira Porcupine Seabight *C. refulgens* was constantly observed attached to coral debris (authors' personal observations) and the hypothesis of reworking of glacial species is here disregarded.

The study of Margreth and others (2009) also documents abundant epifauna in the living coral facies, which represents a suitable substrate. The infaunal species *Melonis barleeanum*, *Globocassidulina subglobosa*, *Cassidulina* spp. and *Gavelinopsis* spp. occuring also in the living coral facies probably lived in the finer sediment fraction between coral branches (Fig. 3.2 A).

Rüggeberg and others (2007) studied the fossil benthic assemblages from the Propeller Mound in this region (Fig. 3.2 B) and identified the epifaunal species *D. coronata*, *L. lobatula*, *P. ariminensis*, *C. refulgens* and *H. sarcophaga* as cold-water coral indicators, *E.*

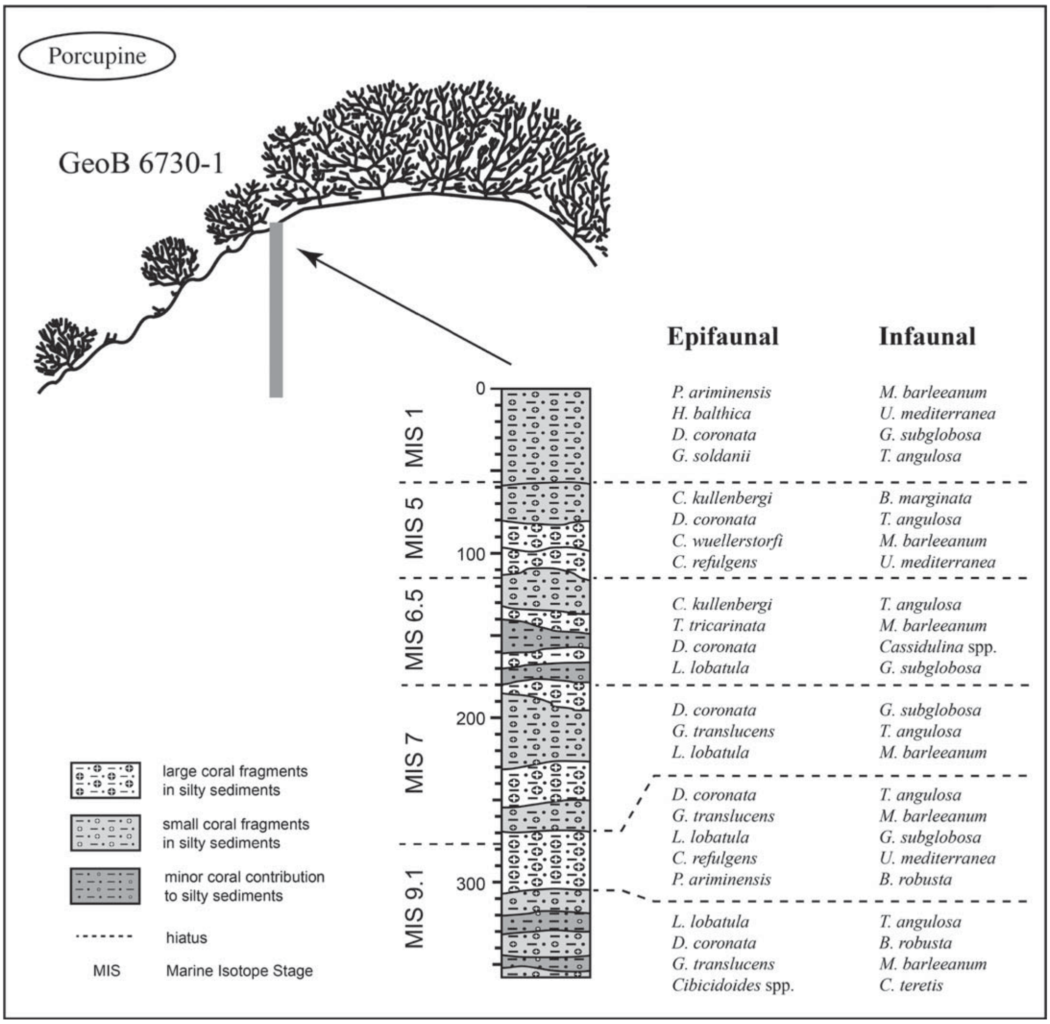


Figure 3.2. B) Epifaunal and infaunal benthic foraminifera of the buried facies recovered in gravity core GeoB6730-1 from Propeller Mound (modified after Rüggeberg and others, 2007).

excavatum f. *clavata*, *C. teretis*, *C. kullenbergi*, and *G. subglobosa* as glacial indicators.

Figure 3.1 and Table 3.2 show the location of our samples (modified after Margreth and others, 2009). The distribution of benthic foraminiferal microhabitats according to different facies summarizing our data is shown in Figure 3.2 A-B. The list and abundances of benthic foraminifera are in Appendix I.

THE NORWEGIAN MARGIN AND THE LOPPHAVET REEF

Several authors have studied benthic foraminifera from the Norwegian margin (see Table 3.1 for references), however, they did not focus on cold-water corals. Only Cedhagen (1994) and Freiwald and Schönfeld (1996) investigated the role of predators and parasitism of the single species *Hyrrokin sarcophaga* in cold-water coral reefs.

Margreth (2010) and Spezzaferri and others (2013) present the distribution of these organisms in several sites from the Oslo Fjord (Skagerrak) to the northernmost discovered cold-water coral reef (The Korallen Reef) (Fig. 3.3). Their study indicates that foraminifera can be used as a tool for the characterization of cold-water coral reef environments. In particular, they describe abundant epifaunal species such as *D. coronata*, *C. refulgens*, *C. aravaensis*, *L. lobatula* living in the living coral framework and also infaunal species e.g., *T. angulosa*, *M. barleeanum*, *E. vitrea*, *A.*

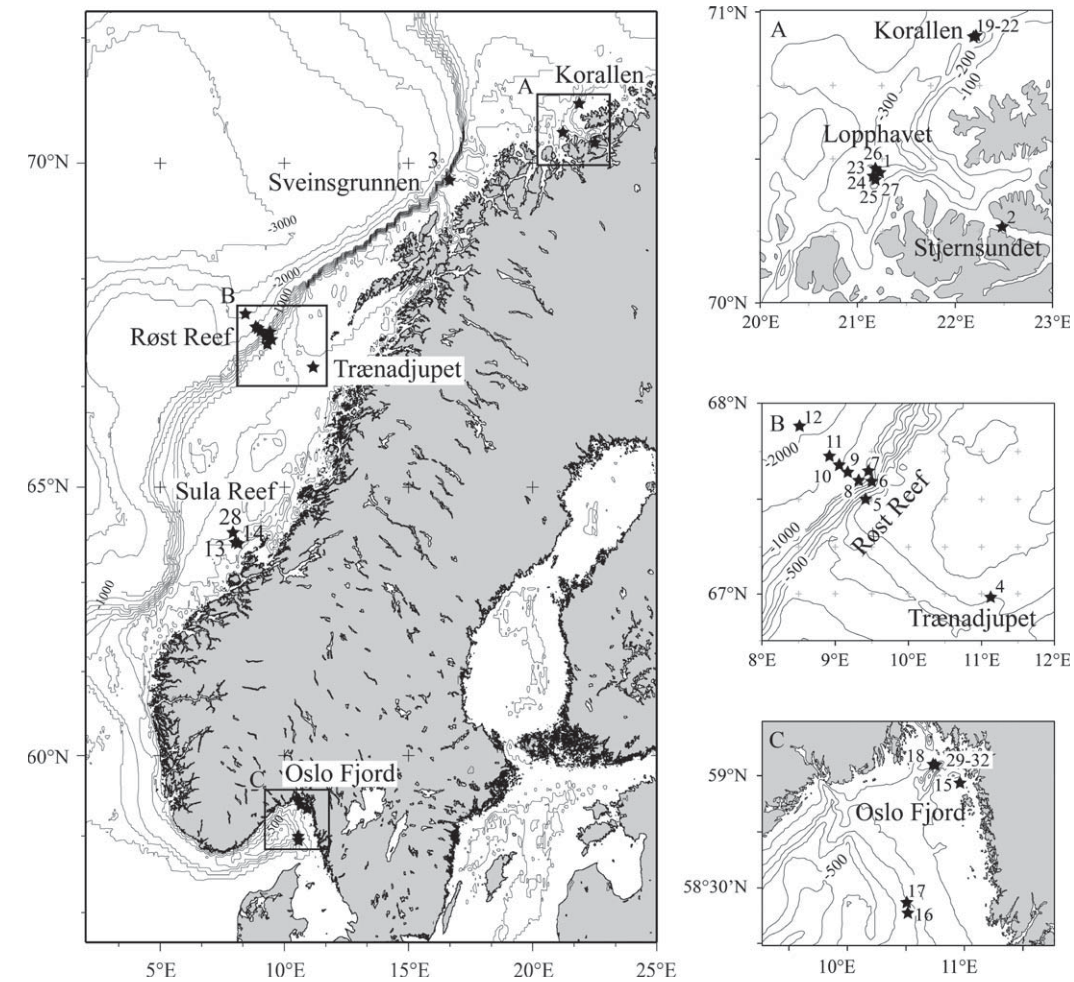


Figure 3.3. Location map of the surface sediment samples from the Norwegian continental shelf (modified after Margreth, 2010 and Spezzaferri and others, 2013). Numbers indicate the sample site in the Oslo Fjord (Skagerrak), Sula, Trænadjupet, Røst Reef, Stjernsundet, Lopphavet and Korallen Reefs.

gallowayi from the muddy to sandy sediments trapped by the living coral framework.

Along the Norwegian margin, epifaunal benthic species are also present in the sediment clogged coral and the pebbly sand facies where dropstones and dead corals provide them with ecological niches. However, uvigerinids, which are abundant in the off-mound facies of the Porcupine Seabight are underrepresented in the off-reef sites. In particular, Margreth (2010) and Spezzaferri and others (2013) have demonstrated that living strategies and microhabitats of benthic foraminiferal assemblages from the Porcupine Seabight and from the Norwegian margin are very similar, although species composition may vary. Microhabitats and facies can develop over hundreds of meters in the Porcupine Seabight, whereas, they may drastically change within tens of meters along the Norwegian margin.

Figure 3.3 and Table 3.3 show the location of the samples. The distribution of benthic foraminiferal microhabitats according to different facies summarizing our data for the modern Lopphavet reef is shown in Figure 3.4 A. The list and abundances of benthic foraminifera are in Appendix II.

The Lopphavet region is located in Northern Norway (Fig. 3.3). During the *RV Poseidon* cruise 391 two cores were retrieved on a cold-water coral reef at about 70°26.946′ N and 21°11.175′ E at a few tens of meters distance (Core POS559/2 and POS559/3).

Core POS391-559/2 consists of 277 cm of coral-rich and other biogenic fragments in a silty matrix. The base of the cores contains more abundant small-sized fragments.

From the top of core POS391-559/3 down to 64 cm, sediments consist of small fragments (3–4 cm), mainly of

Table 3.3. Sample number, latitude and longitude, water depth, region/reef and facies of the investigated samples from reefs along the Norwegian margin.

Nr.	Sample	Lat. N	Long. E	Depth	Region	Facies
1	Hermi-1_1	70°27.71′	21°12.77′	300 m	Lopphavet	*coral rubble facies*
2	POS325 455	70°16.13′	22°29.46′	270 m	Stjernsund	*coral rubble facies*
3	PS70/011-1	69°44.21′	16°33.27′	327 m	Sveinsgrunnen	*coral rubble facies*
4	PS70/023-3	66°58.12′	11°07.79′	324 m	Trænadjupet	*coral rubble facies*
5	PS70/002-2	67°30.40′	9°25.55′	304 m	Røst Reef	*sediment clogged coral framework*
6	PS70/029-3	67°35.23′	9°28.92′	604 m	Røst Reef	*pebbly sand facies*
7	PS70/028-2	67°38.05′	9°26.98′	761 m	Røst Reef	*pebbly sand facies*
8	PS70/037-2	67°35.15′	9°19.22′	889 m	continental slope	*mud facies (deep)*
9	PS70/038-2	67°37.77′	9°10.30′	1214 m	continental slope	*mud facies (deep)*
10	PS70/039-2	67°40.15′	9°03.00′	1514 m	continental slope	*mud facies (deep)*
11	PS70/033-2	67°43.00′	8°55.00′	1824 m	continental slope	*mud facies (deep)*
12	PS70/032-2	67°52.22′	8°30.72′	2098 m	continental slope	*mud facies (deep)*
13	AL316-320	64°06.30′	8°04.80′	296 m	Sula Reef	*pebbly sand facies*
14	AL316 321	64°05.88′	8°05.35′	278 m	Sula Reef	*coral rubble facies*
15	AL 232 1022	58°59.88′	10°57.80′	91 m	Oslo Fjord	*coral rubble facies*
16	AL 232 1025	58°25.88′	10°31.05′	326 m	Oslo Fjord	*mud facies (shallow)*
17	AL 232 1026	58°27.75′	10°30.31′	287 m	Oslo Fjord	*mud facies (shallow)*
18	AL 232 1155	59°04.71′	10°43.90′	106 m	Oslo Fjord	*sediment clogged coral framework*
19	POS 391 534-1	70°55.26′	22°10.71′	214 m	Korallen	*pebbly sand facies*
20	POS 391 535-1	70°55.14′	22°11.26′	201 m	Korallen	*coral rubble facies*
21	POS 391 539-1	70°56.09′	22°11.00′	247 m	Korallen	*pebbly sand facies*
22	POS 391 544-2	70°56.03′	22°12.35′	172 m	Korallen	*coral rubble facies*
23	POS 391 550-1	70°26.72′	21°10.36′	233 m	Lopphavet	*living coral framework facies*
24	POS 391 555-1	70°26.58′	21°10.01′	232 m	Lopphavet	*coral rubble facies*
25	POS 391 556-2	70°26.64′	21°11.61′	320 m	Lopphavet	*coral rubble facies*
26	POS 391 558-1	70°28.29′	21°11.48′	330 m	Lopphavet	*pebbly sand facies*
27	POS 391 559-1	70°26.93′	21°11.10′	230 m	Lopphavet	*pebbly sand facies*
28	POS 391 562-1	64°04.40′	08°01.20′	287 m	Sula Reef	*coral rubble facies*
29	POS 391 567-1	59°06.78′	10°47.46′	140 m	Oslo Fjord	*sediment clogged coral framework*
30	POS 391 570-2	59°05.62′	10°47.95′	110 m	Oslo Fjord	*coral rubble facies*
31	POS 391 571-1	59°05.96′	10°47.67′	117 m	Oslo Fjord	*living coral framework facies*
32	POS 391 584-1	59°03.96′	10°48.37′	290 m	Oslo Fjord	*mud facies (shallow)*

Lophelia pertusa mixed with biogenic fragments such as gastropods, bivalves, brachiopods and abundant sponge spicules in a matrix of fine to coarse silt. Three levels with abundant dropstones (up to 5 cm in diameter) in a silty matrix can be identified from 64–82 cm, 184–188 cm and 274–279 cm. In these intervals coral fragments are absent. The dropstone interval at 64–82 cm represents the base of the coral-rich unit. The remaining sediments consist of fine to coarse silt without apparent sedimentary structures and lacking of coral fragment.

The cores were studied for benthic foraminiferal assemblages with a 3 cm resolution (Stalder and others, 2014). The AMS ^{14}C dating revealed that an extended cold-water coral reef developed on a pre-existing topographical height of glacial origin around 11,000 cal yr BP and persisted at least until around 2,000 cal yr BP.

The Holocene benthic foraminiferal assemblages from this cold-water coral reef show striking similarities with the sub-Recent assemblages from the Norwegian margin, indicating that no significant changes occurred in species composition in the last 11,000 years. The assemblages consist of abundant epifaunal species such as *C. pachyderma*, *D. coronata*, *C. aravaensis*, *L. lobatula*, *H. boueana*, *G. praegeri* and infaunal species including *T. angulosa*, *C. reniforme*, *A. gallowayi*. In core POS391-559/3 the transition to glacial time is well recorded and characterized by high abundances of *N. labradorica*, *E. incertum*, *E. excavatum* f. *clavata* (Figure 3.4 B; Stalder and others, 2014).

THE ALBORAN SEA

Buried Holocene cold-water corals occur in the Eastern Mediterranean on the top of the Dhaka (Core TTR17-MS411G) and Maya (TTR17-MS419G) Mud

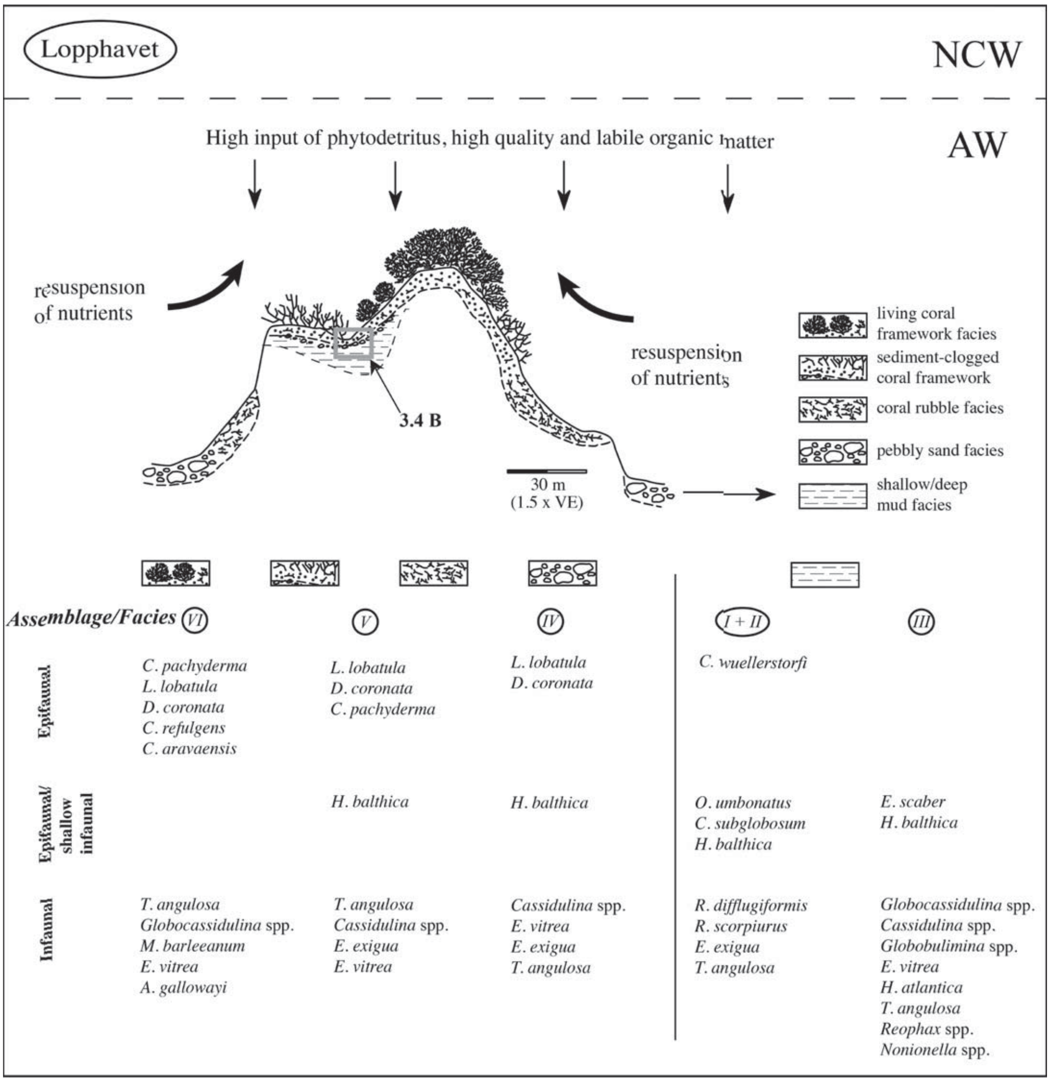


Figure 3.4 A) Model of the distribution of benthic foraminiferal microhabitats on a modern reef according to sedimentary facies at Lopphavet (facies model after Freiwald and others 2002). The influence of the Norwegian Coastal Water (NCW) and Atlantic Water (AW), and the position of Fig. 3.4 B are indicated.

Volcanoes (MV). The MVs are located in the Mud Diapir Province in the Western Alboran Basin (35°25.43′ N, 4°31.89′ W and 35°27.11′ N, 4°37.14′ W) along the Moroccan Coast and were cored during the TTR-17, Leg 1 cruise (Figure 3.5).

The sediments recovered from the two MVs consist of (from top to bottom): 1) a hemi-pelagic uppermost layer (0–30 cm at Dhaka and 0–95 cm at Maya), 2) a cold-water coral fragment-rich level (30–60 cm at Dhaka and 95–125 at Maya), 3) a mud-breccia layer (60–145 cm at Dhaka and from 125 down to the bottom of the core at Maya), and 4) a lowermost level of pelagic sediments mixed with the mud breccia (from 145 cm to the base of the core were retrieved at Dhaka MV).

The mud breccia from the two MVs is composed of a compact and rather stiff dominantly clayey matrix containing clasts. These clasts are composed of marls and lithified to semi-lithified clays up to 20 cm in size at Dhaka and up to 3 cm in size at Maya (Fig. 3.6 A-B).

The level rich in cold-water coral fragments developed between ca. 4175±62 years BP and 2230±59 years BP at Dhaka, and between ca. 15583±185 years BP and 7613±38 years BP at Maya MV, respectively (Margreth and others, 2011).

The complete benthic foraminiferal assemblages from the coral-rich layers and pelagic sediments are documented in Margreth and others (2011). The coral-rich layers contain epifaunal faunas comparable to those

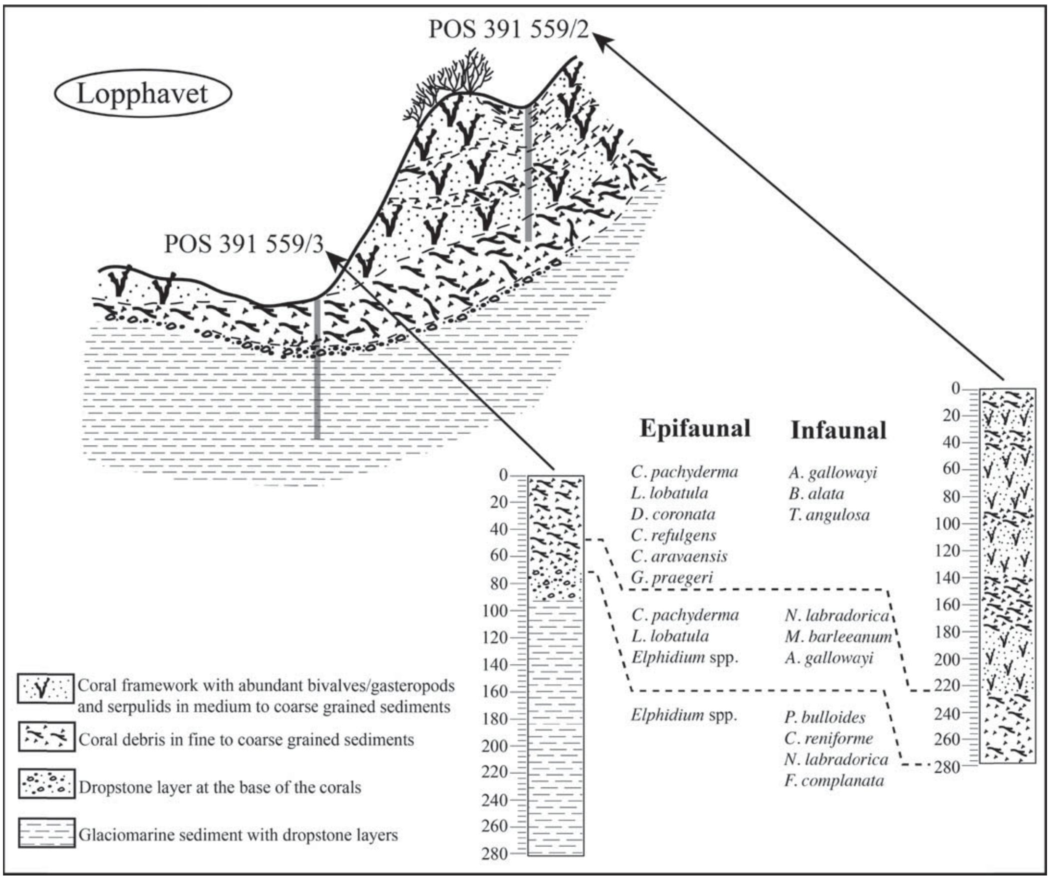


Figure 3.4. B) Buried reef facies recovered in cores POS391-559/2 and 559/3 (location see Fig. 3.4. A). Core POS391-559/2 spans a buried reef and the coral rubble facies at its base. Core POS391-559/3 spans the buried coral reef, coral rubble facies at its base and the passage to glacial sediments rich in dropstones layers (modified after Stalder and others, 2014).

observed for the Atlantic Margin (Porcupine and Norwegian margin sensu lato), although species abundance may vary. In particular, they are composed of *D. coronata*, *C. aravaensis*, *L. lobatula*, shallow infaunal species consist of *H. balthica* and *E. scaber*, and infaunal species are dominated by *G. subglobosa*, *M. barleeanum*, *C. carinata* and rarer uvigerinids (Figure 3.6 A-B). *Uvigerina* spp. (dominantly *U. mediterranea* and *U. peregrina*) are more abundant in the pelagic sediments overlying the coral-fragment rich horizons together with *B. marginata*, *B. difformis*, *A. scalaris*, *M. barleeanum*.

The mud breccia extruded from the mud volcano (Figure 3.6 A) provides the nucleation point for the colonization and development of cold-water corals and associated ecosystems (Margreth and others, 2011). Successive reactivation of the volcanic activity and/or changing climate conditions triggered the decline of the cold-water corals (Figure 3.6 B). Possible periods of slow seep activity with emission of acidic gasses may have selectively dissolved and fragmented the aragonitic corals with respect to associated calcareous organisms (Turley and others, 2007), e.g., foraminifera, which are still abundant in the sediments. The pelagic sedimentation buried the partially dissolved ecosystem (Figure 3.6 B).

SIMILARITIES AND DIFFERENCES AMONG COLD-WATER CORAL REEFS IN SPACE AND TIME

Recent studies on modern cold-water coral communities from the Mediterranean deep sea have revealed that the biodiversity of the macrobenthos is higher than previously known (e.g., Mastrototaro and others, 2010; Danovaro and others, 2010). In particular, these studies indicate that deep-sea Mediterranean communities today are "impoverished" with respect to the NE Atlantic and lack the typical Atlantic cold stenothermic

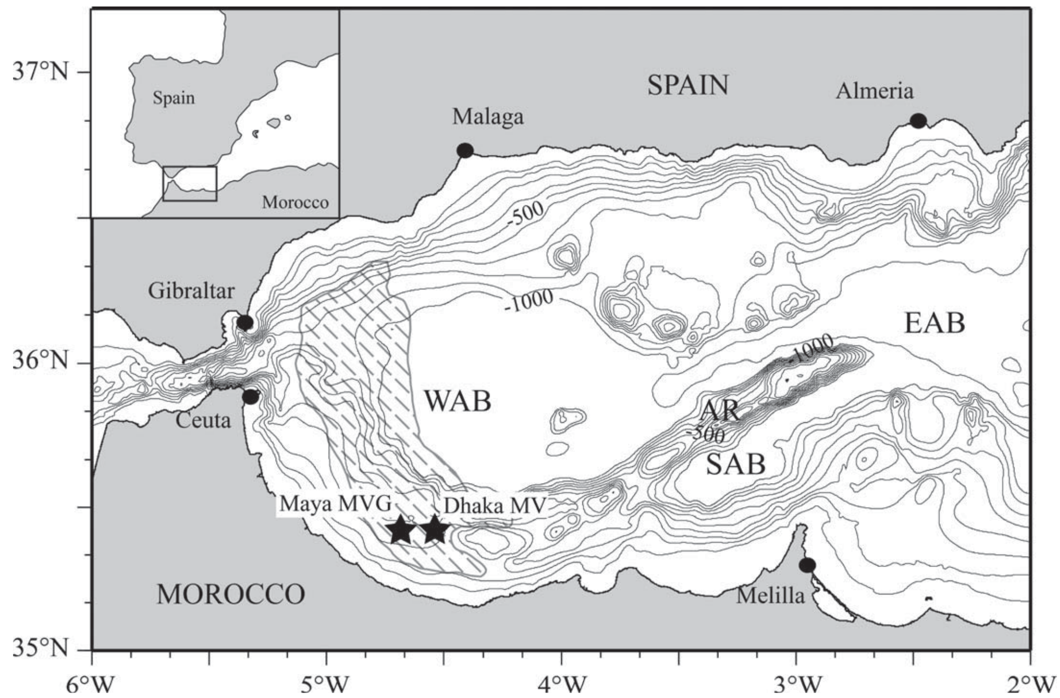
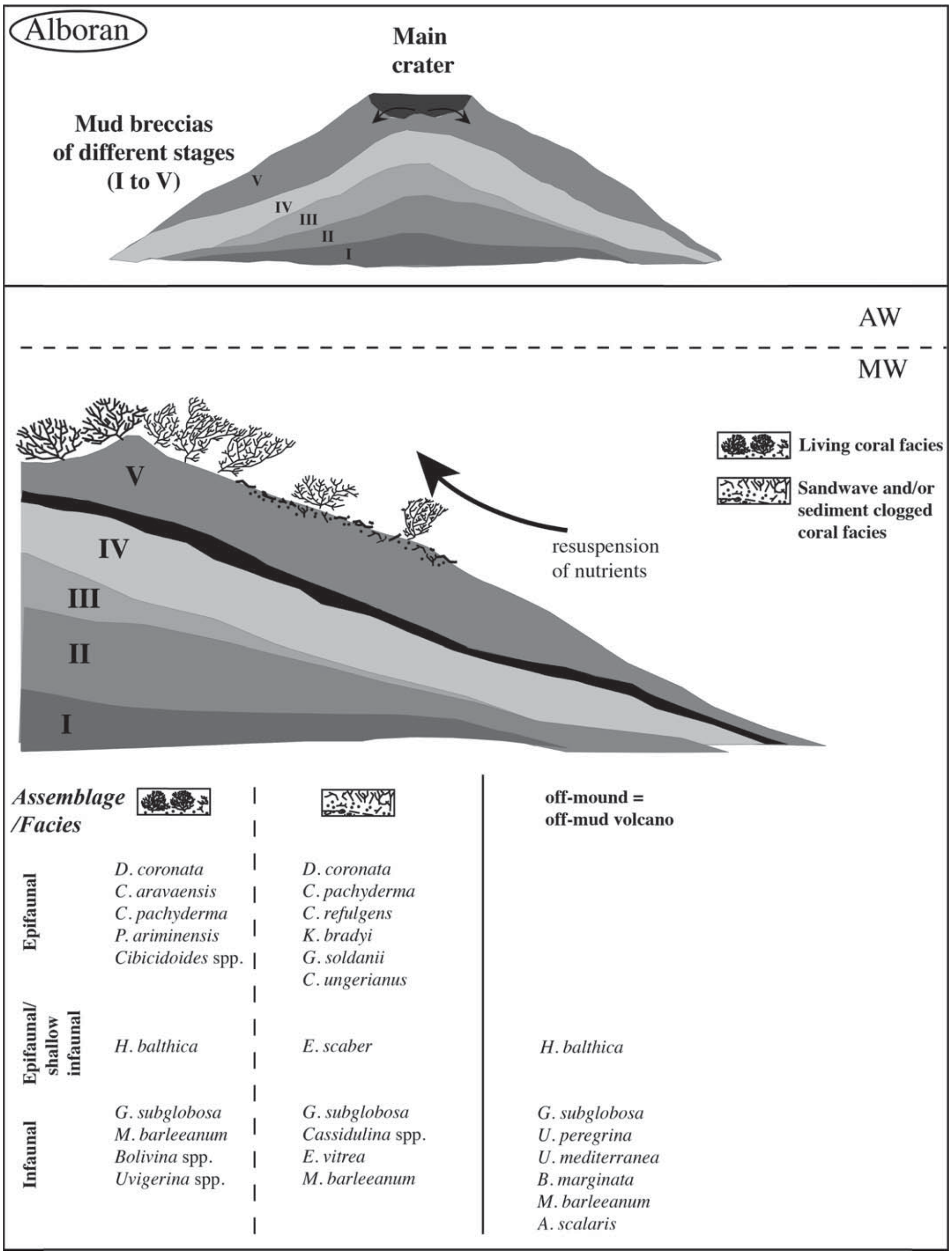


Figure 3.5. Map of the Alboran Sea showing the position of the Dhaka (Core TTR17-MS411G) and Maya (TTR17-MS419G) MVs. Modified after Margreth and others (2011). WAB = Western Alboran Sea; SAB = Southern Alboran Sea; EAB = Eastern Alboran Sea; AR = Alboran Ridge.

species (living at less than 10° at higher latitudes) and, due to the homothermy of the basin, show a higher eurythermy and eurybathy degree. On the contrary, in the Pleistocene, deep-sea Mediterranean benthic fauna was much more similar to that of the modern Atlantic (e.g., Zibrowius, 1980; Di Geronimo and others, 1996; Vertino, 2003).

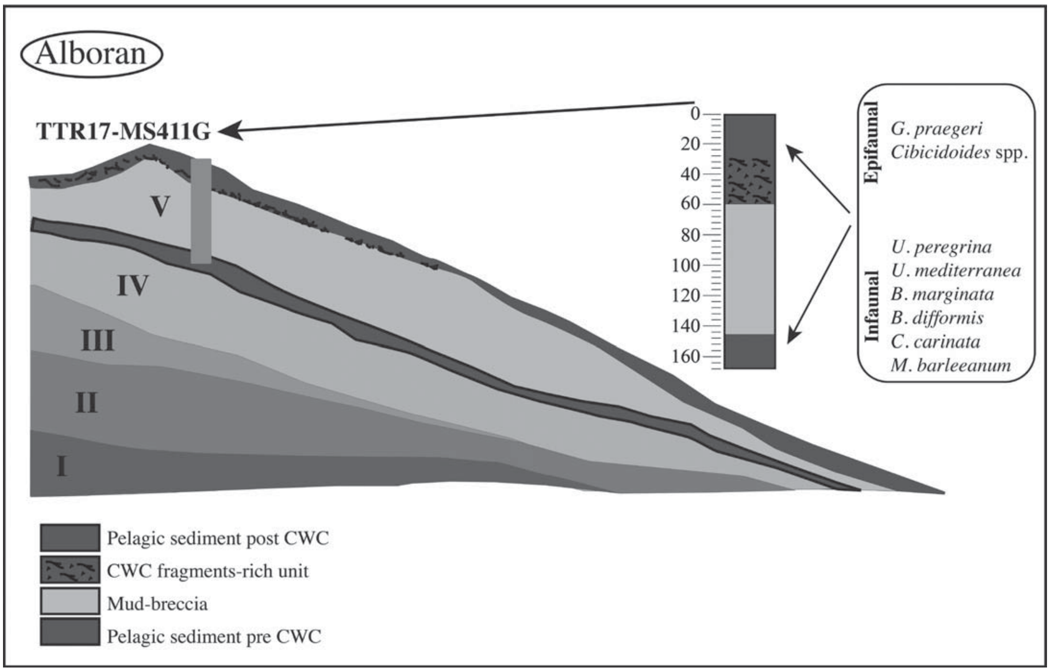
Our data demonstrate that a similar pattern can be observed also within Recent benthic foraminifera in comparison to those from the Holocene. Table 3.4 shows the occurrence of the identified 373 species of benthic foraminifera in the four investigated regions. The regions are categorized: Recent and sub-Recent assemblages of the Porcupine Seabight/Rockall Bank and Norwegian margin, and Alboran and Lopphavet assemblages from Holocene buried sediments. The distribution patterns in the four regions, counted from Table 3.4, can be summarised as follows: thirty-two species occur only in Recent/sub-Recent sediments from the Porcupine Seabight/Rockall region, eighty-one species are present only in Recent/sub-Recent sediments assemblages from the Norwegian margin, fifty species occur only in Holocene sediments of the Alboran Sea, and twenty–eight species are found only in Holocene sediments from Lopphavet. Fourty species are common in all four regions. Holocene assemblages from the Alboran Sea and Lopphavet have only 10 species in common, whereas, the Holocene from the Alboran Sea share fifty-three species with Recent/sub-Recent assemblages from the Norwegian margin indicating that Recent North Atlantic benthic foraminiferal assemblages are more similar to the Holocene Mediterranean assemblages than Holocene assemblages in both regions. Common species include epifaunal such as *C. pachyderma*, *C. kullenbergi*, *C. pseudoungerianus*, *H. sarcophaga*, *D. coronata* and infaunal such as *T. angulosa*, *Bolivina* spp., *Bulimina* spp., cassidulinids and *Nonionella* spp.

The observation of these closer similarities between the Pleistocene and Holocene, deep-sea Mediterranean paleocommunities with those of the modern Atlantic, possibly implies more efficient connections between the two basins at that time and "therefore" more efficient migrations. The large number of the common species present in the four regions is an intriguing feature pointing toward strong similarities of the requirements of both benthic foraminifera and other macrobenthos (including corals) from cold-water coral reefs. The corals require strong currents (e.g., Frederiksen and others, 1992; Freiwald and others, 2002; Rüggeberg and others, 2007) and important input of organic matter (possibly) phytoplankton detritus (Duineveld and oth-



Figures 3.6. A). This model shows the evolution of cold-water corals on a mud volcano in the Alboran Sea and the distribution of benthic foraminiferal microhabitats covering the mud volcano.

ers, 2004). Currents transport the food to the coral polyps and remove the excess of fine sediment (Duineveld and others, 2004; Freiwald and others, 2004; Thiem and others, 2006; White, 2007). The organic matter in the form of fresh and labile organic matter feeds the zooplankton, which is the main food source for cold-water corals (Mortensen, 2001; Freiwald and others, 2002; Duineveld and others, 2007). Additional food source for corals may be the fresh particles derived from production higher on the bank



Figures 3.6. B) Core TTR17-MS411G shows the benthic foraminiferal assemblages of the top 170 cm of Dhaka Mud Volcano, Western Alboran Sea.

resuspended by lateral advection and/or resuspension (Frederiksen and others, 1992; White and others, 2005; Duineveld and others, 2007).

Similar requirements are highlighted by comparing the requirements of corals with the autecology of benthic foraminifera (Table 3.1). In particular, the epifaunal species *D. coronata*, *C. refulgens*, *C. aravaensis*, and *L. lobatula* living attached to cold-water corals are passive suspension feeders preferring fresh and labile components of the organic matter and thrive in highly oxygenated and high energy waters (e.g., Murray, 2006; Fontanier and others, 2002; Margreth and others, 2009). Infaunal species living in the sediments of cold-water coral reefs such as *T. angulosa* prefer coarse-grained sediments and strong currents (Mackensen and others, 1995). Infaunal cassidulinids (*C. laevigata*, *C. carinata* and *G. subglobosa)* are also linked to availability of high quality (labile) organic matter (e.g., Mackensen and Hald, 1988; Murray, 2003; Murray, 2006; Alve, 2010). Buliminids and bolivinids also living in sediments of cold-water coral reefs can tolerate low oxygen levels but are dependent on high fluxes of organic matter. *Pullenia* spp. and *S. bulloides* are typical of cold and oxygenated waters in high productivity regions (e.g., Licari and Mackensen, 2005; Murray, 2006).

These observations indicate that benthic foraminiferal assemblages have a strong potential to serve as bioindicators for paleo-cold-water coral reefs.

CONCLUSIONS AND OUTLOOK

In this Atlas we present a review of benthic foraminifera from cold-water coral ecosystems, and an overview of the factors controlling their distribution. We have documented their presence and abundance within cold-water coral reefs in four regions: Norwegian margin, Lopphavet, Porcupine Seabight/Rockall Bank, and Alboran Basin. We have compared Recent/sub-Recent and Holocene assemblages in different regions and presented poorly documented species in 37 plates (Chapter 4). However, the study of cold-water coral ecosystems is still in its infancy and several years of research will pass before we are able to understand the role of foraminifera in their functioning and the factors triggering their nucleation, growth and demise.

ACKNOWLEDGEMENTS

This research is funded by the Swiss National Science Foundation grants 200021-103482 and 200020-131829/1. AR acknowledges funding also by Deutsche Forschungsgemeinschaft (DFG) Projects

Table 3.4. List of all 373 benthic foraminiferal species identified in the living coral facies, coral rubble, sandwave and dropstones facies. Only species from samples directly related to cold-water coral reefs and containing some coral fragments have been considered in the list to highlight similarities and differences among the cold-water corals in different investigated regions in space and time.

Age	Recent/sub-Recent		Holocene/buried	
Regions	**Porcupine**	**Norw. margin**	**Lopphavet**	**Alboran**
Species				
Adercotryma wrightii Brönnimann and Whittaker, 1987	**X**	**X**		
Allassoida virgola (Brady) = *Sagrina virgola* Brady, 1879				**X**
Ammobaculites agglutinans (d'Orbigny) = *Spirolina agglutinans* d'Orbigny, 1846		**X**		
Ammodiscus incertus (d'Orbigny) = *Operculina incerta* d'Orbigny, 1839		**X**		
Ammolagena clavata (Jones and Parker) = *Trochammina irregularis* d'Orbigny var. *clavata* Jones and Parker, 1860		**X**		
Ammomassilina arenaria (Brady) = *Spiroloculina arenaria* Brady, 1884				**X**
Ammonia beccarii (Linnaeus) = *Nautilus beccarii* Linnaeus, 1758	**X**			
Ammoscalaria pseudospiralis (Williamson) = *Proteonina pseudospiralis* Williamson, 1858	**X**			
Amphicoryna scalaris (Batsch) = *Nautilus scalaris* Batsch, 1791	**X**	**X**		**X**
Anomalinoides globulosa (Chapman and Parr) = *Anomalina globulosa* Chapman and Parr, 1937	**X**		**X**	
Archimerismus subnodosus Brady, 1884				**X**
Astacolus crepidulus (Fichtel and Moll) = *Nautilus crepidulus* Fichtel and Moll, 1798	**X**		**X**	
Astacolus patens (Brady) = *Vaginulina patens* Brady, 1884				**X**
Astacolus beerae Brenner and McMillan, 1976		**X**		
Asterigerinata mamilla (Williamson) = *Rotalina mamilla* Williamson, 1858				**X**
Asterigerinata planorbis (d'Orbigny, 1846)				**X**
Astrononion antarcticus (Parr) = *Nonion stelligerus* d'Orbigny var. *antarcticus* Parr, 1931			**X**	
Astrononion gallowayi Loeblich and Tappan, 1953		**X**	**X**	
Astrononion stelligerum (d'Orbigny) = *Nonionina stelligera* d'Orbigny, 1839	**X**			**X**
Astrorizha catenata Norman, 1877		**X**		
Bathysiphon filiformis M. Sars, 1872		**X**		
Bigenerina cylindrica Cushman, 1922		**X**		
Bigenerina nodosaria d'Orbigny, 1826		**X**		**X**
Biloculinella depressa (Wiesner) = *Biloculina labiata* Schlumberger var. *depressa* Wiesner, 1923		**X**		
Biloculinella fragilis Le Calvez and Le Calvez, 1958	**X**			
Biloculinella globula (Bornemann) = *Biloculina globulus* Bornemann, 1855		**X**	**X**	**X**
Bolivina translucens Phleger and Parker, 1951			**X**	
Bolivina alata (Seguenza) = *Vulvulina alata* Sequenza, 1862	**X**	**X**	**X**	**X**
Bolivina albatrossi (Cushman), 1937		**X**	**X**	**X**
Bolivina difformis (Williamson) = *Textularia variabilis* var. *difformis* Williamson, 1858			**X**	**X**
Bolivina dilatata (Reuss) = *Brizalina dilatata* Reuss, 1850	**X**	**X**		**X**
Bolivina pseudoplicata Heron-Allen and Earland = *Bolivina pseudo-plicata* Heron-Allen and Earland, 1930	**X**	**X**	**X**	**X**
Bolivina pseudopunctata Höglund, 1947	**X**	**X**	**X**	**X**
Bolivina pygmaea Brady, 1881	**X**			
Bolivina spathulata (Williamson) = *Textularia variabilis* var. *spathulata* Williamson, 1858	**X**	**X**	**X**	**X**
Bolivina spinescens Cushman, 1911			**X**	
Bolivina subaenariensis (Cushman) = *Brizalina subaenariensis* Cushman, 1922				**X**
Bolivina subspinescens Cushman, 1922	**X**	**X**		**X**
Bolivinella striatula (Cushman) = *Brizalina striatula* Cushman, 1922	**X**	**X**		**X**
Buccella frigida (Cushman) = *Pulvinulina frigida* Cushman, 1922		**X**	**X**	
Buccella tenerrima (Bandy) = *Rotalia tenerrima* Bandy, 1950		**X**		
Bulimina aculeata d'Orbigny, 1826	**X**	**X**		**X**

Table 3.4. Continued.

Age	Recent/sub-Recent		Holocene/buried	
Regions	Porcupine	Norw. margin	Lopphavet	Alboran
Species				
Bulimina marginata d'Orbigny, 1826	X	X	X	X
Bulimina striata d'Orbigny, 1843			X	X
Buliminella spinigera Cushman, 1922	X			
Cancris auriculus (Fichtel and Moll) = *Nautilus auricula* Fichtel and Moll, 1798			X	X
Cassidulina carinata Silvestri = *Cassidulina laevigata* d'Orbigny var. *carinata* Silvestri, 1896	X	X	X	X
Cassidulina crassa d'Orbigny, 1839		X	X	X
Cassidulina laevigata d'Orbigny, 1826	X	X	X	X
Cassidulina neocarinata Thalmann, 1950			X	
Cassidulina neoteretis Seidenkranttz, 1995		X		
Cassidulina reniforme Nörvang = *Cassidulina crassa* d'Orbigny var. *reniforme* Nörvang, 1945		X	X	
Cassidulina teretis Tappan, 1951		X	X	
Cassidulinoides brady (Norman) = *Cassidulina bradyi* Norman, 1881		X		
Cassidulinoides oblonga (Reuss) = *Cassidulina oblonga* Reuss, 1850				X
Chilostomella oolina Schwager, 1878				X
Cibicides refulgens de Montfort, 1808	X	X	X	X
Cibicides ungerianus (d'Orbigny) = *Rotalia ungeriana* d'Orbigny, 1846	X	X	X	
Cibicidoides aravaensis (Perelis and Reiss) = *Cibicides aravaensis* Perelis and Reiss, 1976	X	X	X	X
Cibicidoides kullenbergi (Parker) = *Cibicides kullenbergi* Parker, 1953	X			X
Cibicidoides mundulus (Brady, Parker, and Jones) = *Trunctulina mundula* Brady, Parker, and Jones, 1888		X		
Cibicidoides pachyderma Rzehak, 1886	X	X	X	X
Cibicidoides pseudoungerianus (Cushman) = *Truncatulina pseudoungeriana* Cushman, 1922		X		X
Cibicidoides wuellerstorfi (Schwager) = *Anomalina wüllerstorfi* Schwager, 1866		X	X	X
Clavulina parisiensis d'Orbigny, 1826				X
Clavulina primaeva Cushman, 1913		X		
Cornoloculina circularis (Chapman) = *Spiroloculina dorsata* Reuss var. *circularis* Chapman, 1915			X	
Cornuspira foliacea (Philippi) = *Orbis foliaceus* Philippi, 1844		X		
Cornuloculina inconstans (Brady) = *Hauerina inconstans* Brady, 1879			X	
Cornuspira involvens (Reuss) = *Operculina involvens* Reuss, 1850	X	X	X	X
Cribrostomoides jeffreysii (Williamson) = *Nonionina jeffreysii* Williamson, 1858	X			
Cribrostomoides subglobosum (Cushman) = *Haplophragmoides subglobosum*, Cushman, 1910		X		
Cycloforina laevigata d'Orbigny, 1839		X		X
Cycloforina stalkeri Loeblich and Tappan, 1953		X		X
Dentalina advena (Cushman) = *Nodosaria advena* Cushman, 1923		X	X	
Dentalina communis (d'Orbigny) = *Nodosaria communis* d'Orbigny, 1826				X
Dentalina cuvieri (d'Orbigny) = *Nodosaria cuvieri* d'Orbigny, 1826	X			
Dentalina flintii Cushman, 1923				X
Dentalina guttifera d'Orbigny, 1846				X
Dentalina lamarki Neugeboren, 1856	X			
Discammina compressa (Goes) = *Lituolina irregularis* Roemer var. *compressa* Goes, 1882		X		
Discanomalina coronata (Parker and Jones) = *Anomalina coronata* Parker and Jones, 1857	X	X	X	X
Discanomalina japonica Asano, 1951	X			X
Discorbinella bertheloti (d'Orbigny) = *Rosalina bertheloti* d'Orbigny, 1839		X	X	X
Eggerella bradyi (Cushman) = *Verneuilina bradyi* Cushman, 1911		X		X

Table 3.4. Continued.

Age	Recent/sub-Recent		Holocene/buried	
Regions	Porcupine	Norw. margin	Lopphavet	Alboran
Species				
Eggerella humboldti Todd and Brönnimann, 1957		X	X	
Eggerelloides scaber (Williamson) = *Bulimina scabrum* Williamson, 1958	X	X		X
Ehrenbergina trigona Göes, 1922	X			
Elphidiella hannai (Cushman and Grant) = *Elphidium hannai* Cushman and Grant, 1927		X		
Elphidium albiumbilicatum (Weiss) = *Nonion pauciloculum* Cushman subsp. *albiumbilicatum* Weiss, 1954		X	X	
Elphidium earlandi Cushman, 1936	X			
Elphidium frigidum Cushman, 1933		X		
Elphidium gerthi Van Voorthuysen, 1957	X			
Elphidium excavatum f. *clavata* Cushman, 1944		X	X	
Elphidium hanzawai Asano, 1939				X
Elphidium groeanlandicum Cushman, 1933		X		
Elphidium incertum (Williamson) = *Polystomella umbilicata* Walker var. *incerta* Williamson, 1858		X	X	
Elphidium magellanicum Heron-Allen and Earland, 1932		X		
Elphidium subarcticum Cushman, 1944		X		
Epistominella exigua (Brady) = *Pulvinulina exigua* Brady, 1884	X	X	X	X
Epistominella vitrea Parker, 1953	X	X	X	X
Favulina hexagona (Williamson) = *Entosolenia squamosa* Montagu var. *hexagona* Williamson, 1858		X	X	X
Favulina melo (d'Orbigny) = *Oolina melo* d'Orbigny, 1839		X	X	X
Favulina squamosa (Montagu) = *Vermiculum squamosum* Montagu, 1803		X	X	X
Fissurina aggazisi Todd and Bronnimann, 1957				X
Fissurina annectens (Burrows and Holland) = *Lagena annectens* Burrows and Holland, 1895		X	X	
Fissurina circularis Todd, 1954	X			
Fissurina clathrata (Brady) = *Lagena clathrata* Brady, 1884		X	X	
Fissurina crassiporosa McCulloch, 1977		X	X	
Fissurina curvitubulosa McCulloch, 1977		X		
Fissurina derogata McCulloch, 1977		X		
Fissurina dublinii McCulloch, 1977	X			
Fissurina eburnea Buchner, 1940		X	X	
Fissurina inflatiperforata McCulloch, 1977		X		
Fissurina kerguelensis Parr, 1950				X
Fissurina lacunata Burrows and Holland (1895)			X	
Fissurina laevigata Reuss, 1850		X		X
Fissurina longpointensis McCulloch, 1977		X	X	
Fissurina lucida (Williamson) = *Entosolenia marginata* Montagu var. *lucida* Williamson, 1848	X	X	X	X
Fissurina marginata (Montagu) = *Vermiculum marginatum* Montagu, 1803	X	X		X
Fissurina nucelloides (Buchner), 1940	X			
Fissurina orbignyana Seguenza, 1862	X	X	X	X
Fissurina piriformis (Buchner) = *Lagena piriformis* Buchner, 1940				X
Fissurina pseudolucida Zheng, 1979		X	X	
Fissurina pseudorbignyana (Buchner) = *Lagena pseudoorbignyana* Buchner, 1940		X		
Fissurina quadrata (Williamson) = *Entosolenia marginata* Montagu var. *quadrata* Williamson, 1858			X	
Fissurina quadricostulata (Reuss) = *Lagena quadricostulata* Reuss, 1870		X		X
Fissurina serrata (Schlumberger) = *Lagena serrata* Schlumberger, 1894			X	
Fursenkoina complanata (Egger) = *Virgulina schreibersiana* var. *complanata* Egger, 1893		X	X	

Table 3.4. Continued.

Age	Recent/sub-Recent		Holocene/buried	
Regions	**Porcupine**	**Norw. margin**	**Lopphavet**	**Alboran**
Species				
Gaudryina rudis Wright, 1900	X	X	X	X
Gavelinopsis caledonia Murray and Whittaker, 2001		X		
Gavelinopsis nitida (Williamson) = *Rotalina nitida*, Williamson 1858		X	X	
Gavelinopsis praegeri (Heron-Allen and Earland) = *Discorbina praegeri* Heron-Allen and Earland, 1913	X	X	X	X
Geminospira bradyi Bermudez, 1952			X	
Glabaratella torrei (Bermudez, 1935)				X
Glabratella patelliformis (Brady) = *Discorbina patelliformis* Brady, 1884			X	X
Glandulina laevigata (d'Orbigny) = *Nodosaria laevigata* d'Orbigny, 1826		X	X	
Glandulina ovula d'Orbigny, 1846				X
Glandulina rotundata Reuss, 1850		X	X	
Globobulimina affinis (d'Orbigny) = *Bulimina affinis* d'Orbigny, 1839			X	X
Globobulimina doliolum (Terquem and Terquem) = *Bulimina doliolum* Terquem and Terquem, 1886	X	X	X	
Globobulimina turgida (Bailey) = *Bulimina turgida* Bailey, 1851				
Globocassidulina subglobosa (Brady) = *Cassidulina subglobosa* Brady, 1881	X	X	X	X
Globulina aequalis d'Orbigny, 1846		X		
Glomospira charoides (Parker and Jones) = *Trochammina squamata* Jones and Parker var. *charoides* Jones & Parker, 1860		X		
Gordiospira elongata (Collins) = *Glomospira elongata* Collins, 1958				X
Gordiospira fragilis Heron-Allen and Earland, 1932				X
Grigelis orectus Loeblich and Tappan, 1994		X	X	
Guttulina communis (d'Orbigny) = *Polymorphina communis* d'Orbigny, 1826	X			X
Guttulina regina (Brady, Parker and Jones) = *Polymorphina regina* Brady, Parker and Jones, 1871	X			
Gyroidina altiformis Steward and Steward = *Gyroidina soldanii* d'Orbigny var. *altiformis* Steward and Steward, 1930				X
Gyroidina laevigata d'Orbigny, 1826		X		X
Gyroidina lamarkiana (d'Orbigny) = *Rotalia lamarkiana* d'Orbigny, 1839				X
Gyroidina neosoldanii Brotzen, 1936	X	X	X	
Gyroidina orbicularis d'Orbigny, 1826	X			
Gyroidina soldanii d'Orbigny, 1826	X	X	X	X
Hanzawaia boueana (d'Orbigny) = *Rotalina boueana* d'Orbigny, 1846	X	X	X	X
Hanzawaia concentrica (Cushman) = *Truncatulina concentrica* Cushman, 1918		X		X
Haplophragmoides membranaceum Höglund, 1947		X		
Haplophragmoides robertsoni (Brady) = *Trochammina robertsoni* Brady, 1887		X		
Haynesina depressula (Walker and Jacob) = *Nautilus depressulus* Walker and Jacob, 1798		X		
Heronallenita lingulata (Burrows and Holland) = *Discorbina lingulata* Burrows and Holland, 1895				X
Heterolepa haidingeri (d'Orbigny) = *Rotalina haidingeri* d'Orbigny, 1846	X			
Hippocrepinella hirudinea Heron-Allen and Earland, 1932		X		
Hoeglundina elegans (d'Orbigny) = *Rotalia (Turbinulina) elegans* d'Orbigny, 1826	X	X	X	X
Homalohedra apiopleura (Loeblich and Tappan) = *Lagena apiopleura* Loeblich and Tappan, 1953			X	X
Homalohedra borealis (Loeblich and Tappan) = *Entosolenia costata* Williamson, 1954		X	X	
Homalohedra eucostata (McCulloch) = *Oolina eucostata* McCulloch, 1977		X	X	
Homalohedra williamsoni (Alcock) = *Entosolenia williamsoni* Alcock, 1865		X	X	
Hormosinella guttifera (Brady) = *Lituola guttifera* Brady, 1881		X		
Hyalinea balthica (Schröter) = *Nautilus balthicus* Schröter, 1783	X	X	X	X
Hyalinonetrion gracillimum (Costa) = *Amphorina gracilis* Costa, 1856		X		

Table 3.4. Continued.

Age	Recent/sub-Recent		Holocene/buried	
Regions	**Porcupine**	**Norw. margin**	**Lopphavet**	**Alboran**
Species				
Hyperammina elongata Brady, 1878		X		
Hyrrokkin sarcophaga Cedhagen, 1994	X	X	X	X
Ioanella tumidula (Brady) = *Truncatulina tumidula* Brady, 1884		X	X	
Islandiella norcrossi (Cushman) = *Cassidulina norcrossi* Cushman, 1933		X	X	
Karreriella bradyi (Cushman) = *Gaudryina bradyi* Cushman, 1911	X	X		X
Labrospira canariensis (d'Orbigny) = *Nonionina canariensis* d'Orbigny, 1839		X		
Labrospira crassimargo (Norman) = *Haplophragmoides crassimargo* Norman, 1892		X		
Labrospira jeffreysii (Williamson) = *Nonionina jeffreysii* Williamson, 1858	X	X		
Labrospira scitula (Brady) = *Lituola (Haplophragmium) scitulum* Brady, 1881	X			
Laevidentalina inflexa (Reuss) = *Nodosaria inflexa* Reuss, 1866			X	
Laevidentalina sidebottomi (Cushman) = *Dentalina sidebottomi* Cushman, 1933			X	X
Lagena gibbera Buchner, 1940				X
Lagena hispida Reuss, 1863	X			
Lagena hispidula Cushman, 1913			X	
Lagena meridionalis Wiesner = *Lagena gracilis* Williamson var. *meridionalis* Wiesner, 1931		X	X	X
Lagena semilineata var. *spinigera* Earland, 1934		X	X	
Lagena spicata Cushman = *Lagena sulcata* Walker and Jones var. *spicata* Cushman, 1950	X			
Lagena squamosoalata Brady, 1881	X			
Lagena striata (Montagu) = *Vermiculum striatum* Montagu, 1803	X	X		X
Lagena substriata Wiliamson, 1848		X	X	
Lagena sulcata (Walker and Jacob) = *Serpula sulcata* Walker and Jacob, 1798	X			
Lagena trigonabicarinata Balkwill and Millett, 1884		X		
Lagena trigonolaevigata Balkwill and Millett, 1884			X	
Lagena williamsoni Harvey and Bailey, 1854				X
Lagenammina arenulata (Skinner) = *Reophax difflugiformis* var. *arenulata* Skinner, 1961		X		
Lagenammina fusiformis (Williamson) = *Proteonina fusiformis* Williamson, 1858		X		
Lagenosolenia bradyiformata McCulloch, 1977		X	X	
Lagenosolenia inflatiperforata McCulloch, 1977			X	
Lenticulina calcar (Linné) = *Nautilus calcar* Linné, 1758				X
Lenticulina gibba (d'Orbigny) = *Cristellaria gibba* d'Orbigny, 1826		X	X	X
Lenticulina inornata (d'Orbigny) = *Robulina inornata* d'Orbigny, 1846	X	X		X
Lenticulina orbicularis (d'Orbigny) = *Robulina orbicularis* d'Orbigny, 1826	X	X	X	X
Lenticulina peregrina (Schwager) = *Cristellaria peregrina* Schwager, 1866				X
Lenticulina vortex (Fichtel and Moll) = *Nautilus vortex* Fichtel and Moll, 1798			X	X
Lepidodeuterammina ochracea (Williamson) = *Rotalina ochracea* Williamson, 1858		X		
Lobatula lobatula (Walker and Jacob) = *Nautilus lobatulus* Walker and Jacob, 1798	X	X	X	X
Marginulina striata d'Orbigny, 1852				X
Melonis barleeanum (Williamson) = *Nonionina barleeana* Williamson, 1858	X	X	X	X
Melonis pompilioides (Fichtel and Moll) = *Nautilus pompilioides* Fichtel and Moll, 1798		X		X
Miliolinella elongata Kruit = *Miliolinella circularis* Bornemann var. *elongata* Kruit, 1955		X	X	X
Miliolinella subrotunda (Montagu) = *Vermiculum subrotundum* Montagu, 1803	X	X	X	X
Mycostomina revertens (Rhumbler) = *Spirillina vivipara* Ehrenberg var. *revertens* Rhumbler, 1906		X	X	
Neoconorbina terquemi (Rzehak) = *Discorbina terquemi* Rzehak, 1888	X	X		X

Table 3.4. Continued.

Age	Recent/sub-Recent		Holocene/buried	
Regions	Porcupine	Norw. margin	Lopphavet	Alboran
Species				
Neoeponides haidingerii (d'Orbigny) = *Rotalina haidingerii* d'Orbigny, 1846		X		
Nodogenerina virgula (Brady) = *Sagrina virgula* Brady, 1884		X	X	
Nodosaria aequalis d'Orbigny, 1826				X
Nonion fabum (Fichtel and Moll) = *Nautilus faba* Fichtel and Moll, 1798		X		
Nonion pauciloculum Cushman, 1944		X		
Nonion pauperatus (Balkwill and Wright) = *Nonionina pauperata* Balkwill and Wright, 1885		X		X
Nonionella grateloupii (d'Orbigny) = *Nonionina grateloupii* d'Orbigny, 1839			X	
Nonionella iridea Heron-Allen and Earland, 1932		X	X	X
Nonionellina labradorica (Dawson) = *Nonionina labradorica* Dawson, 1860		X	X	
Nuttallides umboniferus (Cushman) = *Pulvinulina umbonifera* Cushman, 1933	X		X	X
Nuttallides decorata (Phleger and Parker) = *Pseudoparrella decorata* Phleger and Parker, 1951		X	X	
Oolina ampulladistoma (Jones) = *Lagena vulgaris* var. *ampulla-distoma* Jones, 1874		X		
Oolina eucostata McCulloch, 1977			X	
Oolina globosa (Montagu) = *Vermiculum globosum* Montagu, 1803		X	X	
Oolina hexagona (Williamson) = *Entosolenia squamosa* Montagu var. *hexagona* Williamson, 1848	X			
Oolina laevigata d'Orbigny, 1839		X		
Oolina lineata var. *communis* McCulloch, 1977		X		
Oolina williamsoni (Alcock) = *Entosolenia williamsoni* Alcock, 1865			X	X
Ophthalmidium kilianensis (Rhumbler) = *Ophthalmina* Rhumbler, 1936	X			
Oridorsalis umbonatus (Reuss) = *Rotalina umbonatus* Reuss, 1851		X		X
Ovulina striata Seguenza, 1862		X		
Paliolatella semimarginata (Reuss) = *Fissurina semimarginata* Reuss, 1870			X	
Parabrizalina porrecta (Brady) = *Bulimina (Bolivina) porrecta* Brady, 1881		X	X	
Parafissurina basispinata McCulloch, 1977				X
Parafissurina botteliformis (Brady) = *Lagena botelliformis* Brady, 1881		X		
Parafissurina felsinea (Fornasini) = *Lagena felsinea* Fornasini, 1894		X		
Parafissurina lateralis (Cushman) = *Lagena lateralis* Cushman, 1913		X	X	
Parafissurina marginata (Walker and Boys) = *Serpula marginata* Walker and Boys, 1784			X	
Parafissurina marginoradiata McCulloch, 1977		X		
Parafissurina robusta (Zheng) = *Fissurina robusta* Zheng, 1979		X		
Parafissurina subquadrata (Parr) = *Fissurina subquadrata* Parr, 1945		X		
Paratrochammina challengeri Brönnimann and Whittaker, 1987	X	X		X
Paratrochammina murrayi Brönnimann and Zaninetti, 1984				X
Patellina corrugata Williamson, 1858		X	X	
Pelosina cylindrica Brady, 1884		X		
Planularia costata Cornuel, 1848	X			
Planularia perculata McCulloch, 1977				X
Planulina ariminensis d'Orbigny, 1826	X	X		X
Porosononion ex gr. *granosum* (d'Orbigny) = *Nonionina granosa* d'Orbigny, 1826	X			X
Portatrochammina antarctica (Parr) = *Trochammina antarctica* Parr, 1950		X		
Praeglobobulimina ovata (d'Orbigny) = *Bulimina ovata* d'Orbigny, 1846	X		X	
Procerolagena clavata (d'Orbigny) = *Oolina clavata* d'Orbigny, 1846			X	
Procerolagena gracilis (Costa) = *Amphorina gracilis* Costa, 1856		X		
Protelphidium anglicum Murray, 1965		X		
Protoglobobulimina nescia (Saidova) = *Bulimina nescia* Saidova, 1975			X	
Psammosphaera fusca Schulze, 1875		X	X	

Table 3.4. Continued.

Age	Recent/sub-Recent		Holocene/buried	
Regions	Porcupine	Norw. margin	Lopphavet	Alboran
Species				
Pseudoeponides falsobeccarii (Rouvillois) = *Ammonia falsobeccarii* Rouvillois, 1974		X		X
Pseudotriloculina oblonga (Montagu) = *Vermiculum oblongum* Montagu, 1803				X
Pullenia bulloides (d'Orbigny) = *Nonionina bulloides* d'Orbigny, 1846	X	X	X	X
Pullenia osloensis Feyling-Hanssen = *Pullenia quinqueloba* Reuss var. *minuta* Feyling-Hanssen, 1954		X		
Pullenia quadriloba Reuss = *Pullenia compressiuscula* Reuss var. *quadriloba* Reuss, 1867		X	X	X
Pullenia quinqueloba (Reuss) = *Nonionina quinqueloba* Reuss, 1851	X	X		X
Pullenia subcarinata (d'Orbigny) = *Nonionina subcarinata* d'Orbigny, 1839		X	X	
Pygmaeoseistron laevis ovalis (Williamson) = *Serpula laevis ovalis* Walker and Boys, 1784		X		
Pyrgo anomala (Schlumberger) = *Biloculina anomala* Schlumberger, 1891	X	X	X	X
Pyrgo comata (Brady) = *Biloculina comata* Brady, 1881		X	X	
Pyrgo constricta (Costa) = *Biloculina constricta* Costa, 1856		X		
Pyrgo depressa (d'Orbigny) = *Biloculina depressa* d'Orbigny, 1826				X
Pyrgo elongata (d'Orbigny) = *Biloculina elongata* d'Orbigny, 1826	X	X	X	X
Pyrgo inornata (d'Orbigny) = *Biloculina inornata* d'Orbigny, 1846	X		X	X
Pyrgo lucernula (Schwager) = *Biloculina lucernula* Schwager, 1866		X		
Pyrgo murrhina (Schwager) = *Biloculina murrhina* Schwager, 1866	X			
Pyrgo oblonga (d'Orbigny) = *Biloculina oblonga* d'Orbigny, 1839		X		
Pyrgo rotalaria Loeblich and Tappan, 1953		X		
Pyrgo sarsi (Schlumberger) = *Biloculina sarsi* Schlumberger, 1891		X	X	
Pyrgo subsphaerica (d'Orbigny) = *Biloculina subsphaerica* d'Orbigny, 1840	X	X	X	
Pyrgo williamsoni (Silvestri) = *Biloculina williamsoni* Silvestri, 1923		X	X	
Pyrgoella sphaeroidina Saidova, 1975				X
Pyrulina cylindroides Roemer, 1945		X		
Pyrulina gutta (d'Orbigny) = *Polymorphina* (*Pyruline*) *gutta* d'Orbigny, 1826		X		
Quinqueloculina laevigata d'Orbigny, 1826				X
Quinqueloculina lamarckiana d'Orbigny, 1839		X		
Quinqueloculina arctica Cushman, 1933	X	X	X	
Quinqueloculina cuvieriana d'Orbigny, 1839		X		
Quinqueloculina ectypha Loeblich & Tappan, 1994			X	
Quinqueloculina padana Perconig, 1954				X
Quinqueloculina pygmaea Reuss, 1850		X	X	X
Quinqueloculina seminula (Linné) = *Serpula seminulum* Linné, 1758		X	X	X
Quinqueloculina viennensis Le Calvez and Le Calvez, 1958		X	X	X
Quniqueloculina pseudobuchiana Luczkowska, 1974				X
Rectuvigerina elongatastriata (Colom) = *Angulogerina elongatastriata* Colom, 1952				X
Recurvoides trochamminiformis Höglund, 1947		X		
Reophax difflugiformis Brady, 1879		X		
Reophax scorpiurus de Montfort, 1808		X		
Reussoolina stellula Loeblich & Tappan, 1994			X	
Rhabdammina abyssorum Sars, 1869		X		
Robertinoides pumilum Höglund, 1947			X	
Robertinoides brady Cushman and Parker, 1936		X	X	
Robertinoides subcylindrica (Brady) =*Bulimia subcylindrica* Brady, 1881	X	X		X
Rosalina anomala Terquem, 1875		X		
Rosalina brady (Cushman) = *Discorbina globularis* d'Orbigny var. *brady* Cushman, 1915		X	X	
Rosalina globularis d'Orbigny, 1826		X	X	X

Table 3.4. Continued.

Age	Recent/sub-Recent		Holocene/buried	
Regions	Porcupine	Norw. margin	Lopphavet	Alboran
Species				
Rosalina semipunctata (Bailey) = *Rotalina semipunctata* Bailey, 1851		X		
Rosalina vilardeboana d'Orbigny, 1839		X		X
Rupertina stabilis Wallich, 1877		X		
Saccammina sphaerica Sars, 1868		X		
Saccorhiza ramosa (Brady) = *Hyperammina ramosa* Brady, 1879	X	X		
Saracenaria caribbeanica Hofker, 1976	X			
Sigmoidella elegantissima (Parker and Jones) = *Polymorphina elegantissima* Parker and Jones, 1865		X		
Sigmoilina sigmoidea Brady, 1907				X
Sigmoilinella borealis (Saidova) = *Sigmoinella borealis* Saidova, 1975				X
Sigmoilinita tenuis (Czjzek) = *Quinqueloculina tenuis* Czjzek, 1848		X		X
Sigmoilopsis schlumbergeri (Silvestri) = *Sigmoilina schlumbergeri* Silvestri, 1904	X	X	X	X
Sigmoilopsis woodi Atkinson, 1968		X		
Sigmoinella borealis Saidova, 1975			X	
Siphogenerina columellaris Brady, 1881				X
Siphogenerina dimorpha (Parker and Jones) = *Uvigerina (Sagrina) dimorpha* Parker and Jones, 1865		X		
Siphonina subreticulata Myatliuk, 1953				X
Siphotextularia fretensis Vella, 1957				X
Siphotextularia obesa Parr, 1950	X			
Sphaeroidina bulloides d'Orbigny, 1826	X	X	X	X
Spirillina vivipara Ehrenberg, 1843	X	X	X	
Spiroloculina depressa d'Orbigny, 1826				X
Spiroloculina dilatata d'Orbigny, 1846			X	X
Spiroloculina excavata d'Orbigny, 1846		X		X
Spiroloculina tenuiseptata Brady, 1884		X		X
Spiroplectinella wrighti (Silvestri) = *Spiroplecta wrighti* Silvestri, 1903	X	X		X
Stainforthia concava Höglund, 1946				X
Stainforthia loeblichi (Feyling-Hanssen) = *Virgulina loeblichi* Feyling-Hanssen, 1954		X	X	
Stainforthia skagerakensis (Höglund) = *Virgulina skagerakensis* Höglund, 1947		X		
Stomatorbina concentrica (Parker and Jones) = *Pulvinulina concentrica* Parker and Jones, 1864	X	X	X	X
Takayanagia delicata (Cushman) = *Cassidulina delicata* Cushman, 1927	X			
Textularia agglutinans d'Orbigny, 1839	X	X		X
Textularia earlandi Parker, 1952		X		
Textularia laevigata d'Orbigny, 1826				X
Textularia lateralis Laliker, 1935				X
Textularia pseudogramen d'Orbigny, 1839		X		X
Textularia pseudotrochus Cushman, 1922	X			
Textularia truncata Höglund, 1947	X	X	X	X
Tosaia hanzawai Takanayagi, 1953	X			
Trifarina angulosa (Williamson) = *Uvigerina angulosa* Williamson, 1858	X	X	X	X
Trifarina brady Cushman, 1923	X	X	X	X
Trifarina fornasinii Selli, 1948				X
Triloculina marioni Schlumberger, 1893			X	X
Triloculina oblonga Montagu, 1803			X	
Triloculina tricarinata d'Orbigny, 1826	X	X	X	X
Triloculina trigonula (Lamarck) = *Miliolites trigonula* Lamarck, 1804		X	X	X
Trisegmentina compressa Wiesner, 1923		X		
Tritaxis fusca (Williamson) = *Rotalina fusca* Williamson, 1858		X		
Trochammina conica Earland, 1934				X

Table 3.4. Continued.

	Age	Recent/sub-Recent		Holocene/buried	
	Regions	Porcupine	Norw. margin	Lopphavet	Alboran
Species					
Trochammina inflata (Montagu) = *Nautilus inflatus* Montagu, 1808			**X**		
Trochammina labiosa Höglund = *Trochammina labiosa* Höglund, 1947			**X**		
Trochammina squamata Jones and Parker, 1860			**X**		
Uvigerina auberiana d'Orbigny, 1839		**X**			**X**
Uvigerina mediterranea Hofker, 1932		**X**	**X**	**X**	**X**
Uvigerina peregrina Cushman, 1923		**X**	**X**	**X**	**X**
Uvigerina peregrina parva Lutze, 1986		**X**			
Uvigerina pygmaea d'Orbigny, 1826		**X**			
Vaginulina bradyi Cushman, 1917				**X**	
Vaginulinopsis sublegumen Parr, 1950				**X**	
Valvulineria bradyana (Fornasini) = *Discorbina bradyana* Fornasini, 1900			**X**		**X**
Valvulineria minuta (Schubert) = *Discorbina rugosa* d'Orbigny var. *minuta* Schubert, 1904				**X**	

Summary of Table 3.4 (see text for explanation)

Species present in	#	Species in common	#
All areas	**373**	All areas	**40**
Recent/sub-Recent	**276**	Recent/sub-Recent	**116**
Holocene/buried	**246**	Holocene/buried	**88**
Porcupine	**109**	Porcupine	**32**
Norwegian margin	**232**	Norwegian margin	**81**
Lopphavet	**152**	Lopphavet	**28**
Alboran	**164**	Alboran	**50**

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