Species diversity of Miocene deep-sea benthic foraminifera and watermass stratification in the northeastern Indian Ocean

Anil K. Gupta¹, Sudheer Joseph², and Ellen Thomas^{3,4}

¹Department of Geology and Geophysics, Indian Institute of Technology, Kharagpur - 721 302, India, e-mail: anilg@gg.iitkgp.ernet.in

²Chemical Oceanography Division, National Institute of Oceanography, Dona Paula, Goa – 403 004, India

³Department of Earth & Environmental Sciences, Wesleyan University, 265 Church Street, Middletown CT 06459-0139 e-mail: ethomas@wesleyan.edu

⁴Department of Geology and Geophysics, Yale University, P.O. Box 208109, New Haven, CT 06520-8109 USA

ABSTRACT: The Miocene species diversity of deep-sea benthic foraminifera (expressed as α index, information function H[S], and Sanders' rarefaction values) at DSDP Sites 214 (1671 m) and 216 (2262 m), and ODP Site 758 (2923 m) in the northeastern Indian Ocean was overall higher than the modern diversity, but with major variations. The α and H(S) values were relatively low at the shallowest Site 214, medium at intermediate-depth Site 216, and highest at the deepest Site 758. Across the Oligocene/Miocene boundary, when the Antarctic Circumpolar Current (ACC) might have originated, diversity dropped at Sites 214 and 758. All diversity parameters decreased for a short time at about 17 Ma at all sites (more prominent at Site 216), at which time production of Northern Component Water (NCW) may have peaked. At shallow Site 214 and deep Site 758, the α and Sanders' values show an abrupt decrease at about 12.5 Ma, a time of major expansion of the East Antarctic Ice Sheet (EAIS) and increased production of Antarctic Bottom Water (AABW), Northern Component Water (NCW) and Indonesian Intermediate Water (IIW). These decreases in diversity are not seen in the records of Site 216. In the latest Miocene (about 7.15 to 6.5 Ma) the α and Sanders' values at Sites 214 and 758 decreased further, during the Chron-6 global carbon shift and the Indo-Pacific biogenic bloom in productivity. The H(S) values also show a decrease in this interval at Sites 214 and 758. We suggest that deep-ocean circulation played a significant role in shaping the long-term diversity trends in the northeastern Indian Ocean. Productivity, which might in turn have been influenced by the circulation changes, dominantly affected the diversity in the latest Miocene.

INTRODUCTION

The climate of the Earth has witnessed important changes during the Neogene, including the waning and waxing of the polar ice sheets, changes in ocean circulation, and tectonism, such as mountain building and the opening and closing of oceanic gateways (e.g., Kennett 1977; Ruddiman and Kutzbach 1989; Kennett and Barker 1990; Gupta and Srinivasan 1992a; Wright and Miller 1996). The circulation and chemistry of the deep ocean basins are closely linked to the Earth's climate, and we must understand the interactions between the cryosphere, hydrosphere, atmosphere, and biosphere in order to understand the past, and predict possible future climate changes.

Understanding the climatic and biotic developments of the Miocene is of major importance for understanding these interactions. By the early Miocene (~22 Ma) the ocean basins had essentially assumed their modern shapes, and the Antarctic continent had formed (Ramstein et al. 1997; Cande et al. 2000). The East Antarctic Ice Sheet (EAIS) had become established in the earliest Oligocene (e.g., Ehrmann and Mackensen 1992; Diester-Haass and Zahn 1996; Zachos et al. 1999), when steep thermal gradients between polar and tropical regions were established (e.g., Zachos et al. 1993, 1994, 2001). Surface water productivity increased in the latest Eocene into the Oligocene (e.g., Diester-Haass and Zahn 1996), and the seasonality of ocean surface productivity also increased (Thomas and Gooday 1996).

The Earth cooled from the end of the early Eocene (Zachos et al. 2001), but long-term cooling was interrupted for a period of

warming in the early Miocene. Locally, intermediate ocean waters may have held little oxygen in the early Miocene warm period (Thomas 1986a, 1986b; Smart and Murray 1995). Causes of this warming are not clear, especially because more and more evidence suggests that the Miocene atmospheric CO₂-levels were not higher than preindustrial levels (Flower 1999; Pagani et al. 1999a, 1999b). Cooling resumed in the middle Miocene, when Tethyan outflow into the Indian and Southern Oceans probably ended (Woodruff and Savin 1989). At this time, the rate of production of Northern Component Water (the Miocene equivalent of the modern North Atlantic Deep Water) may have increased substantially (Wright and Miller 1996). Global benthic foraminiferal faunas underwent major restructuring, including changes in diversity (e.g., Douglas and Woodruff 1981; Thomas 1985, 1986a, 1986b).

Many hypotheses have been proposed to explain global biodiversity patterns, including the stability-time hypothesis (Fischer 1960; Hessler and Sanders 1967; Sanders 1968), the spatial heterogeneity hypothesis (Simpson 1964), competition (Dobzhansky 1950; Williams 1964), predation or cropping (Paine 1966, Pianka 1966), productivity (Connell and Orias 1964), and dynamic equilibrium (Huston 1979). The relative importance of individual ecological and biologic factors influencing species diversity remains largely unresolved, however, and causes and effects of biodiversity are actively debated (e.g., Gaston 2000). The deep-sea diversity changed considerably during the major climatic changes of the Cenozoic (e.g., Thomas and Gooday 1996), and studies of benthic foraminifera can thus help to narrow the debate regarding causes of high

TABLE 1 Data from the northeastern Indian Ocean Sites.

TABLE	l	

-		
Con	tinue	a.
0011		

Site	Sub-bottom depth (mbsf)	Age (Ma)	Alpha Index	H(S)	Number of Species (S)	Sanders' values rarefied to 100	Number of specimens
214	70.44	4.89 4.97 5.20	11	2.7 2.7 3.2	32	31 · 27	206
	71.94 76.94	4.97	9	2.7	30	27	240 336
_	76.94	5.20	11	3.2	39	34	336
	78.44 79.94	5.25 5.30	10	2.7	34 30	28 27	256
	81.44	5.30	13	3.1	41	34	236
	82.94	5.38	9	2.8	31	28	278
_	84.30	5.41	6	2.2	22	20	253
	84.30 85.92	5.44	10	2.2 2.8	43	30	724
	86.44	5.45	12	2.8 2.5 2.5	45	32	554
	87.42 88.92	5.47 5.50	8	2.5	32	25	513
	88.92	5.50	6	2.5	27	23	469
	89.44	5.51	6 7	2.3 2.2	27 27	21 22	607 408
	90.42 90.94	5.53	6	2.2	25	22	408
	91.92	5.56	9	2.5	37	30	475
	92.44	5.57	7	2.5 2.2 2.2 2.2	29	26	424
	93.44	5.59	9	2.2	40	26 25	896
	93.94	5.60	5 8	1.7	26	17	656
	95.42	5.63	8	2.3	36	23 21	904
	95.94	5.65	7	2.2	30	21	549
	96.92	5.67	8	2.6 2.8	35	25 26	553 438
	97.44 98.42	5.68 5.71	8	2.8	32 35	20	438
	99.08	5.73	10	2.7	40	28	631
	99.92	5.76	8	2.8 2.4	33	24	565
	100.44	5.77	7	2.6	30	25 20	517
	101.42	5.80	7	2.6 2.0 2.7 2.6	32	20	645
	101.94	5.82	10	2.7	37	28	381
	102.92	5.85	7	2.6	30	24	594
	103.44	5.87	8	2.7 2.9	28	26	296 396
	105.44 106.46	5.95 5.99	10 8	2.9	38 28	32 24	292
	106.46	6.01	8	2.5	32	24	405
	107.96	6.05	9	2.8	30	29	240
	108.46	6.07	9 6	2.4	23	29 22	239
	109.32	6.11	8	2.8	23	23	150
	109.83	6.14	8	2.8	28	25	300
	114.96	6.40	10	3.1	34	32	289
	115.96	6.46	8	2.7	27	27	228
	116.46	6.49	11	3.2	43	36	581
	117.46	6.55	10 10	3.0	42	35 31	580 392
	117.96	6.58 6.64	10	3.1	36	31	452
	118.96	6.68	10	3.3	38	34	417
	119.40	6.74	13	3.1	39	34	270
	120.40	6.78	12	3.0	37	33	270
	121.96	6.85	13	3.1	40	34	307
	122.46	6.89	10	2.7	29	29	183
	123.96	7.00	13	3.4	46	38	402

biodiversity, which typifies the deep ocean biota (e.g., Douglas and Woodruff 1981).

The deep-sea environment has been said to be more stable than the surface environments through geological time (e.g., Douglas and Woodruff 1981; Thiel et al. 1988; Gooday and Lambshead 1989). Recent studies, however, indicate that the deep-sea environment is dynamic and subject to short-term changes in diversity and standing stocks of deep-sea fauna (e.g. Huston 1979; Gooday and Lambshead 1989; Gupta 1990; Thomas 1990; Gupta and Srinivasan 1992a; Smith 1994; Smart and Murray 1995; Smart 1998). Documentation of deep-sea benthic foraminiferal faunas thus is useful within the debate of the stability-time hypothesis. This hypothesis is prominent, but widely discussed among marine scientists (see e.g., Smith 1994; McCann 2000, Stuart et al., in press, Rex et al., in press). The hypothesis asserts that high diversity in the deep sea and in the tropics results from long-term (geological) climatic stability. Under such physically stable conditions biological interactions may stabilize, resulting in an increase in species diversity through niche partitioning. Interruptions of the long-term stability are then predicted to lead to decreased diversity. As an example, Gupta and Srinivasan (1992a) related diversity changes in the northeastern Indian Ocean to variations in Antarctic Bottom Water (AABW) circulation in response to changes in Antarctic ice volume.

Site	Sub-bottom depth (mbsf)	Age (Ma)	Alpha Index	H(S)	Number of Species (S)	Sanders' values rarefied to 100	Number of specimens
	125.36	7.12	13	3.2	43	36	323
	125.96	7.17	10	2.9	37	29	448
	126.86	7.25 7.30	11 10	2.9	39	32 30	319
	127.40	7.39	10	2.9	37	29	465
	128.96	7.45	8	2.4	35	27	559
	129.86	7.54	10	3.0	34	29	306
	130.37	7.59	10	3.1	38	31	401
	131.36	7.69	8	3.0	28	25	308
	133.27 134.91	7.91	9	3.1 2.9	31 45	29 33	248 687
	134.91	8.10 8.17	9	2.9	34	29	397
	136.46	8.30	9	2.6	33	25	405
	136.96	8.37	7	2.5	29	23	463
	137.96	8.50 8.57 8.72	9	2.8	34	29	423
	138.46	8.57	9	1.6	46	27	1491
	139.48	8.72	10	2.9 3.3	47	31	1016
	139.96	8.79 8.93	11	3.3	38 33	33	373 226
	140.90	9.02	9	2.9	28	28	199
	143.46	9.31	9	3.0	32	29	279
	143.96	9.39	9	3.0	26	26	151
	144.96	9.55	7	2.7	20	20	116
	145.46	9.62	9	2.8	32	28	298
	146.46	9.78	11	3.0	36	31	293
	146.96	9.86 10.01	8	3.0 3.0	28 32	27	225 225
	147.96	10.01	10	3.0	33	31	223
	149.46	10.24	12	3.2	34	34	184
	149.96	10.32	12	3.4	42	37	385
	150.96	10.47	12	3.1	44	34	479
	151.46	10.54	11	3.2	36	32	265
	152.96	10.76 10.83	12	3.3	33 48	33	170
_	154.00	10.85	12	3.2	46	35	623
	154.46	10.96	12	3.2	44	35	507
	154.96	11.03	12	3.2	41	34	394
	155.96	11.16	9	3.0	30	29	233
	156.50	11.23	10	3.0	24	24	104
	157.46	11.35	12	3.2 3.1	45	36 34	445 403
	158.96	11.41	12	3.2	37	34	239
	159.46	11.52	14	3.5	45	41	365
	160.44	11.68	12	3.2	36	34	250
	161.02	11.74	14	3.4	44	37	305
	162.54	11.89	15	3.4	43	39	261
	162.97	11.93	13	3.4	46	37 38	445
	164.40	12.06	10	3.3	30	38	198
	165.24	12.00	10	2.9	26	26	138
	165.97	12.17	10	3.1	34	30	297
	166.96	12.24	9	2.9	24	24	119
	167.44	12.27	10	3.1	38	32	477
	168.46	12.33	9	3.0 2.9	28	28	179 413
	168.96	12.36 12.50	11	3.0	40 39	34 32	413
	172.39	12.50	10	3.2	40	32	422
	173.96	12.54	15	3.2	40	36	218
	174.96	12.56	13	3.4	31	29	134
	175.52	12.57	17	3.3	43	36	202
	176.46	12.60	18	3.0	35	34	106
	176.96	12.62	15	3.0	36	32	145
	177.96	12.67 12.70	13	3.0 3.2	38 48	31 36	214 308
	1/8.46	12.70	16	3.2	36	30	135
	181.96	13.04	17	3.2	45	35	231

Cronin and Raymo (1997) demonstrated that Pliocene ostracode diversity patterns dynamically responded to climatically induced change in ocean circulation, temperature, and food availability. They suggested that the deep sea is a temporally dynamic environment marked by orbitally induced climatic changes which affect the deep-sea benthic diversity on 103-104 years time scales; such variability probably existed also in the Miocene (Zachos et al. 1997). Cronin and Raymo (1997) also argued that low diversity values correspond to glacial intervals, whereas diversity was higher during interglacials, when the food supply was greater. This is in contrast with the situation in benthic foraminiferal faunas in the North Atlantic, which were more diverse during the last glacial than they are at present (Thomas et al. 1995). In contrast, Valentine (1971) proposed that abundant and/or unstable food supply results in low diversity values whereas scarce and/or stable food resources lead to increased diversity, in agreement with Huston (1979) and Phleger and Soutar (1973). Thomas and Gooday (1996) docu-

TABLE 1 Continued.

Sanders' values rarefied to 100 Sub-bottom depth (mbsf) Alpha Index Number of Species (S) Number of specimens Age (Ma) H(S) Site 182.96 183.46 184.36 18 19 3.1 3.4 122 13.18 34 13.25 13.39 13.49 37 16 19 3.8 348 184.96 185.96 202 13.66 16 3.2 422 187.46 13.95 189 188.96 14.25 141 14.35 15.00 15.12 15.22 89.40 244 217 192.40 8 193.4 18 43 185 193.96 195.46 195.96 15.33 15.67 15.78 18 85 241 3.1 3.0 109 196.9 197.4 15.99 13 13 108 16.10 2.9 261 93 200.96 202.33 200.4 16.78 18 16.92 2.9 2.8 3.0 112 223 282 17.87 203.92 204.96 205.46 206.38 18.12 12 18.80 19.21 20.06 3.0 206.9 20.61 17 138 307 207.9 21.45 13 21.43 21.80 22.64 208.46 210.46 16 161 16 22.87 22.95 23.07 23.12 211.46 211.96 212.96 213.46 16 10 14 3.0 195 325 180 127 215 291 13 214.46 214.96 215.96 23.20 23.24 23.31 863 378 439 216.52 23.35 23.41 11 14 49 47 23.44 217.96 219.46 16 193 219.96 23.57 23.63 28 23.66 222.46 10 23.74 39 35 223.9 23.8 23.83 224.46 2.6 23.89 23.94 337 313 183 26.0 2.8 226.96 24.00 227.40 229.40 230.40 24.03 24.16 24.22 425 218 2.9 3.0 24.25 2.9 7.10 7.43 7.58 216A 102.38 138 3.5 2.0 103.38 16 104.88 7.82 106.38 8.30 8.49 16 3.1 48107.90 8.89 9.07 269 258 42 40 47 9.43 109.38 109.88 9.61 46 286

mented that lower species richness occurs at seasonally fluctuating food supply, as also argued for the Somali Basin by Gupta (1997).

Observations on spatial variations of deep-sea species diversity are few, and the causes of species diversity patterns in various environments remain elusive (e.g., Stuart et al., in press). Two major spatial trends have been observed: (1) increasing species diversity with decreasing latitude (e.g. Fischer 1960; Valentine 1966; Thomas and Gooday 1996; Rex et al. 1997, in press; Culver and Buzas 2000), and (2) a general increase in species diversity with increasing water depth in the marine environment (Gibson 1966; Hessler and Sanders 1967; Buzas and Gibson 1969), possibly peaking at middle bathyal depths (e.g., Schmiedl 1995). In the Indian Ocean between about 1600 and 4500 m depth, Gupta (1990) observed that species diversity increases (with fluctuations) up to about 3000m, then declines at greater depths owing to the influence of AABW circulation

TABLE 1	
Continued	

Site	Sub-bottom depth (mbsf)	Age (Ma)	Alpha Index	H(S)	Number of Species (S)	Sanders' values rarefied to 100	Number of specimens
s			A				
	111.38	10.11	15 7	2.9 2.8	42	32	240
	112.88	10.27	13	2.8	32 37	32 30	627 233
	112.88	10.67	15	2.7	52	34	504
	114.38	10.90	15	3.1	36	31	146
	114.88 115.88	11.00	21	3.4	51	41	220
	115.88	11.16	10	2.8 2.9	46	31 30	823 756
	117.38	11.35	12	3.0	47	35	535
	117.88	11.39	15	3.3	49	39	409
	118.88	11.47	13	3.4	54	42	780
	119.38 120.88	11.50	15 17	3.4 3.3	55 77	40 40	598
	120.88	11.58	17	3.5	62	36	1470
	122.38	11.64	10	3.1	46	33	968
	122.88	11.66	12	3.2	53	35	872
	123.88 124.45	11.70	13	3.2	56	39	848
	124.45	11.73	14	3.3	58 46	38 36	983 524
	125.92	11.81	13	3.3	52	37	841
	126.88	11.88	13	3.1	53	36	751
	127.38	11.93	12	2.1	48	33	708
	128.38 128.88	12.03	10	2.8	44 49	33 34	778
	130.45	12.10 12.35	13	3.4	59	39	1088
	130.95	12.45	13	3.4	58	38	1101
	131.95	12.65	13	3.4	54	38	735
	132.45	12.76	11 13	2.1 3.3	51	34 37	1017 706
	133.88	13.09	10	3.3	44	35	898
	134.92	13.34	10	3.1	39	34	534
	135.54 136.52	13.49	10	3.2	42	36	567
	130.52	13.83	10	3.5 3.2	37 52	36	406 680
	138.00	14.05	12	3.3	49	35	712
	138.52	14.16	13	3.2	41	34	327
	140.03 140.52	14.45	12	3.3	41	36	384
	140.52	14.53	12	3.3 3.3	40	36 37	363 429
	142.02	14.72	17	3.4	50	40	310
	142.89	14.80	14	3.3	52	39	540
	143.52 144.32	14.84	13	3.3	50	39	590
	144.52	14.87 14.89	14	3.4	58 47	37 37	825 751
	146.02	14.93	12	3.3	49	37	646
	146.52	14.96	10	3.3	45	36	733
	147.52 148.02	15.04	10	3.1 3.2	39 53	32 35	523 687
	149.54	15.39	17	3.3	51	35	321
	150.14	15.55	14	3.3	56	37	731
	151.04	15.86	11	3.3	42	35	457
	151.64 152.54	16.10	12	3.2	43 36	36	384
	152.54	16.88	8	2.7	29	24	333 280
	154.04	17.44	14	3.5	49	39	432
	154.64	17.85	9	3.2	39	30	711
	155.47 155.97	18.44 18.80	13	3.1	44 39	36	377
	155.97	20.38	11	3.2 3.0	39	33 30	386
758A	71.25	5.71	10	3.0	34	29	245
	71.88	5.79	13	3.3	46	34	400
	72.76 73.40	5.92	16	3.4	54	39	500
	73.40 74.14	6.01	19	3.3 3.1	56 39	36 30	380 301
	74.14	6.21	12	3.3	51	30	301
	75.64	6.31	13	3.3	57	36	445

and/or dissolution. Smart (1998) also suggested that dissolution causes decreasing diversity values at the deeper Site 710 (3824m) in the western Indian Ocean.

Benthic foraminiferal tests are comparatively resistant to postmortem environmental changes, thus are suitable for species diversity studies among fossil populations. In this paper we present the species diversity record of benthic foraminifera from the Miocene of Deep Sea Drilling Project (DSDP) Sites 214 and 216, and Ocean Drilling Program (ODP) Site 758 in the northeastern Indian Ocean. The sites offer an opportunity to study the influence of long-term climate changes on species diversity at lower bathyal to abyssal depths, because they have been in the equatorial region during the Miocene (e.g., Peirce et al. 1989; Nomura 1995). We examined the temporal relationship between diversity and environmental stability, as expressed in deep-ocean circulation, global ice-volume, productivity and

TABLE 1

Continued.

TABLE 1 Continued.

Site	Sub-bottom depth (mbsf)	Age (Ma)	Alpha Index	H(S)	Number of Species (S)	Sanders' values rarefied to 100	Number of specimens	
	76.42	6.41	16	3.4	49 50	36	321	
	77.14	6.50	16	3.1	50	32	320	
	77.92	6.60	16	3.2 3.3	52 52	34	381 297	
	78.63	6.68 6.77	15	3.4	54	33	297	
	80.31	6.85	17	3.3	53	38	321	
	80.93	6.93	21	3.4	60	38	342	
	81.63	7.00	20	3.4	59	39	578	
	82.42 83.10	7.08	19	3.3	57 54	35	367 346	
	83.10	7.14	17	3.4	50	36	393	
	83.83	7.19	21	3.5	60	39	339	
	84.62	7.26	16	3.2	49	34	334	
	85.42	7.32	16 23	3.5 3.7	52 64	39 45	344 339	
	86.12 86.84	7.37 7.43	17	3.4	50	36	339	
	87.62	7.49	15	3.5 3.7	56	40	549	
	88.34	7.54	25	3.7	64	44	302	
	89.13	7.61	16	3.3	48	34	321	
	89.83	7.66	18	3.4 3.5	56 60	39 42	364 323	
	90.62 91.33	7.72	21 21	3.5	59	41	323	
	92.12	7.83	18	3.5	59	40	418	
	92.8	7.87	22	3.5	63	42	343	
	92.85	7.89	21	3.4	60 50	38	351 297	
	93.54 94.32	7.94 7.99	17 24	3.3 3.6	63	43	317	
	94.32	8.04	18	3.4	56	38	339	
	95.83	8.10	20	3.5	58	40	328	
	96.53	8.15	18	3.4	53	39	298	
	97.32	8.21 8.26	19	3.5 3.6	56 58	33 46	306 310	
	98.03 98.83	8.26	21 23	3.6	62	40	389	
	99.54	8.36	22	3.5	59	40	313	
	100.32	8.41	21 20	3.6	58	41	329	
	101.04	8.46	20	3.4	58 57	36	345	
	101.83	8.51 8.55	21 22	3.6 3.6	61	42 43	298 318	
	102.40	8.56	17	3.5	52	39	314	
	102.44 103.13	8.60	19	3.5	57	39	335	
	103.92	8.65	20	3.5	56	42	301	
	104.63 105.43	8.69 8.74	18 21	3.5	54 57	39 39	328 301	
	105.45	8.74	21	3.6	60	44	315	
	106.92	8.83	19	3.5	58	39	376	
	107.64	8.87	17	3.4	51	41	314	
	108.42	8.91	16	3.3	48	36 36	316 381	
	109.13 109.92	8.96 9.00	18 23	3.4	60	42	297	
	110.63	9.04	19	3.5	54	39	298	
	111.42	9.08	21	3.5	61	41	364	
	112.10 112.15	9.10	22	3.6	64	42	376	
	112.15	9.12 9.16	19	3.3	58 50	36	400 367	
	112.83 113.62	9.10	20	3.5	57	41	319	
	115.82 114.33 115.12 115.83 116.62 117.33	9.24	16	3.4	50	38	354	
	115.12	9.28	18	3.4	56	40	332	
	115.83	9.32	17	3.4	52 54	40 40	309 310	
	110.02	9.36 9.38	19	3.5	50	36	310	
	118.12	9.55	10	3.6	65	41	513	
	118.91	9.74	17	3.4	52	40	311	
	119.62	9.91	20	3.5	61	41	394	
	120.33	10.09	17	3.4	56	38 42	403	
	121.12 121.70	10.31	16	3.5 3.4	47	37	290	

dissolution. These may be the most important factors shaping the faunal diversity in the Indian Ocean.

LOCATION

DSDP Sites 214 (water depth 1671m, 11°20.21'S and 88°43.08'E), 216 (water depth 2262m, 01°27.72'N and 90°12.48'E), and ODP Site 758 (water depth 2923m, 5°23.049' N and 90°21.693'E) are located on the Ninetyeast Ridge (text-fig. 1). At present, the drift current of the southwest (SW) monsoon induces intense upwelling above these sites leading to seasonally high surface productivity.

Deeper water circulation patterns in the Indian Ocean are not well known. AABW is present below 3800 m (Kolla et al. 1976; Gupta and Srinivasan 1992b). North Atlantic Deep Water or Northern Component Water (NADW or NCW), flowing North into the Indian Ocean from the Antarctic Current component of the Global Ocean Conveyor (Broecker 1995) has been said to

Site	Sub-bottom depth (mbsf)	Age (Ma)	Alpha Index	H(S)	Number of Species (S)	Sanders' values rarefied to 100	Number of specimens
	121.75	10,48	17	3.5	51	40	319
	122.43 123.22	10.48 10.68	20	3.5 3.5 3.5 3.5	55	41	304
	123.22	10.92	16	3.5	48	38	320
	124.01	11.16	19	3.5	58	40	373
	124.72 125.44	11.39	21 18	3.4	59 55	39 37	313 314
	125.44	11.82	16	3.4	48	38	324
	127.01	12.15	22	3.5	57	42	282
	127.72	12.40	18	3.4 3.3	53	35	353
	128.41	12.49	18	3.3	47	36	255
	131.48	13.75	24	3.6 3.5	57 52	43 40	252 310
	132.13 132.92	13.99 14.28	16	3.5	57	40	270
	132.92	14.28	20	3.5	48	38	203
	134.42	14.83	21	3.5 3.3	38	37	106
	135.13	15.09	22	3.5	54	42	256
	135.91	15.38	21	3.4	39	38	108
	136.84 141.02	15.51 17.15	22	3.5 3.4	56 54	42 40	260 301
	141.02	17.15	16	3.3	45	35	255
	142.52	17.62	20	3.6	53	42	242
	143.31	17.87	21	3.7	64	45	390
	144.02	18.08	19	3.4	48	39	239
	144.78	18.29 18.49	18	3.4	43 48	40 42	189
	145.52 146.24	18.49	25	3.2	38	34	150
	150.74	19.74	18	3.6	60	44	136
	151.44	19.88	22	3.4	50	37	308
	152.22	20.04	18	3.5 3.5	42	39	288
	153.01	20.20 20.34	22	3.5	53 45	39 40	121 312
	153.71 154.42	20.34	16	3.5 3.2	37	33	153
	155.21	20.62	16	3.3	36	33	126
	155.21 155.90	20.74	16	3.3	39	35	174
	156.02	20.76	20	3.3	40	36	133
	161.13	21.49	18	3.3 3.4	44 47	38 38	144 223
	161.45 161.91	21.59 21.70	21	3.4	47	40	180
<u> </u>	161.91 162.63 163.41 164.10 164.91 165.63	21.81	22	3.5 3.5	57	41	272
	163.41	21.81 21.92 22.01 22.12	20	3.3 3.3	41	36	139
	164.10	22.01	18	3.3	41	35	163
	164.91	22.12	17	3.1 3.2	40	32	167
	165.63	22.21 22.28	18	3.2	37	35	139
	170.01	22.73	20	3.3	48	38	202
	166.20 170.01 170.72	22.80	22	3.3	37	36	106
	171.51	22.89	25	3.5	47	42	151
	172.39 173.01	22.98 23.04	22	3.4	40	40	102 103
	173.01	23.04	22 20	3.4	39	39	103
	174.51	23.19	25	3.5	48	41	151
	174.51 175.23	23.25	24	3.5	46	44	112
	176.01	23.32	30	3.6	52	47	122
	176.46	23.36	19	3.2	37	34	124
	179.72 180.40	23.64 23.69	16	3.3 3.2	40	34 35	185
	180.40	23.76	21	3.4	41	39	180
	182.01	23.82	15	3.1	43	37	231
	182.71	23.87	21	3.4	49	41	202
	183.41	23.92	16	3.3	46	37	247
	183.99	23.96	17	3.2 3.2	55 39	37	420
	189.32	24.33 24.37	18	3.2	39	34	153
	190.00	24.37	10	2.1			125

occur at intermediate depths, as argued by Tchernia (1980) and Corliss (1983). In contrast, Warren (1982), GEOSECS (1983) profiles and Johnson (1985) suggest that the water between 1200 and 3800m north of 30°S is of north Indian origin. More recently, You (1998) identified three sources of intermediate waters in the Indian Ocean: the Red Sea-Persian Gulf Intermediate Water, the Indonesian Intermediate Water (IIW), and Antarctic Intermediate Water (AAIW). The role of AAIW is ambiguous north of the hydrochemical front at 10°S (Tchernia 1980; You 1998). You (1998) suggested that the Indonesian Intermediate Water (IIW) contributes 50-60% of its water to the northeastern Indian Ocean including the Bay of Bengal.

MATERIALS AND METHODS

Miocene samples of 10cc volume at an interval of ~75-150cm from Site 758 (136 from 24.37-5.71 Ma), Site 214 (172 from 24.25-4.89 Ma), and Site 216 (70 from 20.38-7.10 Ma) have been examined. The samples were soaked in water with half a





spoon of baking soda for 8-12 hours. A few samples with high clay content were processed with hydrogen peroxide (5%). Samples were washed over a 63µm sieve and oven-dried at about 60°C. The >125µm-size fraction was used for benthic foraminiferal analysis at Site 758, and the >149µm-size fraction at Sites 214 and 216. We could not analyze the >125µm-size fraction from Sites 214 and 216 as the samples were pre-washed. The number of specimens analyzed in each sample varies from <100 to >1000. The specimens were counted, identified, and their percentages were calculated. Numerical ages are based on planktic foraminiferal (Vincent 1977; Srinivasan and Gupta 1990 for Sites 214 and 216) and calcareous nannofossil (Peirce et al. 1989 for Site 758) datum levels, and are after Berggren et al. (1995). Sites 214, 216, and 758 have well-preserved Neogene microfaunas and little to no reworking. In the Miocene, water depths at the sites were about 100m shallower than at present (Sclater et al. 1977; Peirce et al. 1989). In the early Miocene the sites were located about 5°S of their present position, in the latest Miocene about 2°S of their present location (Nomura 1995). At Sites 214 and 758A the sediment accumulation was low from 23 to 12.5 Ma and the time resolution therefore is low (text-figs. 2, 3 and 6). At Site 216A, however, the record is available only from 20.0 to 7.0 Ma with more or less uniform sample density (text-figs. 2, 3 and 6).

We describe species diversity in terms of the α index, Sanders' rarefaction number, and information function, H(S) for Site 758 (table1; text-figs. 2 and 3). The α index is a measure of species richness and was first described by Fisher et al. (1943). This value is commonly used in foraminiferal studies (e.g., Murray 1991). We calculated α values following Williams (1964, p. 307-311). Sanders' values are commonly used in studies of deep-sea faunas (e.g., Rex et al. 1997). We calculated these values by rarefying against 100 individuals at all the sites (Sanders 1968) (table 1; text-fig. 6). The values of H(S) were calculated using the Shannon-Wiener Diversity Index (Shannon and Wiener 1949) as follows:

$$H(S) = -\sum_{i=1}^{s} p_i \ln p_i$$

Where S is the number of species in a given sample and p_i is the proportion of the *ith* species in the sample. H(S) takes into account both number of species and the abundance of individuals



TEXT-FIGURE 2 Values of index plotted against numerical ages at northeastern Indian Ocean Sites. Numerical ages are after (Berggren et al. 1995).

in each sample, thus H(S) is a measure of both species richness and evenness. The α , H(S), and Sanders' values have been correlated using linear correlation (text-figs. 7 and 8).

Smart and Murray (1995) found a good correlation between α and H(S) indices indicating that either is a satisfactory measure of species diversity. Alve and Murray (1994), however, suggested that α is a better discriminator in modern environments. We calculated the α values and replotted the H(S) values from Sites 214 and 216 (table 1) based on the >149µm size fraction (Gupta and Srinivasan 1992a), and from the Somali Basin based on the >63µm size fraction (Smart 1998). All data were plotted on the Berggren et al. (1995) time scale for comparison with our values from the $>125\mu m$ size fraction from Site 758A, in order to understand the diversity changes at various depths in the eastern and western sectors of the Indian Ocean. Since the size difference between fractions from Sites 214, 216 (149µm) and 758 (125µm) is very small, we presume that the comparison is realistic. However, our comparison with the Somali Basin sites may be less reliable because Smart (1998) used the >63µm size fraction.

RESULTS AND DISCUSSION

Our data show significant fluctuations in benthic foraminiferal diversity over the Miocene, but the changes differ by depth. Comparison of our data with published work shows that changes also differ by ocean basin. The α , H(S) and Sanders'

values from Sites 214, 216, and 758 are given in table 1, and plotted against numerical ages in text-figures 2, 3, and 6. The α and Sanders' values show more changes than H(S). In general, α , H(S) and Sanders' values are lower at shallower Site 214, medium at the intermediate-depth Site 216, and higher at the deeper Site 758 (text-figs. 2, 3 and 6). This may indicate that environmental disturbances were more severe at intermediate depths than at abyssal depths, and that waters in the northeastern Indian Ocean became more stratified during the Miocene. Such increased stratification might be expected during cooling of the deeper waters while tropical surface waters did not change much in temperature.

The α , H(S), and Sanders' values are low and fluctuate across the Oligocene-Miocene boundary at Sites 214 and 758 (textfigs. 2, 3 and 6). From 23 to 12.5 Ma both α and H(S) values remained high and fluctuated less (text-figs. 2 and 3), suggesting more stable conditions. The food supply was low and deep-sea oxygenation was moderate to high in the northeastern Indian Ocean during this time (Srinivasan and Gupta 1990; Joseph 1999). This interval of relative tranquility might have been interrupted at about 17 Ma by increased production of NCW (Wright and Miller 1996), which strengthened thermal gradients in the water column (Kennett 1986). Although there are not enough data points from this interval at the study sites, a short-lived decrease in all diversity parameters is visible. At this time, deep-sea benthic foraminiferal faunas in the Pacific Ocean also decreased in diversity (Thomas and Vincent 1987).



TEXT-FIGURE 3 Values of H(S) plotted against numerical ages at northeastern Indian Ocean Sites.

At 12.5 Ma the α values show a major and abrupt drop whereas the H(S) values do not show a significant decrease at Site 214 (text-figs. 2 and 3). The Sanders' values also show a major but stepwise decrease at Site 214 during this time (text-fig. 6). The correlation between α and H(S) is high at Site 214 (text-fig. 7), weak at Site 758 (text-fig. 8), and very weak at Site 216 (textfig. 7). This contrasts with the observations by Smart and Murray (1995), indicating that the two functions may behave differently in different environmental setups. At Site 758 there is no shift at 12.5 Ma towards lower values in the parameters (text-figs. 2, 3 and 6), probably due to the coarse sampling interval.

From 12.5 Ma onwards all three parameters show a continuous decrease at Site 214 and a moderate decrease at Site 758. At Site 216, however, the α values show a continuous increase, with fluctuations through the Miocene, and values show no correlation with those at the other sites. This difference in diversity trends at various depths in the northeastern Indian Ocean indicates that different water masses may have been present at the different depths of these sites, perhaps due to strengthened water mass stratification. Smart (1998) also did not see coherence in α and H(S) values between various sites in the Somali Basin (western Indian Ocean). At 12.5 Ma, α values decreased at bathyal to upper abyssal sites, although the data points are at low time resolution (text-figs. 4 and 5). At the deeper Site 710 (water depth 3824m) the shift appears to occur at 12.0 Ma, possibly as a result of the wide sample spacing or a short unconformity.

The decrease in diversity values coincided with the middle Miocene positive oxygen isotope shift resulting from the expansion of the EAIS (e.g. Wright et al. 1992; Savin et al. 1981; Kennett 1986; Vincent et al. 1985), which was also observed at Site 758 (Joseph 1999; Gupta et al. 2000). At this time, increased production of NCW resumed in different ocean basins (Woodruff and Savin 1985; Nomura 1991; Wright and Miller 1996), and the thermal gradients in the water column increased (Kennett 1986). The supply of Tethyan outflow water into the Indian Ocean terminated (Woodruff and Savin 1989; Ramsay et al. 1998). The Indonesian Seaway may have closed about this time as well (ODP website), and this closure may have resulted in increased production of Indonesian Intermediate Water (IIW), influencing the intermediate waters in the northeastern Indian Ocean. In addition, a five-fold increase in terrigenous flux to the northern Indian Ocean started at approximately 12.5 Ma, possibly as a result of rapid uplift of the Himalayas (Rea 1992). Benthic foraminiferal faunas worldwide show major changes in the late middle Miocene at about12.5 Ma in the time scale of Berggren et al. (1995), as documented by many authors (e.g., Douglas and Woodruff 1981; Woodruff 1985; Thomas 1985, 1986a, b, 1992). At this time, the Cibicides wuellerstorfi-Pyrgo murrhina assemblage at Sites 758 and 754 (Nomura et al. 1992; Joseph 1999) occurred in the Atlantic, Indian and at least some parts of the Pacific Ocean (Woodruff 1985; Miller et al. 1987; Nomura 1991), although not in the abyssal eastern equatorial Pacific (Thomas 1985). The coeval increase in relative abundance of Nuttallides umbonifera at Indian Ocean Sites 237 and



TEXT-FIGURE 4 Values of index at Somali Basin Sites (from Smart 1998) replotted against time scale of Berggren et al. (1995). The values have been plotted for comparison with those of the present study.

710 at about 12.5 Ma indicates a change in the Indian Ocean deep circulation at 2000 to 4000m water depths (Smart 1998).

What was the cause for the major and abrupt decrease in diversity parameters at 12.5 Ma? The fact that species diversity decreased at 12.5 Ma, during the increase of Antarctic ice volume, deep-sea cooling, increased thermal gradients, and increased production of NCW, AABW, and IIW, suggests that changes in deep ocean circulation influenced the species diversity of deep-sea benthic foraminifera in the northeastern Indian Ocean. The increased delivery of terrigenous material from the Himalayas (Rea 1992), however, may have caused increased productivity in the surface waters, and the increased productivity may have affected the diversity patterns, as suggested by an increase in high-productivity benthic faunas at ODP Site 758 (Gupta et al. 2000)

The α , H(S) and Sanders' values decreased further between 7.15 and 6.5 Ma at Sites 214 and 758 (text-figs. 2, 3 and 6); at Site 216 there is no record from this interval. The lowest α and H(S) values at Sites 214 and 758 in the uppermost Miocene coincide with the Chron-6 negative Carbon Shift (Vincent et al. 1985), a major expansion of western Antarctic ice volume (Kennett 1977, 1986; Kennett and Barker 1990; Woodruff and Savin 1985), a major regressive phase (Haq et al. 1987), and the occurrence of widespread deep-sea hiatuses (Keller et al. 1987). The surface productivity increased during the "Indo-Pacific biogenic bloom", and oxygen minimum zones (OMZs) expanded over large parts of the Indian Ocean (Berger and Stax 1994; Farrell et al. 1995; Pisias et al. 1995; Filipelli 1997). This was also a period of intense monsoon circulation, widespread upwelling, and increased flux of Himalayan sediment to the northern Indian Ocean (Kroon et al. 1991; Rea 1992; Gupta et al. 2000).

The co-occurrence of abrupt changes in diversity parameters and enhanced production of intermediate or deep waters suggests that the change in deep ocean circulation significantly influenced the diversity of deep-sea benthic foraminifera in the early and middle Miocene Indian Ocean. In the late Miocene, however, changes in productivity became more important. Productivity increased in the Indo-Pacific region in the late Miocene (e.g. Berger and Stax 1994; Farrell et al. 1995; Pisias et al. 1995; Dickens and Owen 1999). The high productivity and low deep water temperatures increased the CO2 levels and intensified the corrosiveness of the deep waters, as indicated by the presence of Nuttallides umbonifera across the Oligocene-Miocene boundary and in the uppermost Miocene at deeper Site 758. We agree with Gupta and Srinivasan (1992a) and Smart (1998), who suggested that long-term species diversity changes in the deep sea are linked to the environmental stability as expressed in deep-ocean circulation. Changes in productivity and deep-sea oxygenation, however, influenced the diversity patterns in deep-sea benthic faunas in the northeastern Indian Ocean between 7.15 and 6.5 Ma, in agreement with Thomas and Gooday (1996) and Smart (1998).



TEXT-FIGURE 5

Values of H(S) at Somali Basin Sites (from Smart 1998) replotted against time scale of Berggren et al. (1995). The values have been plotted for comparison with those of the present study.

Average Miocene α and H(S) values in the Somali Basin (Smart 1998) are lower at deeper Site 710 (3824m) and higher at shallower sites in the Somali Basin. In contrast, in the northeastern Indian Ocean the average Miocene diversity values are higher at deeper Site 758 (2923m) than at the shallower sites. This suggests that different water masses were present in the two regions.

CONCLUSIONS

Species diversity of benthic foraminifera (as defined by α , H(S) and Sanders' values) fluctuated significantly during the Miocene at northeastern Indian Ocean ODP Sites 214 (1671m), 216 (2262m), and 758 (2923m). The values of the diversity parameters are relatively low at the shallower Site 214, medium at the intermediate-depth Site 216, and high at the deepest Site 758. Fluctuations are more prominent and more abrupt at the shallower Site 214 than at the other sites. The average Miocene values are higher than those for the modern ocean (Gupta 1990) at all sites, as also observed by Thomas (1986a) for the Pacific and North Atlantic. Diversity decreased across the Oligocene-Miocene boundary (about 23 Ma) at Sites 214 and 758, but not at Site 216. A short-lived decrease in the diversity parameters (more conspicuous at Site 216) occurred at 17.0 Ma, coinciding with the peak production of NCW. Diversity further decreased at Sites 214 and 758 (but not at Site 216) in the middle Miocene (at about 12.5 Ma), a time of global change in deep-sea benthic foraminiferal faunas (e.g., Woodruff 1985; Thomas 1992). At this time, glaciation on the Antarctic continent increased, and

production of Antarctic Bottom Water (AABW), Indonesian Intermediate Water (IIW) and Northern Component Water (NCW) may have intensified (Wright and Miller 1996), leading to the widespread formation of deep-sea uncomformities (Keller et al. 1987). In the latest Miocene (7.15 to 6.50 Ma) diversity further decreased at Sites 214 and 758. During this time the carbon isotopic composition of total dissolved inorganic carbon in the oceans shifted to lower values (Chron-6 Carbon Shift), and surface productivity in the Indo-Pacific region strongly increased (Farrell et al. 1995).

We conclude that the changes in deep-ocean circulation and strengthened water mass stratification in the northeastern Indian Ocean can explain the long-term changes in species diversity at lower bathyal to abyssal depths during the early through middle Miocene, but productivity-related variations may have dominated during the late Miocene.

ACKNOWLEDGMENTS

The samples for the present study were provided by Ocean Drilling Program to AKG (Req. No. 13626). This study was supported by DST, New Delhi (grant no. ESS/CA/A3-16/94). We thank Chris Smart for allowing us to use his published data from the western Indian Ocean. Martin A. Buzas, Bruce H. Corliss and Chris W. Smart are thankfully acknowledged for their helpful and constructive reviews.



TEXT-FIGURE 6

Sanders' values plotted against numerical ages at Sites 214, 216, and 758.

REFERENCES

- ALVE. E. and MURRAY, J. W. 1994. Experiments to determine the origin and palaeoenvironmental significance of agglutinated foraminiferal assemblages. In: George, A.S. et al., Eds., Proceedings of the fourth International Workshop on Agglutinated Foraminifera, Krakòw, Poland, September 12-19, 1993 Grzybowski Foundation Special Publication, 3: 1-11.
- BERGER, W. H. and STAX, R. 1994. Neogene carbonate stratigraphy of Ontong-Java Plateau (Western Equatorial Pacific): three unexpected findings. Terra Nova, 6: 520-534.
- BERGGREN, W. A., KENT, D. V., SWISHER, C. C. and AUBRY, M.-P. 1995. A revised Cenozoic geochronology and Chronostratigraphy. Society for Economic Paleontologists and Mineralogists, Special Publication, 54: 129-212.
- BROECKER, W. S. 1995. Chaotic Climate. Scientific American, 62-68.
- BUZAS, M. A., and GIBSON, T. G. 1969. Species Diversity: Benthic Foraminifera in the western North Atlantic. Science, 163: 72-75.
- CANDE, S. C., STOCK, J. M., MÜLLER, R. D., and ISHIHARA, T., 2000. Cenozoic motion between East and West Antarctica. Nature, 404: 145-150.
- CONNELL, J. H., and ORIAS, E, 1964, The ecological regulation of species diversity. American Naturalist, 98: 399-414.

- CORLISS, B. H. 1983. Distribution of Holocene deep-sea benthonic foraminifera in the southwest Indian Ocean. Deep-Sea Research, 30: 95-117.
- CRONIN, T. M., and RAYMO, M. E. 1997. Orbital forcing of deep-sea benthic species diversity. Nature, 385: 624-627.
- CULVER, S. J., and BUZAS, M. A., 2000. Global latitudinal species diversity gradient in deep-sea benthic foraminifera. Deep-Sea Research I, 47: 259-275.
- DICKENS, G. R. and OWEN, R. M. 1999. The Latest Miocene-Early Pliocene biogenic bloom: a revised Indian Ocean perspective. Marine Geology, 161: 75-91.
- DIESTER-HAASS, L. and ZAHN, R., 1996. Eocene-Oligocene transition in the Southern Ocean: history of water mass circulation and biological productivity. Geology, 24: 163-166.
- DOBZHANSKY, T. 1950. Evolution in the tropics. American Science, 38: 209-221.
- DOUGLAS, R. G. and WOODRUFF, F. 1981. Deep-sea benthic foraminifera. In: Emiliani, C., Ed., The Oceanic Lithospher, The Sea, 7. New York: Wiley, 1233-1327.
- EHRMANN, W. U. and MACKENSEN, A., 1992. Sedimentological evidence for the formation of an east Antarctic ice sheet in Eocene/Oligocene time. Palaeogeography, Palaeoclimatology, Palaeoecology, 93: 85-112.



TEXT-FIGURE 7

Linear Correlation between and H(S) values ate DSDP Site 214 and 216. The correlation is high positive at Site 214 (r=0.61).

- FARRELL, J. W., RAFFI, I., JANECEK, T. R., MURRAY, D. W., LEVITAN, M., DADEY, K. A., EMEIS, K.-C., LYLE, M., FLORES, J.-A. and HOVAN, S. 1995. Late Neogene sedimentation patterns in the eastern Indian Ocean. Proceedings of the Ocean Drilling Program, Scientific Results. College Station, TX: Ocean Drilling Program, 138: 717-753.
- FILIPELLI, G. M. 1997. Intensification of the Asian monsoon and a chemical weathering event in the late Miocene-early Pliocene: implications for late Neogene climate change. Geology, 25: 27-30.
- FISCHER, A. G., 1960, Latitudinal variations in organic diversity. Evolution, 14: 64-81.
- FISHER, R. A., CORBET, A. S. and WILLIAMS, C. B. 1943. The relationship between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology, 12: 42-58.

- FLOWER, B. P., 1999. Warming without high CO₂? Nature, 399: 313-314.
- GASTON, K. J., 2000. Global patterns in biodiversity. Nature, 405, 220-227.
- GEOSECS, 1983. Indian Ocean Expedition, Hydrographic data, 1977-78. Washington, D.C.: U.S. Government Printing Office, 5:1-48.
- GIBSON, L. B. 1966. Some unifying characteristics of species diversity. contributions from the Cushman Foundation for Foraminiferal Research, 1: 117-124.
- GOODAY, A. J. and LAMBSHEAD, P. J. D. 1989. The influence of seasonally deposited phytodetritus on benthic foraminiferal populations in the bathyal northeast Atlantic: the species response. Marine Ecology Progress Series, 58: 53-67.



TEXT-FIGURE 8 Linear Correlation of H(S) with and Sanders' values at ODP Site 758.

- GUPTA, A. K. 1990. Species diversity in modern deep-sea benthic foraminifera at Indian Ocean DSDP sites. Indian Journal of Geology, 62: 166-172.
- GUPTA, A. K., JOSEPH, S., THOMAS, E., and ZACHOS, J.C., in press. The Indian Monsoon System, surface productivity, and deep-sea ventilation in the late Miocene: Results from the northeastern Indian Ocean (Ocean Drilling Program Site). Palaeogeography, Palaeoclimatology, Palaeoecology.
- GUPTA, A. K., 1997. Paleoceanographic and paleoclimatic history of the Somali Basin during the Pliocene-Pleistocene: multivariate analyses of benthic foraminifera from DSDP Site 241 (Leg 25). Journal of Foraminiferal Research, 27: 196-208.

- GUPTA, A. K., and SRINIVASAN, M.S., 1992a, Species diversity of Neogene deep sea benthic foraminifera from northern Indian Ocean DSDP Sites 214 and 216A: in Takayanagi, Y., and Saito, T. (eds.): Studies in Benthic Foraminifera, Benthos'90, Tokai University Press, p. 249-254.
- GUPTA, A. K., 1992b, Uvigerina proboscidea abundances and paleoceanography of the northern Indian Ocean DSDP Site 214 during the late Neogene: Marine Micropaleontology, v. 19, p. 355-367.
- HAQ, B.U., HARDENBOL, J. and VAIL, P.R. 1987. Chronology of fluctuating sea levels since the Triassic. Science, 235: 1136-1167.
- HESSLER, R. R. and SANDERS, H. L. 1967. Faunal diversity in the deep sea. Deep-sea Research, 14: 65-78.
- HUSTON, M. 1979. A general hypothesis of species diversity. American Naturalist, 113: 81-101.
- JOHNSON, D. A., 1985. Abyssal teleconnetions II. Initiation of Antarctic Bottom Water flow in the southwestern Atlantic. In: Hsu, K.J., and Weissert, H.J., Eds., South Atlantic Paleoceanography. Cambridge University Press, pp. 243-281.
- JOSEPH, S., 1999, Miocene paleoceanography and paleoclimatology of the northeastern Indian Ocean (ODP Site 758A): A faunal and isotopic perspective: Unpublished Ph.D. dissertation, Indian Institute of Technology, Kharagpur, 93.
- KELLER, G., HERBERT, T., DORSEY, R., D'HONDT, S., JOHNSSON, M., and CHI, W. R. 1987. Global distribution of late Paleogene hiatuses. Geology, 16: 199-203.
- KENNETT, J. P., 1977. Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and their impact on global paleoceanography. Journal Geophysical Research, 82: 3843-3860.
- —, 1986. Miocene to early Pliocene oxygen and carbon isotope stratigraphy of the Southwest Pacific DSDP Leg 90. In: Kennett, J.P., von der Borch, C.C. et al., Eds. Initial Reports of the Deep Sea Drilling Project. Washington, D.C.: U.S. Government Printing Office, 90: 1383-1411.
- KENNETT, J. P., and BARKER, P. F. 1990. Latest Cretaceous to Cenozoic climate and oceanographic developments in the Weddell Sea, Antarctica: An ocean-drilling perspective: Proceedings of Ocean Drilling Program, Scientific Results. College Station, TX: Ocean Drilling Program, 113: 937-960.
- KOLLA, V., SULLIVAN, L., STREETER, S. S., and LANGSETH, M. G. 1976. Spreading of Antarctic bottom water and its effects on the floor of the Indian Ocean inferred from bottom water potential temperature, turbidity, and sea-floor photography. Marine Geology, 21: 141-189.
- KROON, D., STEENS, T., and TROELSTRA, S.R., 1991. Onset of monsoonal related upwelling in the western Arabian Sea as revealed by planktonic foraminifers. In: Prell, W.L., Niitsuma, N. et al., Eds., Proceedings of the Ocean Drilling Program, Scientific Results. College Station, TX: Ocean Drilling Program, 117: 257-263.
- McCANN, K. S., 2000. The diversity-stability debate. Nature, 405, 228-233.
- MILLER, K. G., FAIRBANKS, R. G., and MOUNTAIN, G. S. 1987. Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. Paleoceanography, 2: 1-19.
- MURRAY, J. W., 1991. Ecology and paleoecology of benthic foraminifera. Harlow, Essex, UK : Longman Scientific and Technical Publishers, 451 p.

NOMURA, R., 1991. Oligocene to Pleistocene benthic foraminifer assemblages at Sites 754 and 756, eastern Indian Ocean. In: Weissel, J., Peirce, J., Taylor, E., et al., Eds. Proceedings of the Ocean Drilling Program, Scientific Results. College Station, TX: Ocean Drilling Program, 121: 31-75.

—, 1995. Paleogene to Neogene deep-sea paleoceanography in the eastern Indian Ocean: benthic foraminifera from ODP Sites 747, 757 and 758. Micropaleontology, 41: 251-290.

- NOMURA, R., SETO, K., and NIITSUMA, N., 1992. Late Cenozoic Deep-sea Benthic Foraminiferal Changes and Isotopic Records in the Eastern Indian Ocean. In: Takayanagi and Saito, T., Eds., Studies in Benthic Foraminifera, BENTHOS' 90. Sendai: Tokai University Press, p. 227-233.
- PAGANI, M., ARTHUR, M. A. and FREEMAN, K. H. 1999a. Miocene evolution of atmospheric carbon dioxide. Paleoceanography, 14: 273-292.
- PAGANI, M., FREEMAN, K. H. and ARTHUR, M. A., 1999b. Late Miocene atmospheric CO2 concentrations and the expansion of C4 grasses. Science, 285: 876-879.
- PAINE, R.T., 1966, Food web complexity and species diversity: American Naturalist, 100: 65-75.
- PEIRCE, J., WEISSEL, J., and others 1989. Proceedings of the Ocean Drilling Program, Initial Reports. College Station, TX: Ocean Drilling Program, 21: 359-837.
- PHLEGER, F. B. and SOUTAR, A. 1973. Production of benthic foraminifera in three east Pacific oxygen minima. Micropaleontology, 19: 110-115.
- PIANKA, E. R., 1966, Latitudinal gradients in species diversity: A review of concepts. American Naturalist, 100: 33-46.
- PISIAS, N. G., LAYER, L. A., and MIX, A. C. 1995. Paleoceanography of the eastern Pacific during the Neogene: Synthesis of Leg 138 drilling results. Proceedings of the Ocean Drilling Program, Scientific Results. College Station, TX: Ocean Drilling Program, 138: 5-21.
- RAMSAY, A. T. S., SMART, C. W., and ZACHOS, J. C. 1998. A model of early to middle Miocene deep ocean circulation for the Atlantic and Indian oceans. In: Cramp, A., MacLeod, C.J., Lee, S.V., and Jones, E.J.W., Eds., Geological evolution of ocean basins: results from the Ocean Drilling Program. Special Publication of the Geological Society, London, 131: 55-70.
- RAMSTEIN, G., FLUTEAU, F., BESSE, J., and JOUSSAUME, S., 1997. Effect of orogeny, plate motion and land-sea distribution on Eurasian climate change over the past 30 million years. Nature, 386: 788-795.
- REA, D. K. 1992. Delivery of Himalayan sediment to the Northern Indian Ocean and its relation to global climate, sea level, uplift, and seawater strontium. American Geophysical Union, Monograph, 70: 387-402.
- REX, M. A., ETTER, R. J., and STUART, C. T., 1997. Large-scale patterns of species diversity in the deep-sea benthos. In: R. F. G. Ormond and J. D. Gage, Eds., Marine Biodiversity: Patterns and Processes. Cambridge: Cambridge University Press.
- REX, M. A., STUART, C. T., and COYNE, G., in press. Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. Proceedings of the National Academy of Sciences, USA.
- RUDDIMAN, W. F., and KUTZBACH, J. E. 1989. Forcing of Late Cenozoic northern hemisphere climate by plateau uplift in southern

Asia and the American West. Journal Geophysical Research, 94: 18,409-18,427.

- SANDERS, H. L. 1968. Marine benthic diversity: A comparative study. American Naturalist, 102: 243-282.
- SAVIN, S. M., DOUGLAS, R. G., KELLER, G., KILLINGLEY, J. S., SHAUGHNESSY, L., SOMMER, M. A., VINCENT, E., and WOODRUFF, F., 1981. Miocene benthic foraminiferal isotope records: A synthesis. Marine Micropaleontology, 6: 423-450.
- SCHMIEDL, G. 1995. Late Quaternary benthic foraminiferal assemblages from the eastern South Atlantic Ocean: reconstruction of deep water circulation and productivity changes. Reports on Polar Research, Alfred Wegener Institüt fur Polar- und Meeresforschung, 160, 207 pp.
- SCLATER, J. G., ABBOTT, D. and THIEDE, J. 1977. Paleobathymetry and sediments of the Indian Ocean. In: Heirtzler, J.R., Bolli, H.M., et al., Eds., Indian Ocean geology and biostratigraphy. Washington, D.C.: American Geophysical Union, 25-59.
- SHANNON, C. E. and WIENER, W. 1949. The mathematical theory of communication. Urbana, III., 1-125.
- SIMPSON, G. G., 1964. Species diversity of North American Recent mammals. Systematic Zoology, 13: 57-73.
- SMART, C. W., 1998. Diversity patterns of Miocene benthic foraminifera in the Somali Basin, northwestern Indian Ocean. Micropaleontology, 44: 256-264.
- SMART, C. W. and MURRAY, J.W. 1995. Miocene deep-sea benthic foraminifera from the Atlantic and Indian Oceans: Diversity patterns and paleoceanography. Revista Española de Paleontología, No. Homenaje al Dr. Guillermo Colom, 59-68.
- SMITH, C. R., 1994. Tempo and mode in deep-sea benthic ecology: punctuated equilibrium revisited. Palaios, 9: 3-13.
- SRINIVASAN, M. S. and GUPTA, A. K. 1990. Miocene benthic foraminifera and paleoceanography of DSDP sites along Ninetyeast Ridge, northern Indian Ocean. Journal Palaeontological Society of India, 35: 61-72.
- STUART, C. T., REX, M. A., and ETTER, R. J., in press. Large-scale spatial and temporal patterns of deep-sea benthic species diversity. In: Tyler, P. A., Ed., Ecosystems of the World: Ecosystems of Deep Oceans. Elsevier Sciences.
- TCHERNIA, P. 1980. Descriptive regional oceanography. New York: Pergamon Press, 1-253.
- THIEL, H., PFANNKUCHE, SCHRIEVER, G., LOCHTE, K., GOODAY, A. J., HEMLEBEN, CH., MANTOURA, R. F. G., TURLEY, C. M., PATCHING, J. W., and RIEMANN, F. 1988. Phytodetritus on the deep-sea floor in a central oceanic region of the northeast Atlantic. Biological Oceanography, 6: 203-239.
- THOMAS, E., 1985. Late Eocene to Recent deep-sea benthic foraminifers from the central equatorial Pacific Ocean. Initial Reports Deep Sea Drilling Project, 85: 655-679
- ———, 1986a. Changes in composition of Neogene benthic foraminiferal faunas in equatorial Pacific and north Atlantic. Palaeogeography, Palaeoclimatology, Palaeoecology, 53: 47-61
- —, 1986b. Early to middle Miocene benthic foraminiferal faunas from DSDP Sites 608 and 610, North Atlantic. Geological Society London Special Publication, 21: 205-218
- —, 1990. Late Cretaceous through Neogene deep-sea benthic foraminifers (Maud Rise, Weddell Sea, Antarctica). In: Barker, P.F.,

Kennett, J.P. et al., Eds., Proceedings of the Ocean Drilling Program, Scientific Results. College Station, TX: Ocean Drilling Program, 113: 571-594.

- —, 1992. Cenozoic deep-sea circulation: evidence from deep-sea benthic foraminifera. Antarctic Research Series, 56: 141-165.
- THOMAS, E., BOOTH, L., MASLIN, M., and SHACKLETON, N. J., 1995. Northeastern Atlantic benthic foraminifera during the last 45,000 years: productivity changes as seen from the bottom up. Paleoceanography, 10: 545-562
- THOMAS, E., and GOODAY, 1996. Cenozoic benthic foraminifers: Tracers for changes in oceanic productivity. Geology, 24: 355-358.
- THOMAS, E., and VINCENT, E., 1987. Major changes in benthic foraminifera in the equatorial Pacific before the middle *Miocene* polar cooling. Geology, 15: 1035-1039
- VALENTINE, J.W. 1966. Numerical analysis of marine molluscan ranges on the extra-tropical northeastern Pacific Shelf. Limnology and Oceanography, 11: 198-211.
- —, 1971. Resource supply and species diversity patterns. Lethaia, 4: 51-61.
- VINCENT, E., 1977. Indian Ocean Neogene planktonic foraminiferal biostratigraphy and its paleoceanographic implications. In: Heirtzler, J. R., Bolli, H.M. et al., Eds., Indian Ocean geology and biostratigraphy. Washington, D.C.: American Geophysical Union, pp. 469-584.
- VINCENT, E., KILLINGLEY, J. S., and BERGER, W. H., 1985. Miocene oxygen and carbon isotope stratigraphy of the Tropical Indian Ocean. In: Kennett, J. P., Ed., The Miocene Ocean: paleoceanography and biogeography. Geological Society of America, Memoir, 163:103-130.
- WARREN, B. A., 1982. The deep water of the Central Indian Basin. Marine Research, 40:823-860.
- WILLIAMS, C. B., Editor, 1964. Patterns in the balance of nature. New York: Academia, 324 p.

- WRIGHT, J. D. and MILLER, K. G. 1996. Control of North Atlantic Deep Water circulation by the Greenland-Scotland Ridge. Paleoceanography, 11: 157-170.
- WRIGHT, J. D., MILLER, K. G., and FAIRBANKS, R. G., 1992. Early and middle Miocene stable isotopes: implications for deep water circulation and climate. Paleoceanography, 7: 357-389.
- WOODRUFF, F., 1985. Changes in Miocene deep-sea benthic foraminiferal distribution in the Pacific Ocean: relationship to paleoceanography. In: Kennett, J.P., Ed., The Miocene Ocean: Paleoceanography and Biostratigraphy, Geological Society of America, Memoir, 163: 131-176.
- WOODRUFF, F., and SAVIN, S.M. 1985. ¹³C values of Miocene Pacific benthic foraminifera: correlations with sealevel and biological productivity. Geology, 13: 119-122.
- WOODRUFF, F., 1989. Miocene deepwater oceanography. Paleoceanography, 4: 87-140.
- YOU, Y., 1998. Intermediate water circulation and ventilation of the Indian Ocean derived from water-mass contributions. Journal of Marine Research, 56:1029-1067.
- ZACHOS, J.C., LOHMANN, K.C., WALKER, J.C.G., and WISE, S.W., 1993. Abrupt climate change and transient climates during the Paleogene: A marine perspective. Journal of Geology, 101: 191-123.
- ZACHOS, J. C., FLOWER, B. P., and PAUL, H., 1997. Orbitally paced climate oscillations across the Oligocene/Miocene boundary. Nature, 388: 567-570.
- ZACHOS, J. C., OPDYKE, B. N., QUINN, T. M., JONES, C. E., and HALLIDAY, A. N., 1999. Early Cenozoic glaciation, Antarctic weathering, and seawater ⁸⁷Sr/⁸⁶Sr: is there a link? Chemical Geology, 161: 165-180.
- ZACHOS, J. C., STOTT, L. D., and LOHMANN, K. C., 1994. Evolution of early Cenozoic marine temperatures. Paleoceanography, 9: 353-387.
- ZACHOS, J., PAGANI, M., SLOAN, L., THOMAS, E., and BILLUPS, K., in press. Trends, Rhythms and aberrations in global climate 65 ma to Present. Science, 292: 686-693.

Manuscript received June 22, 2000 Revised manuscript accepted May 16, 2001