Palaeontologia Electronica
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BENTHIC FORAMINIFERA FROM THE DIATOMACEOUS MUD BELT OFF NAMIBIA: CHARACTERISTIC SPECIES FOR SEVERE ANOXIA

Carola Leiter and Alexander V. Altenbach

ABSTRACT

Surface sediments were recovered at 35 stations from the oxygen depleted diatomaceous mud belt off Namibia, at water depths from 28 to 152 m. The oxygen content of the bottom near water masses was dysoxic (0.2 to 0.8 ml l^{-1}) at 16 stations, microxic (0.1 ml l^{-1}) at nine stations, and free of dissolved O_2 at 10 stations. Four species of benthic foraminifera were repeatedly found living (stained) in anoxic and sulfidic environments of the central part of the diatomaceous mud belt. *Virgulinella fragilis* is restricted to sulfidic, anoxic, and weakly dysoxic environments, with a distinct upper threshold of dissolved oxygen in the bottom near water masses at 0.3 ml O_2 l^{-1}. *Nonionella stella, Fursenkoina fusiformis,* and *Bolivina pacifica* were found stained under such oxygen depleted conditions, but also in better oxygenated environments. These four species were recovered stained also from deep infaunal habitats where sulfate reduction persists. They also represent the main contributors to the thanatocoenosis. Lateral advection of unstained test and migrational tries of some other species is favored by prevailing landward bottom currents. Among all species observed, *V. fragilis* is considered a characteristic element of sulfidic to dysoxic environments. Even the earliest records of the genus are linked to carbonate aggressive, sulfidic, or oxygen depleted palaeoenvironments.

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KEY WORDS: anoxia; sulfidic; inner shelf; *Virgulinella fragilis*; Benguela-current

INTRODUCTION

Early assumptions about anaerobic respiration and autogenic denitrification in benthic foraminifera considered lethal effects on the long term, due to anoxia and sulfate reduction (Bernhard and Reimers 1991). Today, however, a set of ultrastructural, symbiotic, and kleptoblastic structures is under discussion for benthic foraminifera, all providing independence from dissolved O_2 (Bernhard 2003, Bernhard and Bowser 2008). Facultative but

PE Article Number: 13.2.11A

Submission: 3 February 2009. Acceptance: 27 April 2010

Leiter, Carola and Altenbach, Alexander V., 2010. Benthic Foraminifera from the Diatomaceous Mud Belt Off Namibia: Characteristic Species for Severe Anoxia. *Palaeontologia Electronica* Vol. 13, Issue 2; 11A:19p;
http://palaeo-electronica.org/2010_2/188/index.html

autogenic and complete denitrification was recently observed from laboratory cultures, as well as from field investigations (Risgaard-Petersen et al. 2006, Høgslund et al. 2008). Such biochemical activities of benthic foraminifera at redox boundary conditions are speculated to contribute significantly to the global nutrient cycle, rather than providing rare abnormalities of negligible impact (Høgslund et al. 2008). The diatomaceous mud belt off Namibia is one of the most inhospitable, oxygen depleted, and sulfidic open shelf environments on Earth (Baturin 2002a, 2002b, van der Plas et al. 2007). Oxygen concentrations of bottom waters are below detectability in the central area, suggesting denitrification and anaerobic ammonia oxidation (anammox) in the water column (Emeis et al. 2007). Methane and hydrogen sulfide accumulate over large areas within the sediment column (Emeis et al. 2004), and the blow outs of these toxic gases are frequently recorded at the ocean surface (Weeks et al. 2004). Sulfide diffusion from this mud is detoxified by blooms of nitrate-reducing chemolithotrophic bacteria near the sediment surface under completely anoxic conditions (Lavik et al. 2009). Our investigation aimed at recovering living benthic foraminifera from the diatomaceous mud belt in order to provide evidence for the capability of these organisms to permanently survive and thrive in this type of extreme environment.

ENVIRONMENTAL SETTINGS

High primary production off Namibia is supported by the inflow of nutrient rich, oxygen depleted South Atlantic central water (SACW) from the Angola Gyre in austral summer, and Eastern SACW (ESACW) during the winter season (Hagen et al. 2001). The main driving force for the upwelling of these subsurface water masses is the Ekman offshore transport induced by southeast trade winds, which result in coherence in lowered sea surface temperatures (SST) and offshore wind stress (Giraudeau et al. 2000, Hagen et al. 2001). All near surface water masses over the shelf and slope off Walvis Bay are considered to have a net northward flow, inducing onshore bottom Ekman transport for the inner shelf (Giraudeau et al. 2000). This onshore flow may reach close to the coastline during intense upwelling (Hagen et al. 2001). Thus, the diatomaceous mud belt (DMB) is produced by the onshore flow on the inner shelf (van der Plas et al. 2007). On the outer shelf and slope, the deeper, poleward compensatory flow turns the configuration during the upwelling season (Giraudeau et al. 2000). An offshore bottom Ekman transport prevails, gathering the bulk of particles transported downslope (Giraudeau et al. 2000, Bremner 1978).

On the inner shelf, the flux rate of diatom frustules and organic matter accumulates the DMB from 19 to 25 degrees south, with nearshore amounts of 50 to 80% opal, decreasing to 5 to 40% seawards, and organic matter contents of above 7% (Bremner 1980, 1983). Annual accumulation rates do not normally exceed approximately 1 mm (Struck et al. 2002, Bremner 1978). The landward flank is enriched in aeolian and riverine sand, silt, and terrigenous debris, whereas the seaward flank is enriched in particulate organic matter, clay, planktonic foraminifera, and shell gravel (Bremner and Willis 1993). Depending on local bathymetry and dynamic current intensity (Mohrholz et al. 2008), the landward flank is found at 15 to 104 m water depth, and the seaward flank from 45 to 151 m (Bremner and Willis 1993). Re-suspension by bottom currents is most pronounced at Palgrave Point (near 22 degrees 30 minutes south), where a shoal at 50 m water depth hinders accumulation of opal and clay by wave induced turbulence (Bremner 1980). This causes a single interruption of the DMB within a stretch of 740 km. Seismological analyses revealed a sediment thickness of up to 15 m, most pronounced in between 21 to 23 degrees south (Bremner 1980, Emeis et al. 2004). This range coincides with local oxygen concentrations of the bottom waters below detectability, suggesting denitrification and anammox even in the water column.

An innermost range with free hydrogen sulfide in supernatant waters of multicorers was detected from Cape Cross to Walvis Bay, down to 125 m water depth (Emeis et al. 2007). Gas accumulations of methane and H_2S were observed within the DMB in all areas exceeding 12 m sediment thickness, and in 20 to 60% of the locations characterized by a sediment thickness of 6 to 10 m (Emeis et al. 2004). Gas blow outs of methane and hydrogen sulfide were common in the years 2001 and 2002, producing clouds of elementary sulfur visible from space (Weeks et al. 2002, 2004). Such massive gas extrusions from the sediment column result in biochemical stress for the benthic fauna, as well as in the re-suspension of surface sediment layers (Weeks et al. 2004, Emeis et al. 2007). Even buoyancy of gas laden sediment layers was observed as drifting, mud islands‘ (Emeis et al. 2004). Enhanced advection of slightly oxygenated water masses to the sediment surface provides temporal oxygen availability (Chapman and Shannon 1987), but the benthic consumption rates on the inner shelf are sufficient for subsequent complete reduction (van der Plas et al. 2007). Oxygen deficits of up to 150 µmol l^{-1} were recorded, due to local consumption (Mohrholz et al. 2008). Within the uppermost sediment column, sulfate-reducing bacteria were found in all cores sampled by Brüchert et al. (2003) on the Namibian shelf. Their sulfate reduction rates culminate at the sediment surface or within the uppermost centimeters of the sediment column, providing a net flux of hydrogen sulfide from the sediment column into the bottom water (Brüchert et al. 2003). This sulfide is detoxified by blooms of chemolithotrophic bacteria that occur within an anoxic bottom water mass reaching several meters above the sea floor (Lavik et al. 2009).

Despite its widespread occurrence in several 1000 km^2 of the shelf, this newly recovered bacterial process remains unnoticed in the upper water column. The decreased visibility detected by the ROV of the GeoBio-Center^{LMU} at 20 m above the ocean floor at station 181 (Table 1) was considered resuspended matter onboard (Appendix). Surprisingly, this did not coincide with the inflow of oxygenated water masses, but rather with the complete anoxia in the bottom water (Table 1). Therefore, the video provided here (Appendix) may as well visualize the dense blooms of chemolithotrophic bacteria described by Lavik et al. (2009). Reduced visibility starts at 27 m above the seafloor, and gradually increases to <1 m near the sediment surface.

MATERIAL AND METHODS

Surface sediments were sampled off Namibia with multicorers during the RV Meteor cruises M48/2 in the year 2000 and M57/3 in 2003 (cruise reports in Emeis 2002, Brüchert 2005, respectively). The water depth at the stations ranges from 28 to 152 m (Table 1, Figure 1). Samples were taken in steps of 1 cm from one to four core tubes, depending on availability and recovery. Densely suspended or flocculent matter within the lowermost supernatant bottom water was collected with a spoon and added to the surface sample. Three multicorer tubes were sampled down core in larger sections, lumping together layers of homogenous sediment facies. All samples were stained onboard with a solution of 2 g Rose Bengal (C.I. 45440) l^{-1} ethanol immediately after recovery. This solution does not affect subsequent isotopic measurements (Serrano et al. 2008). About 200 cm^3 of the solution were added per 100 cm^3 sample wet volume in a translucent plastic container (Kautex-bottle). The penetration of the preservative was enhanced by softly shaking the closed container, until no more unstained sediment lumps or bacterial mucus tubers attached to its wall. The best staining results with Rose Bengal are obtained if the sediment is exposed to the stain for three (sandy or silty sediment) or six weeks (sticky clay). Shorter exposure will reduce staining efficiency (Lutze and Altenbach 1991). This methodology was cross-checked by comparison of biomass measurements of stained foraminifera and living foraminifera picked from fresh sediments, both sampled from periodically dysoxic sediments of the Baltic Sea (Lutze and Altenbach 1991). These control measurements gave proof for a reliability of the detection of living, protoplasm filled tests above the 96 % level. The usage of lowered ethanol concentrations or water as a solvent for Rose Bengal, other preservatives, or short-term staining, will adversely affect staining efficiency (Lutze and Altenbach 1991). During cruise M48, the Tübingen working group isolated living foraminifers with protruding reticulopodia from our sampling sites for DNA analysis (Ertan et al., 2004).

Gas bubbles were observed in several samples during recovery, producing an intense smell of hydrogen sulfide, sometimes even foaming up within the multicorer tubes. In some instances, excess sediment falling from the multicorer tubes reduced the wooden ship planks within minutes (Appendix). A sediment volume correction was deduced in compensation of either the additional matter sampled from the nepheloid layer, or for the expanding gas volumes. After storage for several weeks, all particles had settled below the supernatant liquid, leaving a clear, translucent Rose Bengal solution. The sediment surface, clearly visible through the translucent sample container, was marked with a water- resistant felt tip. Subsequent to pouring the sample on the sieve, this mark was refilled with water for the detection of the settled and gas free sample volume. This procedure led to corrections ranging from +10 to -40 % of the theoretical volume calculated based on the diameter of the multicorer. The resulting sample volumes of approximately 100 to 300 cm^3 are sufficient for the detection of a standing stock (stained tests) down to 0.1-0.03 specimens per 10 cm^3. Samples were wet sieved for size fractions >63 µm and >250 µm, and dried at 40ºC. The fraction 150 to 250 µm was dry sieved from the fraction 63-250 µm.

TABLE 1. Station numbers, position, water depth, and oxygen content of bottom near water masses of the 35 stations sampled during *RV Meteor* cruises M48/2 and M57/3 on the inner Namibian shelf. Stations underlined did not produce foraminiferal tests. Oxygen values from CTD measures several meters above the sea floor; O_2 values underlined indicate calibration by Winkler titration onboard for these stations. Prefix 226 for cruise M48/2 and prefix 57 for cruise M57/3 are omitted in the text.

Station	Latitude [S]	Longitude [E]	Depth [m]	O2 [ml l-1]
57165	23°°00.00'	14°18.99'	74	0
57166	23°59.98'	14°12.98'	108	0
57178	23°45.51'	14°15.99'	114	0.4
57179	23°09.96'	14°19.35'	84	0.2
57180	22°52.66'	14°24.58	48	0.8
57181	22°54.61'	14°23.38'	62	0
57182	23°10.01'	14°04.92'	132	0.3
57183	23°05.03'	14°16.07'	99	0.2
57184	23°00.02'	14°22.05'	44	0.5
57185	23°00.00'	14°19.00'	74	0
57187	23°00.05'	14°02.92'	130	0.2
57188	22°59.95'	13°51.95'	143	0.1
57198	21°45.79'	13°43.41'	93	0.5
57199	22°00.22'	13°51.50'	91	0.3
57200	22°50.94'	14°28.35'	28	0.1
57201	22°46.26'	14°27.98'	38	0.1
57202	22°38.26'	14°18.26'	70	0
57203	22°10.22'	14°03.80'	70	0.1
57212	22°59.92'	13°40.98'	152	0.5
226620	22°45.51'	14°18.87'	83	0
226670	23°46.30'	14°18.17'	107	0.1
226680	23°46.52'	14°17.96'	109	0.1
226690	23°46.81'	14°15.74'	109	0
226720	22°09.98'	14°04.07'	69	0
226730	22°00.17'	13°51.52'	91	0
226740	21°55.10'	13°51.93'	79	0.2
226770	21°22.97'	13°40.00'	51	0
226780	20°59.95'	13°21.99'	81	0.1
226790	19°47.00'	12°51.61'	50	0.2
226800	19°48.83'	12°46.36'	93	0.3
226810	19°50.66'	12°40.50'	116	0.7
226830	21°44.00'	13°53.02'	35	0.1
226880	19°00.97'	12°20.62'	98	0.1
226890	19°01.00'	12°16.54'	109	0.4
226900	19°01.01'	12°13.74'	119	0.3

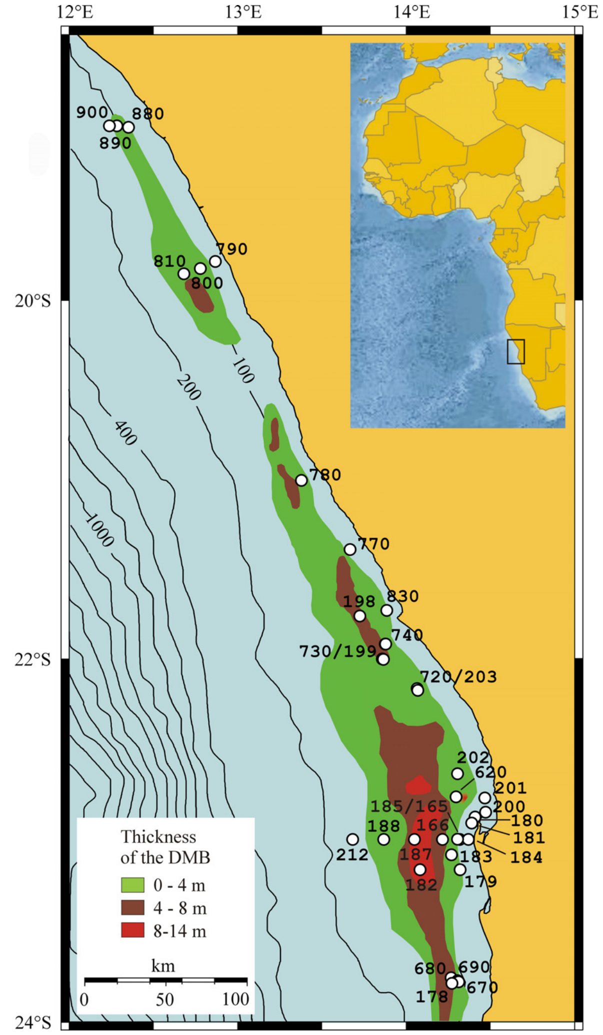

FIGURE 1. Stations of cruises M48 and M57 off Namibia. Thickness of the diatomaceous mud belt (DMB) modified from Bremner and Willis (1993), and Emeis et al. (2004).

Size fraction >250 µm was counted in all surface samples. This size fraction rules out, or at least reduces, increasing lateral advection for decreasing test sizes (Lutze 1980). The size fraction 150-250 µm was counted in all samples from cruise M57/3, in order to estimate the imprint of smaller size classes. Counting this size fraction was much more time-consuming in comparison to the fraction >250 µm. We estimate a factor of about two to 10 times, depending on the increasing number of diatom frustules. The size fraction 63 to 150 µm of the DMB was impossible to count quantitatively because of the absolute dominance of diatom frustules. Other particles were only occasionally found on picking trays. Organic debris and bacterial mucus caught in a fabric with diatoms resulted in large aggregates in the dried sample. Splitting this small fraction in a Micro-Splitter led to static adhesion of diatoms on the walls of the splitter and the containers, and clouds of diatom frustules floated in the air for seconds. Bremner (1983) was successful in point counting the >63 µm fraction of the DMB by treating the samples with fresh water onboard and storing them for longer periods under room temperature. We presume that the chemical breakdown of the organic matter before drying was crucial for his success. However, such treatment would operate to the detriment of protoplasm staining, an indispensable prerequisite for our study. Foraminifers were identified and quantified per sample volume on a picking tray under a Wild M3Z dissecting microscope. Selected specimen were investigated with a Wild M10 with a Planapo 1.6 objective and by scanning electron microscopy (SEM CARL ZEISS LEO 1430 VP). Tests were fixed on isolating wax, fluted with argon, and sputter-coated with gold in a Polaron E 5000.

Data on near bottom oxygen concentrations (Table 1) were obtained with a multi-sensor probe (CTD) at about 5 m above the ocean floor during cruise M48/2. Derived oxygen measures were calibrated by Winkler measurements from Niskin bottles for several stations (Emeis 2002). Mean bottom oxygen values for the stations of cruise M57/3 were calculated from a grid of 1709 measures provided by the database of the South African Oceanographic Center (Sadco 2007). The Standard deviation of Winkler calibrated CTD oxygen values from M48/2 were correlated with the Sadco (2007) derived oxygen values for the same stations; the resulting standard deviation is 0.3 ml O_2 l^{-1}. This range corresponds to the accuracy considered for standard CTD probes in general and is threefold below the mean seasonal variability of oxygen concentrations recorded on the Namibian shelf (Kristmannsson 1999). Given environmental terms for observed oxygen ranges follow Bernhard and Sen Gupta (1999).

RESULTS

Stained Benthic Foraminifera >250 µm

Of the 35 samples obtained from the inner Namibian shelf (Table 1), four were found completely barren of foraminiferal tests, and 15 were barren of stained foraminifers in the size class >250 µm. Of the remaining 16 samples, *Virgulinella fragilis* (Grindell and Collen) was detected in 12 samples (Table 2, Figure 2.1-3.), and thus can be considered a common species. Nonionella stella Cushman and Moyer (Figure 2.7-8.) and *Discam-*

TABLE 2. Standing stock (stained tests) of the size fraction >250 µm as individuals per 10 cubic centimeters surface sediment.

Station	*Virgulinella fragilis*	*Nonionella stella*	*Discammina compressa*	*Ammonia beccarii*	*Crithionina pisum*	*Hyperammina sp.*
165	0.03	-	-	-	-	-
178	0.05	-	-	-	-	-
179	0.07	-	-	-	-	-
203	-	-	2.3	-	-	-
212	-	-	8.4	11.8	-	-
620	0.98	-	-	-	-	-
670	0.05	-	-	-	-	-
680	0.44	-	-	-	0.06	0.06
690	0.1	-	-	-	-	-
730	0.67	-	-	-	-	-
770	-	0.63	0.95	-	-	-
780	0.07	0.06	-	-	-	-
790	-	2.1	1.1	-	-	-
830	0.24	0.02	-	-	-	-
880	0.05	0.14	0.02	-	-	-
900	0.07	-	-	-	-	-

mina compressa (Goes) occur in five samples. *Crithionina pisum* Goes and *Hyperammina* sp. each were found once, i.e., at station 680. All named species occur within low dysoxic to anoxic conditions (0 to 0.3 ml l^{-1}). On the outermost edge of the DMB, at 152 m water depth, the oxygen values rise to 0.5 ml l^{-1}. *Ammonia beccarii* (Linné) exclusively occurs in this area, where it co-occurs with *D. compressa.* The standing stock of this community (station 212, Table 2) is elevated by about two orders of magnitude, in comparison to the more oxygen depleted DMB stations from 74 to 132 m water depth. For these shallower sites, the standing stock of the populations consistently ranges below 1 ind. per 10 cm^3, with *V. fragilis* as a constant member. This depth range corresponds to the depth range of the bacterial blooms and anoxic bottom water masses described by Lavik et al. (2009). Towards nearshore, at 70-50 m water depth, *N. stella* and *D. depressa* display an increased standing stock, while *V. fragilis* is absent. The shallowest station yielding stained foraminifera occurs at 35 m water depth and contains both *V. fragilis* and *N. stella* (station 830, Table 2). Enhanced methane production by submarine seepage of Namibian groundwater aquifers has been postulated for the shallow shelf, but reliable near shore seepage quantifications are available for only one aquifer at present (see Altenbach and Struck 2006).

Unstained Tests >250 µm

The most common species at 35 m water depth, as well as for the depth range from 74 to 132 m is *Virgulinella fragilis,* and sporadically cooccuring *Nonionella stella* and *Discammina compressa.* At 50-70 m water depth, *D. compressa* and *N. stella* are most common in the unstained assemblage (Figure 3). This corresponds with the distributional pattern observed for the stained species (Table 2). *Ammonia beccarii* is most common at the outermost edge of the DMB (station 212), where it co-occurs with *D. compressa.* In addition, *Cibicides lobatulus* Walker and Jacob (referred to *Lobatula* by some authors), *Uvigerina mediterranea* Hofker, *Cancris auriculus* (Fichtel and Moll), *Hyalinea balthica* (Schroeter), two elphidid, and two quinqueloculinid species are indicative of more open marine conditions. However, a large number of heavily corroded and fragmented tests of textulariid, miliolid, or calcitic origin (gen. et. sp. indet.) suggest that reworking and onshore transportation from the outer shelf may have occurred. These intruders are found sporadically in the DMB, either introduced by temporal migration during increased oxygen availability, or by lateral advection. They usually occur close to the edges of the mud, at water depths of either above 74 m (greenish marker colors in Figure 3) or deeper than 132 m (yellow to reddish marker colors in Figure 3). The only exception is represented by *Cibicidoides pseudoungerianus* (Cushman) and *C. lobatulus* (stations 730 and 810 in Figure 3). These taxa, which have a typical epibenthic lifestyle are most commonly advected over broad distances within shelf environments and down slope (Hald and Vorren 1987, Mudie et al. 1984). At station 810, elevated oxygen concentrations (0.7 ml l^{-1}) indicate the local intrusion of more oxygen saturated water masses contemporary to our sampling. In water depths shallower than 74 m, *Nonion asterizans* (Fichtel and Moll) and *Quinqueloculina venusta* Karrer are the most important taxa (Figure 3). Light

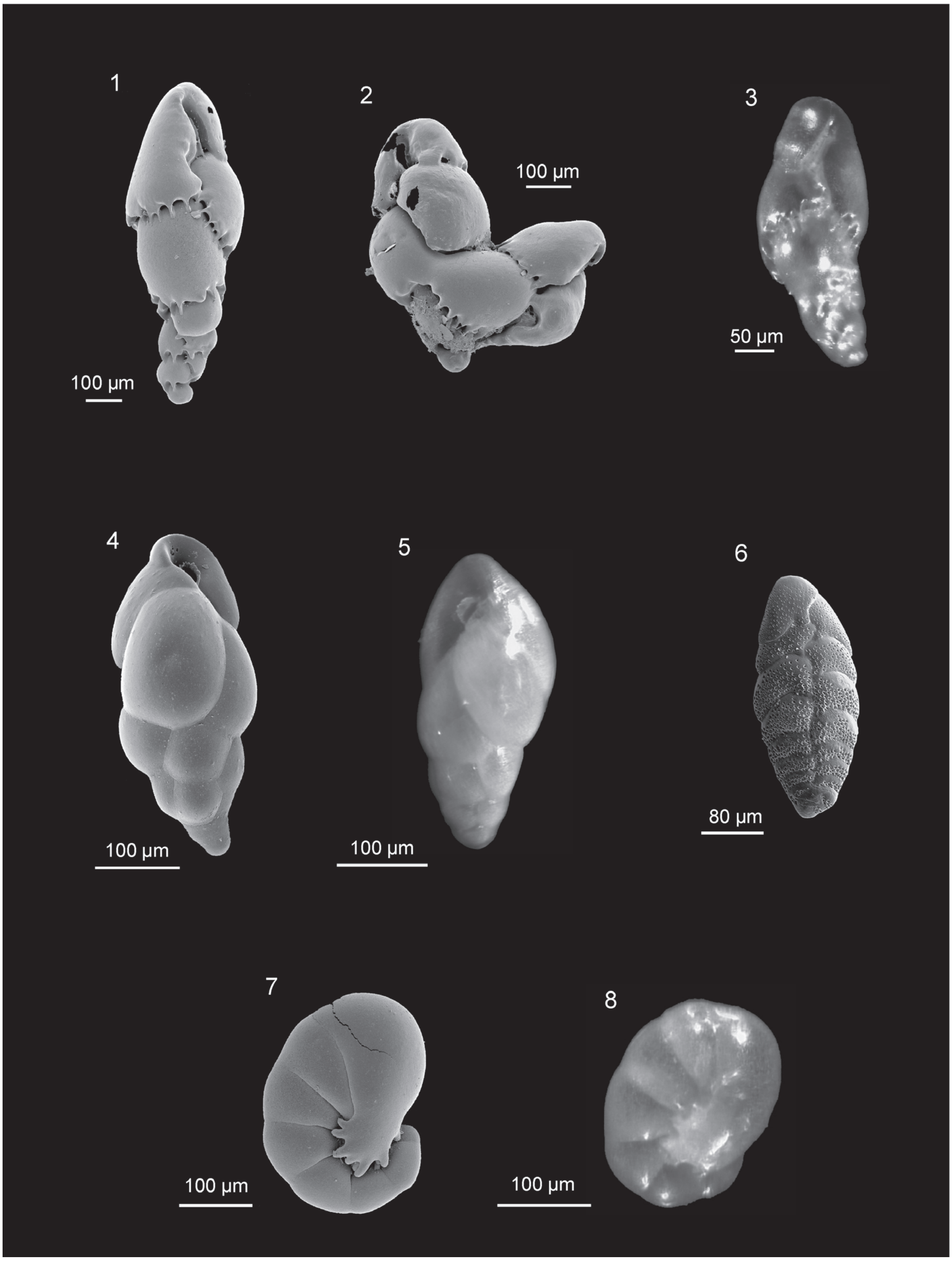

FIGURE 2.1-2.8. Benthic foraminifera of the Namibian diatomaceous mud belt. 1-3. *Virgulinella fragilis* Grindell and Collen 1976. 1. SEM figure. 2. Twin-building teratological tests, derived by the fusion of two embryonic macrospheres, REM figure. 3. Light microscope with digital camera. 4-5. *Fursenkoina fusiformis* (Williamson 1858). 4. REM figure. 5. Light microscope with digital camera. 6. *Bolivina pacifica* Cushman and McCulloch 1942, REM figure. 7-8. *Nonionella stella* Cushman and Moyer 1930. 7. REM figure. 8. Light microscope with digital camera.

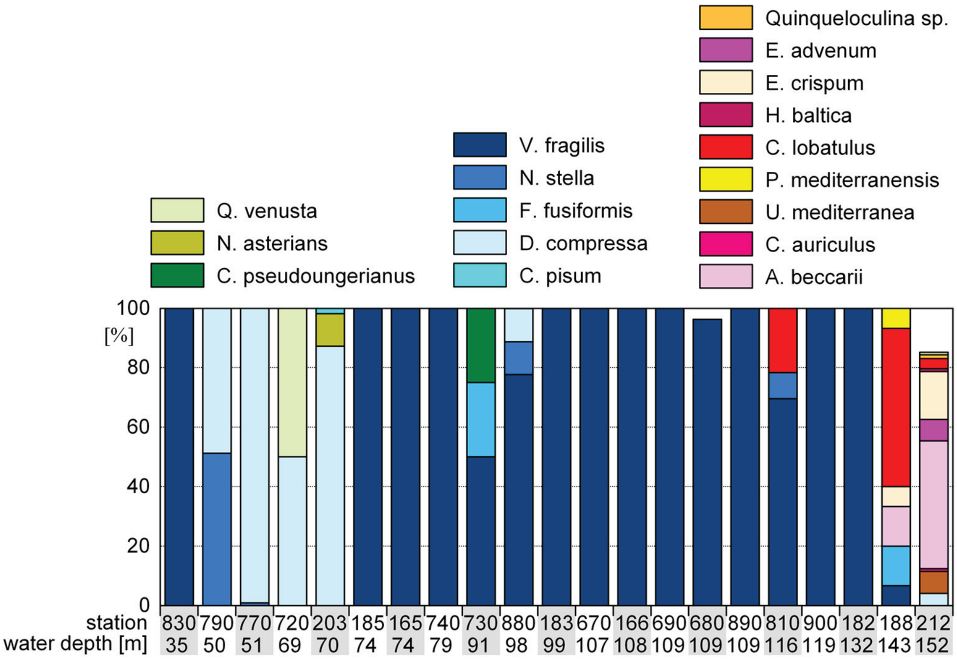

FIGURE 3. Percentage of unstained benthic foraminifera recovered from surface sediments, size fraction >250 µm (omitted stations 181, 184, 187, 199; see text). Columns not reaching 100% indicate the amount of test fragments with gen. et sp. indet.

to dark blue marker colors indicate the species that also were recovered stained from the DMB, and thus can be considered autochthonous (Figure 3). Four stations were omitted in Figure 3: stations 187 and 199 only contained test fragments (gen. et sp. indet.), while station 181 yielded only a single test of *Cassidulina* cf. *teretis* (or the sibling shallow water morphotype described by Seidenkrantz 1995), and from station 184 one slightly corroded test of *Cribrostomoides* cf. *jeffreysi* (referred to *Labrospira* by some authors) was recovered.

TABLE 3. Standing stock (stained tests) of the size fraction 150 to 250 µm as individuals per 10 cubic centimeters surface sediment.

Station	***Virgulinella fragilis***	***Nonionella stella***	***Fursenkoina fusiformis***	***Bolivina pacifica***	***Ammonia beccarii***
178	-	1.6	20.27	0.53	-
179	-	0.13	-	-	-
185	0.27	-	-	0.2	-
187	-	-	0.17	0.04	-
188	-	-	21.33	1.7	-
199	-	-	0.08	0.08	-
212	-	-	-	-	6.74

Stained Benthic Foraminifera 150-250 µm

Stained benthic foraminifers were recovered from seven of 19 stations (Table 3). Four of these produced *Virgulinella fragilis, Nonionella stella,* or *Ammonia beccarii* at identical depth ranges as compared to the larger fraction. Due to shape and size, *Bolivina pacifica* Cushman and McCulloch (Figure 2.6.) was only recovered from this size fraction at five stations with O_2 concentrations from 0-0.4 ml l^{-1}. *Fursenkoina fusiformis* (Williamson) (Figure 2.4-5., referred to *Stainforthia* by some authors) was observed from four stations, with high standing stock (>20 ind. per 10 cm^3) at stations 178 and 188 in spite of the microxic conditions. This species was also recovered from the larger size fraction, but did only occur in the dead count, together with a number of unstained tests of other species.

Stained *V. fragilis, N. stella, F. fusiformis* and *B. pacifica* were also recovered deep infaunal from core 199 (Figure 4). *F. fusiformis* occurs in all samples down to 15 cm, *V. fragilis* and *B. pacifica* occur at 9-11 cm, and *N. stella* settles in the deepest layer at 11-19 cm sediment depth. The standing

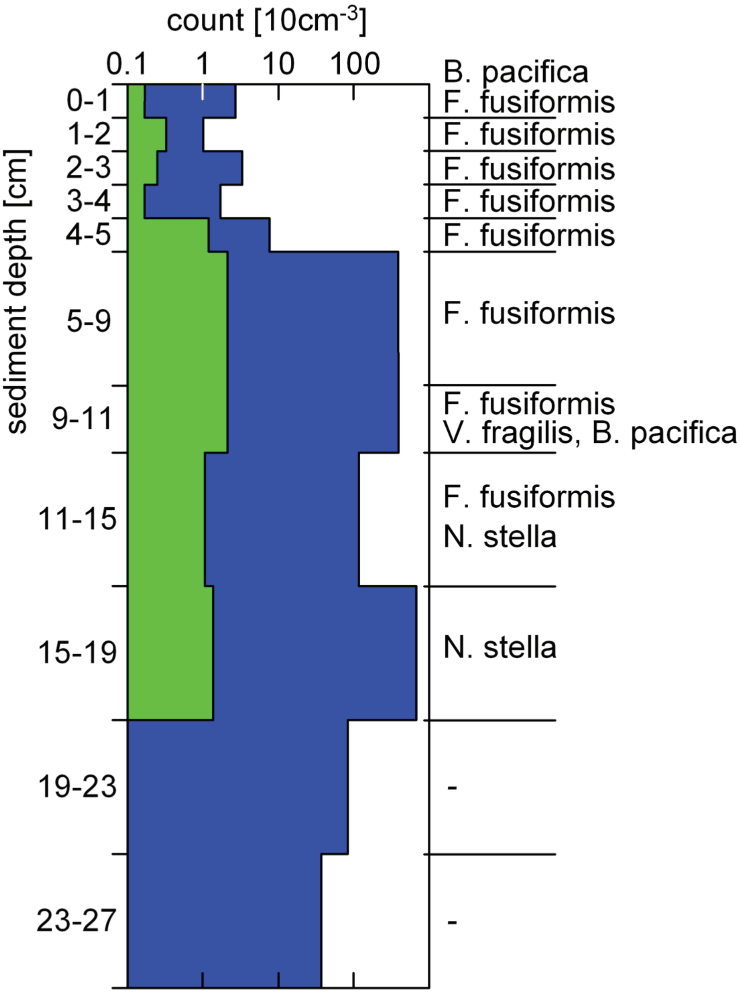

FIGURE 4. Standing stock (green) and number of unstained tests (blue) of benthic foraminifera recovered per 10 cm^{-3} from station 199, in 11 depth slices from 0 to 27 cm sediment depth. Species recovered living (stained) are named right hand of the respective depth slices.

stock of these populations increases at 3-5 cm sediment depth by nearly one order of magnitude, in comparison to the sediment surface; all shifts of standing stock down core are closely connected to the amount of unstained tests preserved (Figure 4).

Unstained Tests 150-250 µm

A pattern of co-occuring *Fursenkoina fusiformis, Virgulinella fragilis, Nonionella stella,* and *Bolivina pacifica* stretches from 70 to 143 m water depth. Intruders are found seaward from 152-143 m water depth, and from 44-74 m on the landward flank of the DMB (Figure 5), similar to the larger size fraction (Figure 3). The dominance of unstained *Discammina compressa* at 50-70 m water depth (Figure 3, >250 µm) is not recognizable in the smaller fraction (Figure 5). The abundance of *V. fragilis* in the larger size fraction (Figure 3) is less significant in the smaller size fraction (Figure 5).

The taphocoenoses represented by core 199 are composed of the four species recovered stained downcore, together with sporadic occurrences of *Uvigerina mediterranea* at 3 to 4 cm, *Cibicides lobatulus* at 4 to 5 cm, *Ehrenbergina undulata* Parker at 9 to 11 cm, and *Nonionella grateloupi* (d‘Orbigny) at 15 to 19 cm sediment depth. The number of unstained tests increases by about two orders of magnitude at 3 to 5 cm sediment depth (Figure 4).

Imprint of Size Classes

Of a total of 16 surface samples from cruise M57/3, unstained tests were detected in 12 samples representing the size fraction >250 µm (Figure 3). This recovery increases by 25% if the size frac-

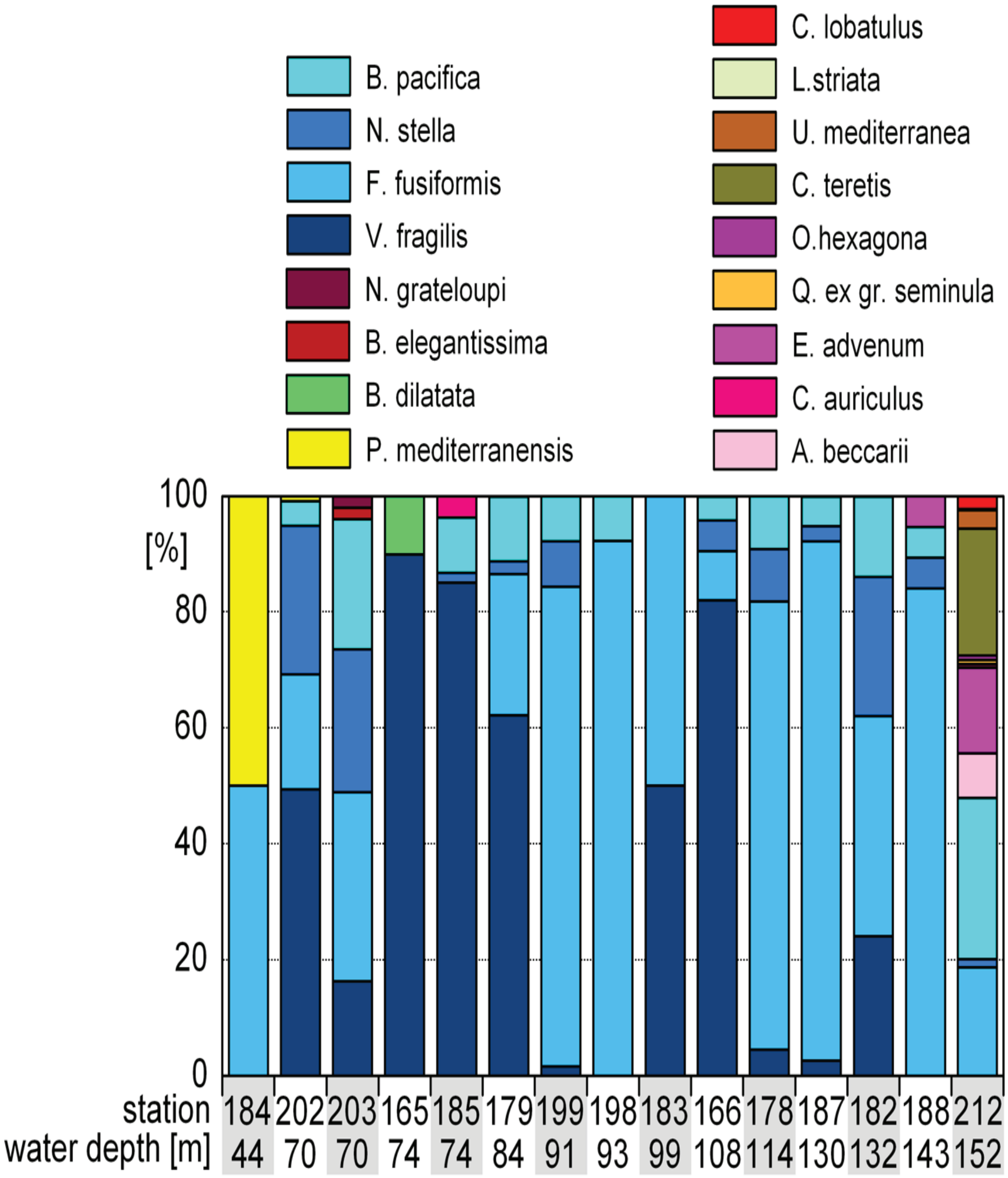

FIGURE 5. Percentage of unstained benthic foraminifera recovered from surface sediments, size fraction 150 to 250 µm.

tion considered is extended down to >150 µm (15 stations, Figure 5). Six additional taxa are recorded, which is inevitably the case for all early ontogenetic stages, and all taxa with a small or slender growth, such as many bolivinids and buliminids. However, this advantage can only be retained when the samples are scrutinized completely. If smaller grid sizes are used for sieving foraminifera, even a small split fraction of the sample may contain an abundance of small-sized species. This may suggest that the analysis of a small sample volume derived from a split fraction is sufficient in order to adequately assess the diversity of foraminifera. However, by restricting the screening process, the likelihood of discovering a rare species is reduced because these species may only be represented by one individual in the entire sample. The abundance of stained foraminifera within the DMB is usually near 1 to 0.1 individual per 10 cm^3 sediment. Dale and McMillan (1998) studied the small fraction (i.e., >125 micron) from the DMB based on sample sizes of 10 g of dry sediment and discovered a diverse fauna with many small growing species. However, the two taxa most commonly stained in our samples, *Virgulinella fragilis* and *Nonionella stella,* were not discovered by these

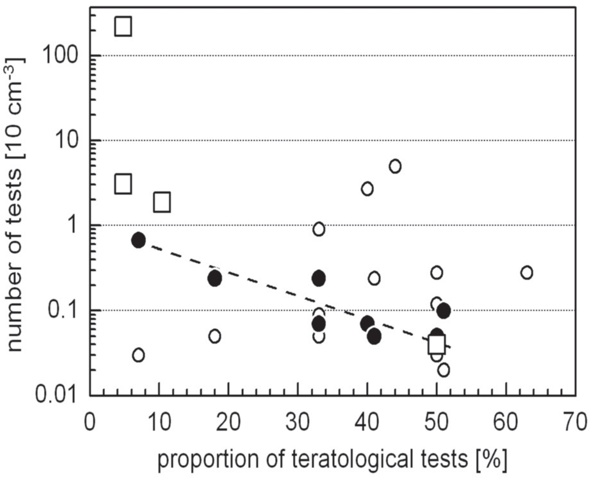

FIGURE 6. Proportion of teratological tests in the DMB. The amount increases with decreasing standing stock (stained tests) in the year 2000 (cruise M48, black circles, fraction >250 µm). The dashed line indicates exponential regression (n=8, r = 0.95, p >99.9%). This tendency is not derived from the unstained tests (cruise M48, open circles, fraction >250 µm). The juvenile generation which went extinct some time between the years 2000 and 2004 (cruise M57, fraction 150-250 µm) is marked by open squares.

authors. Based on the preceding considerations we submit that the analysis of foraminifera from extreme environments should be based on the screening of particularly large samples.

Smaller specimens of *Virgulinella fragilis, Nonionella stella,* and *Fursenkoina fusiformis* were recorded stained for six stations in the size fraction 150-250 µm (Table 3), but none of these stations contained stained tests in the size fraction >250 µm (Table 2). Vice versa, adult stages of *V. fragilis* were recovered from three stations in the size fraction >250 µm, but these stations lacked specimens in the smaller size fraction. Such isolated cohorts result from rare and irregular reproduction, or from repeated and complete loss of recruitment.

Teratological tests of *Virgulinella fragilis* were commonly observed from the size fraction >250 µm in the year 2000 (cruise M48/2), ranging at 7-63% for the counts of stained and unstained tests. Most of the teratological tests display fusion of two embryonic macrospheres, or attachment of a juvenile to an adult test (figured in Altenbach and Struck 2006). With decreasing standing stock of the population, proportion of teratological tests increases significantly (Figure 6, black circles; linear regression, r = -0.85, p >99%; exponential regression exp(-0.0634 * x), r = 0.95, p >99.9%). No correlation is indicated for the number of unstained tests (Figure 6, open circles). Three years later (cruise M57/3), not a single teratological structure was recovered from the size fraction of >250 µm, neither from the stained, nor from unstained tests. In the size fraction 150-250 µm, however, unstained juvenile specimens with teratological tests were observed from 4 surface samples (Figure 2.2.; Figure 6, open squares). All these tests were slightly to heavily corroded or broken.

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Stained tests were mentioned in the typus description of *Virgulinella fragilis* only from the former dumping area off Wellington, but unstained tests were reported from all over the harbour area (Grindell and Collen 1976). Regardless of their own results derived from Rose Bengal staining, these authors suggested that the new species thrived in oxygen- saturated environments. Consequently, most subsequent publications regarded *V. fragilis* as a normal marine shelf foraminifer (references in Revets 1991). Reduced oxygen availability and large amounts of organic debris in decomposition were noted for the first time for habitats of modern virgulinellids by Sellier de Civrieux (1977, referred to *Virgulinella pertusa*), and vital populations of *V. fragilis* were subsequently described by Bernhard (2002) and Altenbach et al. (2002) from anoxic and sulfidic environments. All following studies that included live stains and oxygen measures corroborated these findings. *V. fragilis* was found in sulfur-oxidizing bacterial mats in the Cariaco Basin and the Arabian Sea (Bernhard 2003, Erbacher and Nelskamp 2006), or attributed to microxic and sulfidic conditions off Japan and India (Takata et al. 2005, Nigam et al. 2007). It occurs in the shallow Ria de Vigo estuary in Spain (Diz and Frances 2008, referred to *V. pertusa*), a habitat that is characterized by seasonal oxygen depletion and benthic methanogenesis (Kitidis et al. 2007). Multiple survival strategies have been discussed for this heterotrophic eukaryote, such as symbiotic sulfur oxidizing bacteria, functional kleptoplasts, and peroxisome proliferation (Bernhard 2003, Horak et al. 2004, Bernhard and Bowser 2008). *V. fragilis* meanwhile can be considered a characteristic species for microhabitats near redox boundary conditions.

Nonionella stella, Fursenkoina fusiformis, and *Bolivina pacifica* occur under normal marine conditions on the upper continental slope off Namibia (Leiter 2008), as well as in other areas with enhanced organic carbon flux rates to the sea floor off western Africa (Lutze 1980, Altenbach et al. 2003, Licari and Mackensen 2005). However, these species have also been reported from anoxic or dysoxic environments (Bernhard and Sen Gupta 1999). Highest standing stock was recorded for *F. fusiformis* from dumping areas (Alve 2003). Laboratory experiments revealed an increased survival rate of *F. fusiformis* under anoxia (Bernhard and Alve 1996) that was further supported by the availability of large amounts of organic matter (Ernst et al. 2005). *B. pacifica* co-occurs with *V. fragilis* in sediments covered with the sulfur bacteria *Thioploca* and *Beggiatoa* in the oxygen minimum zone off Pakistan (Erbacher and Nelskamp 2006).

Laboratory experiments of Risgaard-Peterson et al. (2006) suggest that *Nonionella* cf. *stella* and *Stainforthia* sp. are capable of complete denitrification near the chemocline. The results were later corroborated by field investigations off Chile (Høgslund et al. 2008). Similar to *Virgulinella fragilis,* the function of kleptoplasts and peroxisome proliferation has also been discussed for *Nonionella stella* and *Fursenkoina fusiformis* (Bernhard and Alve 1996, Grzymski et al. 2002, Horak et al. 2004, Bernhard and Bowser 1999, 2008). For the central part of the DMB, the sediment column below zero to five cm has to be considered anoxic and sulfidic (Brüchert et al. 2003). The deep infaunal occurrence of *V. fragilis, F. fusiformis, N. stella,* and *Bolivina pacifica* (Figure 4) may indicate long-term adaptability to such conditions.

For the occurrence of *Discammina compressa,* amplifying towards the outer edges of the DMB, and for the single occurrence of *Hyperammina* sp. and *Crithionina pisum* under microxic conditions species specific ecological data remain conjectural. These taxa have been reported from oxic environments of the NW-African upwelling area and the Gulf of Guinea (Lutze 1980, Altenbach et al. 2003). Within the DMB, stained *D. compressa* specimens display a detritic, coarse overlay around the test that is glued together by organic matter intensively colored by Rose Bengal stain. This overlay is either missing on empty tests, or occurs in the form of an unstained, patchy residue. Coarsely agglutinated larger textulariid taxa, such as *Hyperammina* sp., may perform enormous hydrolytic activities, exceeding values reported for symbiotic bacterial-macrofaunal interactions (Koester et al. 1991, Meyer-Reil and Koester 1991). Richardson and Cedhagen (2001) noted extracellular digestion for *Crithionina granum,* and, quoting the work of Meyer-Reil and Koester, they mentioned that bacteria will benefit from exoenzymes produced by foraminifera. However, we can only speculate about gardening, or commensal, or symbiotic interactions at present.

DISCUSSION

Extraordinary organic matter contents and severe dysoxic to anoxic conditions are characteristic of the sediments of the DMB. This allows live staining of foraminifers with Rose Bengal even several months after death (Murray and Bowser 2000). Therefore, our staining indicates living specimens only with regard to this time span. However, the four stained species recovered repeatedly from surface sediments and deep infaunal habitats (Table 2, 3; Figure 4) are the main contributors to the thanathocoenoses. *Virgulinella fragilis* undoubtedly thrives under the harsh conditions of the DMB. It was recovered living with protruded reticulopodia from surface sediments, occurs Rose Bengal stained only at stations ≤ 0.3 ml l^{-1} O_2, and was not recovered outside the DMB (Leiter 2008). For *Nonionella stella, Fursenkoina fusiformis,* and *Bolivina pacifica* one might suggest lateral advection from more oxygenated habitats, and a limited time span of their subsequent survival. All three species occur stained at deeper stations seaward of the DMB, and thus could be transported by the prevailing landward bottom currents. In this case, it seems improbable that none of the many other unstained species that were recovered (Figure 3, 5) displays a similar type of advection and staining of decaying protoplas10 cm^3 unusually rare occurrences. More sophisticated live staining techniques may perhaps provide a better resolution of ratio of living and dead stained individuals (Bernhard et al. 2006a). However, increased numbers of dead stained individuals does not automatically mean that lateral advection of living species into the DMB has occurred. With regard to the severe environmental fluctuations and gas outbreaks, high mortality rates must be considered a pulsed attendant for established populations as well. As a result, we consider the syntopic occurrence of *V. fragilis, N. stella, F. fusiformis,* and *B. pacifica* as characteristic for the oxygen depleted DMB. Moreover, we conclude that our thanathocoenoses firmly transmit the ecological basics derived from the stained taxa (Murray and Alve 1999). The standing stock of most populations ranges at <1 individual 10 cm^{-3}, sometimes even <0.1 ind. 10 cm^{-3}. Staining with CellTracker Green would most probably result in an even smaller standing stock (Bernhard et al. 2006a). Such populations are nearly impossible to recover from common split fractions of sample sizes equivalent to 10 cm^{-3} or less. Much larger sample sizes would have to be scrutinized in order to recover the tiny, but widespread populations. It is likely that the absence of foraminifera considered for other extreme environments is due to sample size, rather than the actual absence of foraminifera.

Taxa recovered exclusively as unstained tests show increased abundances towards the outer sedimentary edges of the DMB. They indicate sedimentological advection and/or unsuccessful migrational attempts. The 'rich' benthic foraminiferal fauna reported on previously from the mud belt was either restricted to the outmost seaward edge (Bremner 1983), or presented as a total assemblage with questionable origin (Dale and McMillan 1998).

The deep infaunal occurrence of four stained foraminiferan taxa probably represents the most significant result of our study. Several centimeter-long annelids of uncertain affinity were recovered during cruise AHAB 5 at the crater, gasdome 2‘ (Altenbach and Struck 2006). Several polychaetes thrive under microxic conditions on the northernmost Namibian shelf (Zettler et al. 2009), and worm feces are considered abundant for the Namibian mud belt (Dale and McMillan 1998). This suggests that passive transport of stained tests downcore may have occurred through bioturbation. On the other hand, worm borrows strongly affect lateral migration of foraminifera and their colonisation behaviour in deeper sediment layers (Thomsen and Altenbach 1993). Core 199 was carefully selected, because it did not show indications of bioturbation or sediment replacement from ascending gas bubbles. The number of stained and unstained tests is lowest within the top 5 cm, and increases in below-positioned layers. An erratic transport downcore would probably lead to a decline in test numbers with increasing sediment depth. Stained taxa occur in distinct depth layers, accompanied by varying numbers of preserved unstained tests (Figure 4). This coincidence perhaps is a result of the imprint of various microbial and biogeochemical processes. Depth defined layers typically occur in areas in which certain reduction rates of sulfate and nitrate are present within the uppermost 30 cm of the Namibian shelf sediments (Brüchert et al. 2003). The sulfate reduction rates of the DMB were modelled to rapidly increase above 15 cm sediment depth and sharply decrease in the deeper sediment column (Dale et al. 2009). This depth layer coincides with the last appearance of *F. fusiformis* and the first occurrence of *N. stella* downcore (Figure 4).

Teratological tests of *Virgulinella fragilis* were commonly observed in the year 2000 (cruise M48) in the size fraction of >250µm. Three years later (cruise M57/3) no teratological tests were recovered from this size fraction, neither stained nor unstained. Numerous gas blow outs of hydrogen sulfide and methane were recorded within this time span (Weeks et al. 2004). These short-term perturbations of pH and redox conditions in the bottom and pore water are known to trigger fusions of embryonic stages (Stouff et al. 1999), and subsequently lead to the corrosion of foraminiferal tests (Keir 1980). The taphonomic loss of the teratological tests likely occurred rapidly and resulted in complete test dissolution, because no *V. fragilis* advected from the DMB was recovered in 2003, neither on the outer shelf nor downslope (Leiter 2008). Offspring of the populations of *V. fragilis* was detected in size fraction 150-250 µm, with relatively high numbers of teratological tests. None of these specimens, however, had matured, and all tests were slightly to heavily corroded, in transfer to dissolution. The extremely thin wall of *V. fragilis* (approximately 1 µm, according to Grindell and Collen 1976) might offer an explanation for these observations. If post mortem dissolution of calcitic foraminiferal tests can be considered a logarithmic function of wall thickness (Keir 1980), the exceptionally thin test walls will rapidly dissolve after death, if they remain in carbonate-aggressive sites. The lateral transport over long distances can only occur if empty tests are advected towards more normal marine hydrochemical conditions. As a result, environmental ranges deducted from sites that only produced unstained tests of *V. fragilis* are most likely exaggerated towards more normal marine conditions (Grindell and Collen 1976, Bhatia and Kumar 1976, Nigam and Setty 1982, Takata et al. 2003).

For palaeoecological investigations, the genus *Virgulinella* provides a very interesting extant species because of it’s environmental thresholds within dysoxic to reducing conditions. All other taxa recovered stained from the DMB can also persist under normal marine conditions, as well as all other agglutinated, miliolid, or rotaliid taxa that have been recorded to date from anoxic environments (Bernhard and Sen Gupta 1999; for an exceptional allogromiid see Bernhard et al. 2006b). The first modern record of the genus *Virgulinella* can be found in Todd and Brönnimann (1957), including a reference to a collection of extant tests at the San Marcos University (Lima/Peru). These authors assigned their material to *Virgulinella pertusa* and regarded the taxa *Virgulinella gunteri* and *Virgulinella miocenica* as 'very similiar or possibly identical' with this species. The first record of stained specimens was provided by Seibold (1975), including a note on modern virgulinellids recovered from the NW African shelf (Lutze in Seibold 1975). Seibold (1975) noted the problem of assigning a Cenozoic fossil form to a modern taxon, and placed the specimens under *Virgulinella* cf. *gunteri*. The specimens illustrated in this paper, however, reveal a morphology that appears to be intermediate between *Virgulinella fragilis* and the Pliocene *Virgulinella lunata.* One year later, the only modern species *V. fragilis* Grindell and Collen 1976 was described, with *V. lunata* named as the most similar fossil taxon. Nevertheless, Nigam and Setty (1982) reported on the variability of the modern taxon. These authors described modern species assignable to both *V. guntheri* and *V. pertusa.* This is consistent with our observations. We found considerable variability with regard to the size of the sutural openings, the interposed arches, and the chamber elongation. Grindell and Collen (1976) have included all these morphological variations in the differential diagnosis for *V. fragilis.* As a result, it appears that the extreme fragility represents the sole specific diagnostic feature of *V. fragilis.* The description of the type material indicates that the wall of the later chambers is approximately 1 μm. This stands in contrast to the more robust specimen recovered from the Cenozoic (Haman 1977, Haman et al. 1993). Several authors did not consider fossil taxa in their evaluation of modern virgulinellids for various reasons, including fewer sutural bridges in comparison to the fossil taxa (Seibold 1975), presumed problems related to reworking (Zobel 1973), or more general considerations (Bhatia and Kumar 1976). However, several authors did not recognize considerable morphological differences between the fossil taxa and their modern virgulinellids (Todd and Brönnimann 1957, Sellier de Civrieux 1977, Setty and Nigam 1980, Diz and Frances 2008). Some fossil taxa reported from surface sediments of the eastern Pacific ocean may fall within the intraspecific pattern of *V. fragilis* (Hayward et al. 1999). We see the need to more precisely define the patterns of variability for the Cenozoic and modern species, until synonymy or separation can be handled precisely. A detailed discussion on the structure and taxonomy of the genus *Virgulinella* proposes to elevate this taxon to superfamily status and to remove it from the buliminids (definition in Revets 1991, rebuttal in Haman et al. 1993). Regardless of these taxonomic problems, the question remains as to whether a relatively homogenous test morphology implies corresponding ecological layouts for extant and fossil species.

It has been proposed that upwelling and dysoxic conditions existed at the Namibian shelf since the Miocene (Baturin 2002a). During the Pliocene-Pleistocene, reducing conditions amplified towards conditions comparable to the modern DMB (Baturin 2002b). This indicates that the spread of the genus *Virgulinella* off south-western Africa could have taken place under severe environmental conditions since the Miocene. One Miocene taxon first appeared at the African west coast (Haman et al. 1993).

However, even the earliest records of the genus *Virgulinella* from the middle to upper Oligocene come from areas that are believed to represent anoxic and sulfidic environments. For example, *Loxostomum chalkophilum* Hagn is described for a pyritic fill-out of a foraminiferal test interior. Already Hagn discussed a possible relationship between this Rupelian stone core and *Virgulinella pertusa.* But in the absence of apertural structures, he preferred to select a more primitive genus for the typus description (Hagn and Hoelzl 1952). Our study of the holotype specimen (BSPG Prot. 1952-8) revealed a chamber arrangement and sutural bridges that are in fact quite similar to that seen in the genus *Virgulinella.* Hagn's discussion is exhaustive. Mineralization and test dissolution must have occurred under sulfidic and carbonate aggressive hydrochemical gradients. In the Upper Oligocene, *Virgulinella* ex gr. *pertusa* is recovered from several outcrops of the Eastern Paratethys; oxygen depleted or sulfidic palaeoenvironments are evident from sedimentological and geochemical data for all these sites (Stolyarov 2001).

In conclusion, our results add support to the hypothesis that *Virgulinella fragilis* represents a characteristic species for environments in which sulfate reduction occurs (Bernhard 2003). We also conclude that, wherever fossil or modern virgulinellids are recovered, it is reasonable to assume temporal or stagnant anoxia for the source stratum or adjacent areas. The co-occurring *Nonionella stella* and *Fursenkoina fusiformis* may expand this supposition towards foraminiferal denitrification at redox boundary conditions (additional taxa discussed in Risgaard-Petersen et al. 2006, Høgslund et al. 2008). Increasing numbers of other benthic foraminiferal taxa indicate increasing lateral advection, and increasing distance from oxygen depleted environments.

ACKNOWLEDGMENTS

The first hint on benthic foraminifera living within the anoxic diatomaceous muds off Namibia came from Dr. U. Struck (Leibniz-Museum für Naturkunde, Berlin). Thanks are due, as always, to the professional captains and crews of the research-vessel *Meteor* for perfect support and cooperation. We acknowledge the valuable ships' time offered by the chief scientists Volker Brüchert/ Bremen and Kay-Christian Emeis/Hamburg for the ROV cruises from onboard *RV Meteor* and *RV Alexander von Humboldt.* Two anonymous reviewers considerably improved the quality of the manuscript, and M. Krings refined our abilities to write in English. We also thank J. Bernhard, P. DeDeckker, K.-C. Emeis, D.K. Kristensen, J. Lipps, and C. Schröder-Adams for discussions about the DMB, virgulinellids, and suggestions on earlier drafts of the manuscript. The Bavarian State Collection for Palaeontology and Geology granted access to the holotype of *Loxostomum chalkophilum* Hagn (BSPG Prot. 1952-8). Funding by the Deutsche Forschungsgemeinschaft (Al 331/7 and Al 331/14) is gratefully acknowledged.

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APPENDIX

The video system of a ROV records the decreasing visibility near the sediment surface at station 57181 during cruise M57 of *RV Meteor.* Whitish microbial clusters are visible all over the water column, and the sea bottom at 62 m water depth is densely covered by mats of sulfur bacteria. The blooms of floating sulfur bacteria described by Lavik et al. (2009) may contribute to the severely reduced visibility in the anoxic bottom water. See palaeo-electronica.org/2010_2/188 for movie.