

Miocene planktonic foraminiferal biogeography and paleoceanographic development of the Indo-Pacific region

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ABSTRACT

Biogeographic patterns of Pacific planktonic foraminifera have been quantitatively mapped for two time-slices in the early Miocene (22 and 16 Ma) and one in the late Miocene (8 Ma). Important differences are apparent between the early and late Miocene that resulted from changes in surface water circulation within the Pacific Ocean and between the tropical Pacific and Indian Oceans.

In the early Miocene, tropical Pacific planktonic foraminifera were dominated by different taxa in the eastern and western areas, but by the late Miocene the assemblages were similar across the entire tropical Pacific. East to west faunal differences were probably due to differences in the surficial water-mass structure and temperature. It is likely that a deeper thermocline existed in the west favoring shallow water dwellers such as *Globigerinoides* and *Globigerina angustumbricata*, and a shallower thermocline in the east favoring slightly deeper-dwelling forms, especially *Globorotalia siakensis* and *G. mayeri*. During the late Miocene a trans-equatorial assemblage developed, dominated by *Globorotalia menardii*-*G. limbata* and *Globigerinoides* groups. These faunal changes are interpreted to reflect both the development, during the middle Miocene, of the Equatorial Undercurrent system when the Indonesian Seaway effectively closed and the general strengthening of the gyral circulation and Equatorial Countercurrent that resulted from increased Antarctic glaciation and high-latitude cooling during the middle Miocene.

The trans-equatorial planktonic foraminiferal distribution patterns typical of the late Miocene did not persist to the present-day oceans when east-west differences are again evident. However, these differences in modern assemblages are exhibited within forms that usually inhabit deeper waters. There is a successive changing dominance from west to east of *Pulleniatina obliquiloculata* to *Globorotalia tumida* to *Neoglobobulimina dutertrei*. The modern west to east differences in these deeper-dwelling forms reflect an intensification of the Equatorial Undercurrent system and its shallowing towards the east to depths well within the photic zone. Shallow-water forms, such as *Globigerinoides*, maintain trans-tropical distribution patterns in the modern ocean un-

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like the early Miocene that lacked an effective equatorial countercurrent system in the Pacific.

The distribution of faunas in the North Pacific indicates that the gyral circulation system was only weakly developed in the early Miocene, but was strong by the late Miocene. In the northwest Pacific, temperate faunas were displaced northward as the Kuroshio Current intensified in the late Miocene. In the South Pacific, more distinct latitudinal faunal provinces appeared during the middle to late Miocene along with a northward expansion of the polar-subpolar provinces and contraction of the tropical province. These faunal changes resulted from the continued areal expansion of the polar and subpolar water masses as Australia drifted northward from Antarctica and from the steepening of pole to equator thermal gradients related to increased Antarctic glaciation.

INTRODUCTION

A major objective of paleoceanography is to better understand patterns of surface-water circulation and the character of the upper part of the water column in ancient oceans. There are two principal approaches: determination of regional gradients in the oxygen isotopic composition of planktonic foraminiferal tests which, in part, reflect changes in temperature and salinity related to paleocirculation; and changes in the distribution and character of planktonic microfossil assemblages. Modern planktonic microfossil groups represent sensitive tracers of surface and near-surface water masses (Bradshaw 1959; Bé 1977; Vincent and Berger 1981; Kennett 1982). In particular, planktonic foraminifera have long been used to study oceanic surface-water paleocirculation in many regions (Ingle 1967; Kennett 1967; Bandy 1968; Keller 1981a, b, c). A major objective of the Cenozoic Paleoceanography (CENOP) project (see Kennett 1981) has been to quantitatively map biogeographic distribution patterns for a number of planktonic microfossil groups on a broad scale to better understand the history of surface-water circulation of the Miocene ocean. CENOP has attempted to produce a synoptic picture of biogeographic patterns from selected intervals of time in the Miocene and represents the first large-scale biogeographic mapping project of the global ocean prior to the Pleistocene Period (CLIMAP 1976; 1981).

The purpose of this contribution is to present quantitative biogeographic maps of planktonic foraminifera in the Indo-Pacific region for three intervals of time during the Miocene that have been used in all of the CENOP time-slice studies: the earliest Miocene (22 Ma, Zone N4B); the late early Miocene (16 Ma, Zone N8) and the late Miocene (8 Ma, Zone N16/N17). Hodell and Kennett (1985) discuss similar data from the South Atlantic that are also shown on our species distribution maps. The biogeographic patterns are employed to define, in broad terms, the nature of surface-water circulation during each of these intervals. It is of particular interest to examine changes in biogeographic patterns that might exist between the three time-slices. This in turn will help in understanding the evolution of surface-water circulation and its structure during the Miocene. It is well known that Oligocene and Neogene planktonic foraminiferal faunas exhibit a continuing trend towards latitudinal differentiation (Kennett 1977; Berggren 1984). Oligocene assemblages exhibit a

marked uniformity over a large latitudinal extent, a pattern that was replaced during the Neogene by numerous distinct latitudinal provinces.

The three time-slices were chosen for two main reasons. First, they generally represent periods of deep-sea sediment accumulation rather than erosion and unconformities (Keller and Barron 1983). Second, these periods were chosen to characterize biogeographic patterns at times when the oceans were potentially quite different. Thus an interval was selected to include the earliest Miocene at a time of Oligocene to Miocene biogeographic transitions and to include the beginning of the well-known Neogene evolutionary radiations in marine microfossil groups (Cifelli 1969; Berggren 1969; Lipps 1970; Kennett 1977, 1983; Thunell 1981; Keller 1981a). Another interval was selected in the late early Miocene during a distinct climatic warming following the major early Miocene evolutionary radiation and preceding the distinct oxygen isotopic shift of the middle Miocene interpreted by many (e.g. Shackleton and Kennett 1975; Savin et al. 1975; Kennett 1977; Woodruff et al. 1981) but not all workers (Matthews and Poore 1980) to represent a major growth phase of the east Antarctic ice sheet. A third interval was selected from within the late Miocene, following this major global climatic/glacial event and before the distinct $\delta^{13}\text{C}$ shift (Keigwin 1979; Haq et al. 1980) and further major climatic deterioration during the latest Miocene generally associated with the Messinian salinity crisis (Kennett 1967; Adams et al. 1977). Questions addressed in this investigation include: Were there significant changes in biogeographic patterns during the Miocene? If so when did the changes occur? What do the changes indicate about the development of surface-water circulation and what may have caused the changes?

Almost all of the stratigraphic sections used in this mapping experiment (Figures 1, 2, and 3) were drilled as part of the Deep Sea Drilling Project (DSDP). Also used in the 8 Ma time-slice are a piston core from the North Pacific (RC12-418) and the Newport Beach section, in southern California. The modern position, water depth, and stratigraphic intervals encompassed in the time-slices and the number of samples counted for each slice are listed in Table 1. In general, core coverage is poor and is perhaps still the most severe restriction upon such ocean mapping experiments. For the Pacific Ocean, there are slightly fewer available

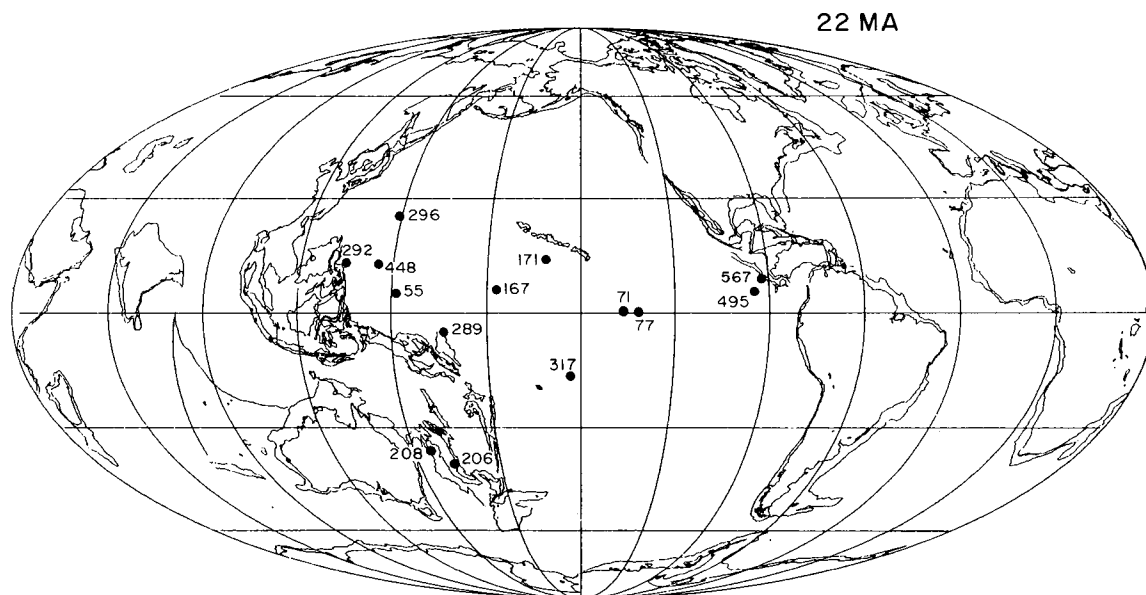


Figure 1. Earliest Miocene global paleogeography (22 Ma) (Sclater et al. 1985) showing location of DSDP sites used for mapping paleobiogeography of planktonic foraminifera within this time-slice.

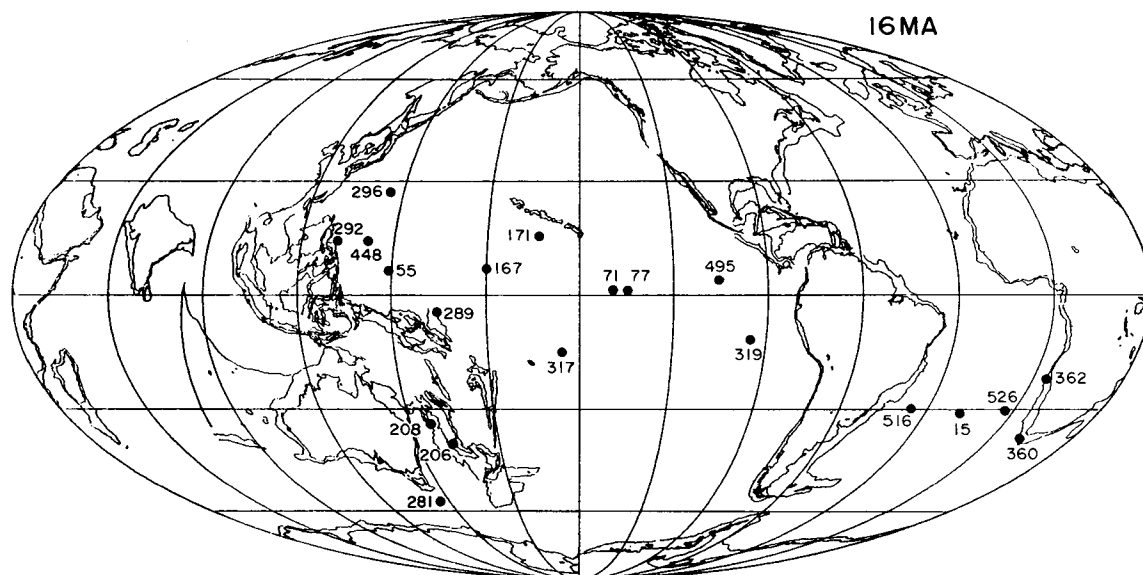


Figure 2. Latest early Miocene (16 Ma) global paleogeography (Sclater et al. 1985) showing location of DSDP sites used for mapping paleobiogeography of planktonic foraminifera within this time-slice.

sections of appropriate age in the early Miocene, as expected from the incomplete deep sea sedimentary record (Moore et al. 1978); 14 sections for the 22 Ma time-slice; 15 for 16 Ma; and 19 for 8 Ma. Large areas have no drilled sections; this is especially true of the southeast and south central Pacific and the higher latitudes of the North Pacific. Core coverage is best in the tropical to subtropical latitudes of the Pacific Ocean. Although cores of suitable ages are few in number, broad trends can be defined. Future drilling should provide needed additional materials to enhance mapping studies of the ancient ocean.

Biogeographic patterns are plotted on global paleogeogra-

phic maps of Sclater et al. (1985). (Figures 1–3) and individual sites have been accordingly backtracked. The most significant changes in the ocean basins potentially effecting Indo-Pacific circulation during the Miocene were the steady constriction and final effective closure to surface circulation of the Indonesian Seaway; the constriction of deep water flow through the central American Seaway and the expansion of the circum-Antarctic Current and polar-subpolar surface waters as Australia drifted northward from Antarctica. Tectonic changes at each of these interocean gateways almost certainly would have had major effects upon surface-water circulation. Tectonic changes that may

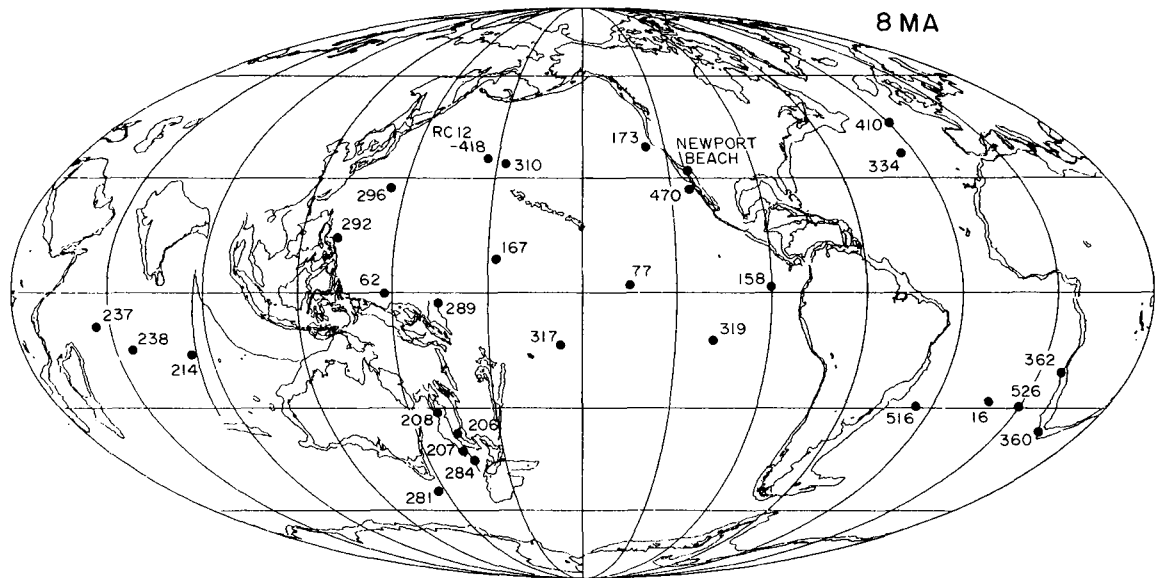


Figure 3. Late Miocene (8 Ma) global paleobiogeography (Sclater et al., 1985) showing location of sections used for mapping paleobiogeography of planktonic foraminifera within this time-slice.

have affected the character of deep and intermediate water circulation during the Miocene are not considered here.

METHODS

Quantitative counts were made of planktonic foraminifera in the $>150 \mu\text{m}$ size fraction. Samples were oven-dried at 50°C , weighed, disaggregated in hot Calgon solution, washed over a $63 \mu\text{m}$ Tyler screen, dried, and reweighed. Samples were microsplit to obtain an average of 300 specimens per sample. Samples were counted and identified following the taxonomy of Kennett and Srinivasan (1983). Up to 20 samples were analyzed for each time-slice interval in each deep sea core, with an average of 6 or 7 samples per core for each time-slice interval. Samples were averaged to obtain a representative faunal assemblage and plotted on maps to show individual species distributions. Assemblages were not included in the data set when they clearly showed alteration resulting from calcium carbonate dissolution. Nevertheless, assemblages from deeper waters must have been affected to some extent by dissolution, although this was not quantitatively analyzed.

The species percent data for the Pacific were analyzed for each time slice using Q-mode factor analysis, a multivariate statistical technique (Imbrie and Kipp 1971). The Atlantic data were not included in this analysis. This technique examines the relative proportions of species within each sample in a data set, groups the data into a predetermined number of factors (in this study, five factors have been employed to define assemblages; Table 2) and ranks each sample by providing a factor value within each assemblage indicating its compositional similarity to that assemblage. Thus, biogeographic patterns in the oceans are revealed by the changes in the factor values.

PHYSICAL OCEANOGRAPHY

The most conspicuous features of modern ocean, surface-water circulation in the Pacific (Figure 4) are the large anticyclonic gyres (clockwise in the North Pacific; counterclockwise in the Southern Hemisphere) of each ocean. The North Pacific gyre is separated from the South Pacific gyre by a well-defined series of eastward and westward zonal surface currents, including an eastward-flowing undercurrent near the equator (Reid 1962; Wyrtki 1967). In each gyre, the flow is most narrow and intense on the western side of the ocean (such as the Kuroshio Current), and more weak and diffuse in the eastern regions. The western boundary currents (Kuroshio and East Australian currents) flow in the direction of the poles. Conversely, the eastern boundary currents (California and Peru-Chile currents) flow back toward the equator as cold currents, thus completing the system of gyral circulation.

The major ocean currents near the equator are more complex and are a response to the wind system. The equatorial circulation consists of three primary components: the westward-flowing north and south equatorial currents (Figure 4) that lie beneath the trade winds; a relatively narrow eastward-flowing Countercurrent that occurs between the trade wind belts at the zone of minimum wind stress; and the eastward flowing Equatorial Undercurrent (Cromwell Current), found directly on the equator beneath the sea surface (Wyrtki 1967). The Equatorial Countercurrent returns warm water to the eastern Pacific. The equatorial wind system produces some upwelling along the equator and along the northern fringes of the surface Countercurrent. The Pacific Equatorial Undercurrent is narrow (300 km) and thin (200 m) and its depth of flow is centered at about 200 m in the west and rises to less than 50 m in the eastern Pacific where it

TABLE 1. SAMPLE LOCATION DATA FOR EACH OF THE THREE MIOCENE TIME-SLICES EMPLOYED IN THIS STUDY (22 MA, 16 MA, AND 8 MA)

Time Slice	Site	Position	Present-Day Water Depth (M)	Paleo Water Depth (M)	Interval Sampled	Depth Below Surface (M)	Interval Thickness (M)	Number of Samples
22 MA	55	9°18.1'N;142°32.1'E	2850	1998	12-2, 52- 58 cm	105.32-	9.43	7
					13-2, 75- 80 cm	114.75		
	71	4°28.28'N;140°18.91'W	4419	4051	30-6, 87- 92 cm	270.37-	27.60	7
					33-6, 15- 19 cm	297.65		
	77(B)	0°28.90'N;133°13.70'W	4291	3732	30-5,103-104 cm	275.33-	13.71	5
					31-6,104-105 cm	289.04		
	167	7°04.1'N;176°49.5'W	3176	3161	9 cc	232.00	0.00	1
	171	169°27.6'W; 19°07.9'N	2290	2055	3-6,147-150 cm	54.97	0.00	1
	206(C)	32°00.75'S;165°27.15'E	3196	3119	2-2, 48- 50 cm	414.98-	25.02	9
					4 cc	440.00		
	208	26°06.61'S;161°13.27'E	1545	1439	23-3,100-102 cm	375.00-	29.50	14
					24-4,100-102 cm	404.50		
	289	0°29.92'S;158°30.69'E	2206	2398	65-3, 28- 42 cm	611.38-	41.00	10
					69-5, 38- 42 cm	652.38		
	292	15° 9.11'N;124°39.05'E	2943	2366	13-6,140-144 cm	119.90-	14.00	10
					15-3, 90- 94 cm	133.90		
	296	29°20.41'N;133°31.52'E	2920	2308	34-1, 45- 56 cm	310.95-	6.07	5
				34-5, 52- 60 cm	317.02			
317(B)	11°00.09'S;162°15.78'W	2598	2520	25-1,142-143 cm	226.42-	4.50	2	
				25-4,142-143 cm	230.92			
448	16°20.46'N;134°52.45'E	3483	2725	6-1, 78- 82 cm	43.78-	2.12	2	
				6-1,140-144 cm	45.90			
495	12°29.78'N; 91°02.26'W	4140	2764	38-1, 80- 82 cm	352.30-	10.10	2	
				39-1,140-144 cm	362.40			
567	12°42.96'N; 90°55.99'W	5529	5339	12-1,101-105 cm	5827.00-	17.80	6	
				13 cc	5845.20			
16 MA	15	30°53.38'S; 17°58.99'W	3938	3286	6-6, 46- 50 cm	112.96-	4.02	2
					7-4, 48- 57 cm	118.98		
	55	9°18.1'N;142°32.1'E	2850	2287	10-1, 42- 50 cm	82.72-	7.50	6
					10-6, 42- 50 cm	90.22		
	71	4°28.28'N;140°18.91'W	4419	4133	19-2,140-144 cm	163.90-	33.60	10
					22-6,100-102 cm	197.50		
	77(B)	0°28.90'N;133°13.70'W	4291	3929	26-2, 92- 94 cm	237.22-	9.10	5
					27-2, 92- 94 cm	246.32		
	167	7°04.1'N;176°49.5'W	3176	3163	7-5, 70- 72 cm	154.70-	3.30	2
					7 cc	158.00		
	171	169°27.6'W; 19°07.9'N	2290	2125	2-6,147-150 cm	36.97	0.00	1
	206	32°00.75'S;165°27.15'E	3196	3136	31-1, 90- 92 cm	277.90-	17.10	20
					32 cc	295.00		
	208	26°06.61'S;161°13.27'E	1545	1492	21-3,100-102 cm	319.00-	3.55	7
					21-6,105-107 cm	322.55		
	281	47°59.84'S;147°45.85'E	1591		10-3, 53- 54 cm	87.03-	4.87	7
					10-6, 90- 91 cm	91.90		
	289	0°29.92'S;158°30.69'E	2206	2373	52-2, 82- 90 cm	486.82-	30.06	13
					55-3, 88- 92 cm	516.88		
	292	15°49.11'N;124°39.05'E	2943	2552	12-2,140-144 cm	104.40-	2.62	3
					12-4,102-103 cm	107.02		
	296	29°20.41'N;133°31.52'E	2920	2543	28 cc	263.00-	10.68	6
					30-1,118-119 cm	273.68		
	317(B)	11°00.09'S;162°15.78'W	2598	2551	18-1, 86- 90 cm	159.36-	2.68	2
					18-3, 54- 58 cm	162.04		
	319	13°01.04'S;101°31.46'W	4296	3492	11-4, 50- 52 cm	100.00-	6.48	6
					12-2, 48- 50 cm	106.48		
360	35°50.75'S; 18°05.79'E	2949	3021	22-2, 74- 79 cm	319.24-	6.72	2	
				22-6,146-150 cm	325.96			
362	19°45.45'S; 10°31.95'E	1325	1580	36 cc	606.00-	12.45	2	
				37-2,145-159 cm	618.45			
448	16°20.46'N;134°52.45'E	3483	2963	3-2, 40- 42 cm	16.40-	0.54	2	
				3-2, 94- 98 cm	16.94			
495	12°29.78'N; 91°02.26'W	4140	3521	26-1, 75- 79 cm	238.50-	8.50	15	
				26-6,103-107 cm	247.00			
516	30°16.59'S; 35°17.10'W	1313	1227	21-1, 51- 55 cm	86.61-	5.89	2	
				22-2, 50- 54 cm	92.50			
526(A)	30°07.36'S; 03°08.28'E	1054	758	21-1, 50- 54 cm	116.50-	4.11	2	
				21-4, 11- 16 cm	120.61			

TABLE 1. SAMPLE LOCATION DATA FOR EACH OF THE THREE MIOCENE TIME-SLICES EMPLOYED IN THIS STUDY (22 MA, 16 MA, AND 8 MA) (continued)

Time Slice	Site	Position	Present-Day Water Depth (M)	Paleo Water Depth (M)	Interval Sampled	Depth Below Surface (M)	Interval Thickness (M)	Number of Samples	
8 MA	16	30°20.15'S; 15°42.79'W	3526	3061	9-1, 58- 65 cm	135.08-	15.12	2	
					10-5, 50- 55 cm	150.20			
	62(.1)	1°52. 2'N;141°56. 3'E	2591	2452	23-5, 47- 51 cm	222.47-	5.46	6	
					24-2,143-147 cm	227.93			
		77(B)	0°28.90'N;133°13.70'W	4291	4127	15-4, 30- 34 cm	142.00-	6.80	8
					16-2,100-104 cm	148.80			
		158	6°37.36'N; 85°14.16'W	1953	1592	19-6, 40- 44 cm	169.90-	10.48	9
					21-1, 38- 42 cm	180.38			
		167	7°04. 1'N;176°49. 5'W	3176	3169	4 cc	75.00	0.00	1
		173	39°57.71'N;125°27.12'W	2927		16-2, 01- 02 cm	140.00-		
						17 cc	157.50	17.50	5
		206	32°00.75'S;165°27.15'E	3196	3205	24-1,106-107 cm	211.06-		
						24 cc	219.00	7.94	7
		207(A)	36°57.75'S;165°26.06'E	1389	1330	6-3, 43- 48 cm	95.43-		
						6-6,100-104 cm	100.50	5.07	8
		208	26°06.61'S;161°13.27'E	1545	1525	16-1, 50- 51 cm	194.50-		
						16-5, 50- 51 cm	200.50	6.00	6
		214	11°20.21'S; 88°43.08'E	1671	1578	14-1, 40- 42 cm	123.90-		
						15-2, 10- 12 cm	134.60	10.70	10
		237	7°04.99'S; 58°07.48'E	1623	1533	12-6, 01- 03 cm	109.00-		
						13-2, 01- 03 cm	112.50	3.50	5
		238	11°09.21'S; 70°31.56'E	2832	2707	24-1, 01- 03 cm	215.00		
						27-5, 50- 52 cm	250.00	35	12
		281	47°59.84'S;147°45.85'E	1591		6-4, 45- 46 cm	50.45-		
						7-4,105-106 cm	60.55	10.10	13
		284	40°30.48'S;167°40.81'E	1078		20-1, 81- 82 cm	180.31-		
						21-6, 40- 41 cm	196.90	16.59	13
		289	0°29.92'S;158°30.69'E	2206	2283	17-5,142-150 cm	254.42-		
						29-3, 38- 46 cm	269.38	14.96	9
		292	15°49.11'N;124°39.05'E	2943	2761	9-1, 93- 97 cm	73.93-		
						9 cc	82.50	8.57	11
		296	29°20.41'N;133°31.52'E	2920	2782	21-6, 60- 62 cm	195.10-		
						23 cc	215.50	20.40	14
		310	36°52.11'N;176°54.09'E	3516	3474	8-5, 50- 52 cm	68.50-		
						8-6,147-150 cm	70.97	2.47	11
		317(B)	11°00.09'S;162°15.78'W	2598	2580	9-5,143-144 cm	80.43-		
					10-2, 66- 67 cm	84.66	4.26	7	
	319	13°01.04'S;101°31.46'W	4296	3955	3-2,118-120 cm	21.68-			
					3-3,118-120 cm	23.18	1.50	3	
	334	37°02.13'N; 34°24.87'W	2619	2185	8-2,112-114 cm	189.12-			
					14-1,108-110 cm	244.58	55.46	9	
	360	35°50.75'S; 18°05.79'E	2949	2984	8-2, 50- 55 cm	148.00-			
					11-6, 50- 55 cm	182.50	34.50	2	
	362	19°45.45'S; 10°31.95'E	1325	1460	24-1, 52- 56 cm	350.02-			
					27-6, 52- 57 cm	414.52	64.50	2	
	410	45°30.51'N; 29°28.56'W	2975	2584	28-1, 94- 96 cm	255.44-			
					31-2, 54- 56 cm	285.04	29.60	8	
	470	28°54.46'N;117°31.11'W	3549	3193	9-1, 54- 59 cm	76.54			
					9 cc	85.50	8.96	4	
	516	30°16.59'S; 35°17.10'W	1313	1276	13-1, 70- 72 cm	51.60			
					14-3, 70- 72 cm	59.00	7.40	2	
	526(A)	30°07.36'S; 03°08.28'E	1054	940	9-1, 50- 54 cm	63.70-			
					11-3, 55- 59 cm	75.55	11.85	2	
	Newport Beach	22°38'N;177°53'W	onshore		N7A	256.00-			
					N5	235.00	21.00	5	
	RC12-418	38°06'N;170°01'E	3842		452 cm	4.52-			
					636 cm	6.36	1.81	8	

TABLE 2. SCALED VARIMAX FACTOR SCORES (Q-MODE FACTOR ANALYSIS) FOR PLANKTONIC FORAMINIFERAL ASSEMBLAGES AT 22 MA, 16 MA, AND 8 MA

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Earliest Miocene (22 Ma)					
<i>Globigerina angustumbricata</i>	1.342	-0.020	-0.084	1.704	-0.571
<i>Globigerina praebulloides</i>	0.030	-0.159	0.343	-0.276	3.200
<i>Globigerina woodi</i> and <i>woodi connecta</i>	0.016	-0.029	0.088	0.205	0.261
<i>Globigerinita glutinata</i>	-0.170	-0.055	2.934	0.740	-0.408
<i>Globigerinoides</i> spp.	-0.341	-0.260	-0.588	2.594	0.959
<i>Dentoglobigerina altispira</i>	-0.078	-0.004	-0.115	0.889	-0.175
<i>Globoquadrina praedehiscens</i>	-0.153	0.181	0.090	0.774	-0.093
<i>Globoquadrina venezuelana</i>	0.037	0.221	0.332	0.306	0.001
<i>Globorotalia opima nana</i>	-0.071	-0.273	0.324	0.015	0.052
<i>Globorotalia siakensis</i> and <i>mayeri</i>	-0.114	3.419	-0.134	0.174	0.185
<i>Globorotalia kugleri</i>	3.161	0.109	0.081	-0.332	0.282
<i>Catapsydrax dissimilis</i>	0.089	0.206	1.628	-0.277	0.348
Early Miocene (16 Ma)					
<i>Globigerina praebulloides</i>	0.193	0.027	3.252	-0.008	-0.014
<i>Globigerina woodi</i>	-0.034	0.049	0.009	0.436	0.107
<i>Globigerinita glutinata</i>	-0.132	0.167	0.271	0.959	1.395
<i>Globigerinoides</i> spp.	3.268	-0.051	-0.178	-0.021	-0.126
<i>Dentoglobigerina altispira</i>	0.207	-0.282	-0.177	0.042	2.959
<i>Globoquadrina dehiscens</i>	0.239	0.175	-0.066	2.452	-0.395
<i>Globoquadrina venezuelana</i>	0.047	-0.295	-0.011	0.042	0.007
<i>Globorotalia continua</i>	0.048	-0.254	0.548	-0.056	-0.075
<i>Globorotalia conoidea</i> and <i>miozea</i>	-0.302	0.030	-0.024	1.819	-0.265
<i>Globorotalia peripheroronda</i>	0.236	-0.474	-0.002	0.744	-0.063
<i>Globorotalia siakensis</i> and <i>mayeri</i>	-0.108	-3.237	0.009	0.094	-0.192
Late Miocene (8 Ma)					
<i>Globigerina nepenthes</i> and <i>druryi</i>	3.046	0.018	-0.069	-0.087	0.091
<i>Globigerina bulloides</i>	0.003	3.146	0.009	0.291	-0.055
<i>Globigerina woodi</i>	-0.344	0.019	-0.198	1.000	0.808
<i>Globigerinita glutinata</i>	0.330	0.055	-0.446	-0.077	2.479
<i>Globigerinoides</i> spp.	0.346	-0.100	1.958	0.540	0.423
<i>Dentoglobigerina altispira</i>	-0.064	-0.018	0.443	0.058	0.672
<i>Globoquadrina venezuelana</i>	0.259	0.038	0.634	-0.108	-0.445
<i>Neogloboquadrina acostaensis</i>	-0.520	-0.000	0.812	0.102	1.440
<i>Globorotalia conoidea</i>	0.179	-0.292	-0.127	2.918	-0.394
<i>Globorotalia menardii-limbata</i>	-0.038	0.067	2.157	-0.265	-0.366

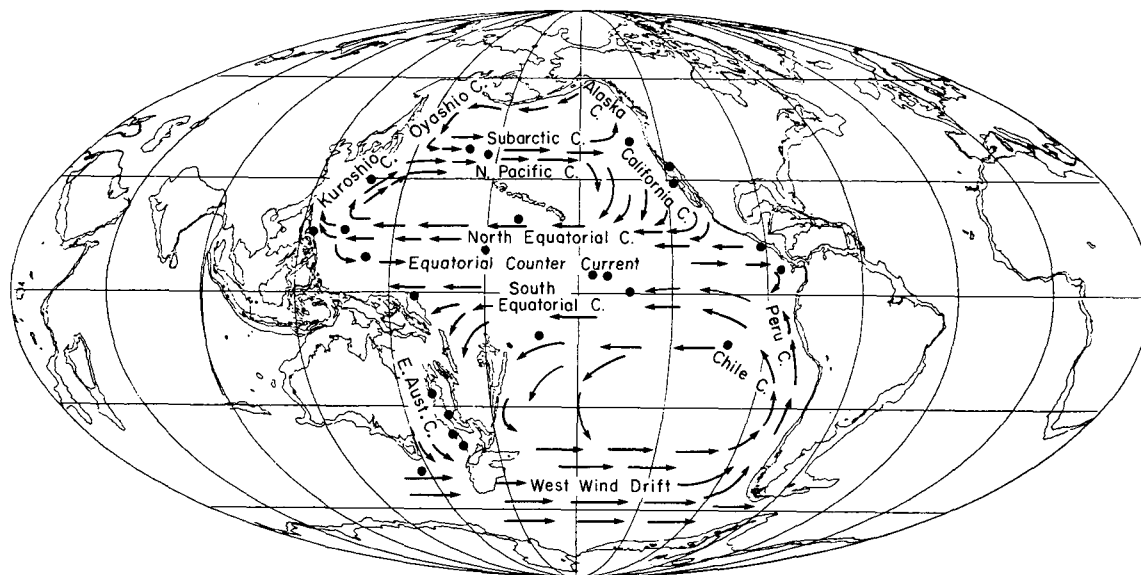


Figure 4. Major components of Modern Pacific Ocean surface circulation.

becomes involved with upwelling created by wind induced divergence (Pak and Zaneveld 1974; Wyrski 1967; Reid 1962). The origin of the Pacific Equatorial Undercurrent seems to be linked with the balancing of geostrophic flow near the equator as a result of an increasing pressure gradient towards the west.

A weak cyclonic gyre (counterclockwise) occurs in the sub-polar area and the North Pacific (Figure 4) with the Alaskan and Oyashio Currents as the main components. An equatorial Southern Hemisphere gyre is lacking because mid-latitude zonal flow is not obstructed by continental barriers. Instead, the Antarctic Circumpolar Current circles Antarctica and flows eastward at all depths.

As the major gyres circulate around the oceans, they either receive or give up heat to the atmosphere or to adjacent currents. Surface-water temperatures thus change around the circuit. Near the equator, the westward-flowing portion of the gyre is heated by high insolation and heat transfer from the warm atmosphere and adjacent warm parts of the central gyres, whereas at high latitudes the eastward-flowing part of the circuit loses heat to the atmosphere and cool subpolar waters. Thus the poleward-flowing western boundary currents are considerably warmer than the eastern boundary currents with consequent displacement of associated planktonic biota along the ocean margins.

Also of biogeographic importance are the division of surface waters into distinct water masses separated by oceanic fronts. Of particular importance in this study are the Subtropical Convergence in the South Pacific that separates Subantarctic from temperate (cool subtropical) surface waters and the Subtropical Divergence (Tasman Front) that separates temperate from warm subtropical surface waters. In the modern ocean each of these fronts is known to have an important effect upon the distribution of planktonic microfossils forming sharp transition zones (Parker 1971; Eade 1973; Bé 1977; Kennett 1978).

Modern ocean circulation would not be expected to be completely analogous to that of the Miocene Ocean. The changing configuration of continents forming the boundaries of the ocean basins created different circulation patterns in key areas, and changes in the latitudinal temperature gradient affected the strength of the circulatory system. There should have been large differences in tropical Pacific circulation patterns during the early Miocene when the Indonesian and Central American seaways were open to surface circulation. During the early Miocene, largely uninterrupted westward equatorial surface currents flowed from the eastern Pacific (or perhaps even the equatorial Atlantic) through the Indonesian Seaway north of Australia-New Guinea (Audley-Charles et al. 1972; Hamilton 1979) and into the Indian Ocean (Edwards 1975). Return-flow in the form of the Equatorial Undercurrent probably did not originate in the west Pacific as today, but in the Indian Ocean upon contact with Africa. The Equatorial Countercurrent system was weaker due to lower equator to pole thermal gradients and reduced wind strengths in the tropics. Largely uninterrupted westward flow of tropical currents into the Indian Ocean also reduced the volume and strength of the tropical waters directed into the western boundary currents in

the North and perhaps the South Pacific. One of the most important oceanic changes during the Miocene was the closure of the Indonesian Seaway by the middle Miocene (Moberly 1972; Hamilton 1979), which should have resulted in important circulatory changes and affected the biogeographic distribution of plankton (Edwards 1975; Kennett 1977, 1978).

STRATIGRAPHY

CENOP workers chose three time-slice intervals for detailed study close to major Miocene paleoceanographic events so as to describe the evolving Miocene Ocean and its paleobiogeographic evolution. The three time-slice intervals are the earliest Miocene at 22 Ma, corresponding to Zone N4b of Srinivasan and Kennett (1981); late early Miocene at 16 Ma, Zone N8 which straddles the early-middle Miocene boundary; and the late Miocene at 8 Ma, corresponding to the boundary between Zones N16 and N17. These three time-slice intervals are biostratigraphically defined and discussed in detail by Barron et al. (1985). Uncertainties of correlation are minimized by study of multiple samples from each of the time-slice intervals in various stratigraphic sections. The multidisciplinary time-scale developed by Barron et al. (this volume) and employed by CENOP Project workers allows resolution of Miocene time approaching 100,000 years. Correlations between temperate and tropical sections approach a time resolution of between 200,000 and 500,000 years although in a few sections this was expanded to up to one million years to alleviate problems of nonrecovery during parts of the interval. Such lengthy intervals sometimes contained large quantitative faunal oscillations, but the counting of an average of 6 or 7 samples per time-slice in each core provided average values that produce coherent biogeographic patterns in the oceans when plotted on maps.

RESULTS

General Trends

It is well established that modern planktonic foraminiferal species are limited in their distribution to certain water masses and latitudinal ranges (Bé 1977; Ruddiman et al. 1970; Parker 1971). Similarly the distribution of fossil planktonic foraminifera in stratigraphic sections shows that they were also latitudinally restricted in the past ocean. The latitudinal ranges of most Neogene planktonic foraminifera are now fairly well known because of investigations by large numbers of workers on DSDP sections from a wide range of latitudes (for summary of literature see Srinivasan and Kennett 1981; Kennett and Srinivasan 1983; Barron and Keller, 1983). General microfossil assemblages have been mapped for particular intervals during the Neogene (San-cetta 1978; Thunell and Belyea 1982). However, this is the first time that planktonic foraminiferal species patterns have been quantitatively mapped on a broad scale. The centers of evolution and biogeographic distribution of most species lie either in tropi-

cal or temperate water masses, although the maximum extent of individual species often includes several water masses.

Table 3 lists the most important planktonic foraminiferal species making up assemblages associated with different water-masses during seven intervals from the latest Oligocene and Miocene. Four broad assemblages are shown in Table 2: Subantarctic; temperate-transitional; warm-subtropical; and tropical. An Antarctic assemblage also occurred but it is not included in the table. Equatorial assemblages, distinct from more broadly distributed assemblages, also occurred at times. In the modern ocean, the Subantarctic water mass lies between the Antarctic Convergence (Polar Front) and the Subtropical Convergence, generally between 60° and 45° south of the equator. Temperate water masses are those that occur at latitudes of about 35° to 45° south or north of the equator. Transitional assemblages are most similar to the temperate, but also contain significant proportions of subtropical elements. The warm subtropical area is immediately adjacent to the tropics between about latitudes 20° to 30° north and south of the equator. Tropical assemblages are those that are largely restricted to areas within the present day tropics between 20° north and south of the equator.

Biogeographic knowledge of modern planktonic foraminifera is of limited value in the study of Miocene assemblages because of the different taxonomic composition of the two assemblages due to evolution and extinction. The species distribution patterns now mapped for each time-slice provide the basis for our paleoceanographic interpretations. During the Miocene, a number of species or lineages adjusted their environmental preferences. For example, *Globigerina praebulloides* exhibited the highest frequencies in warm subtropical-transitional areas in the early Miocene but later developed a preference for the subpolar-temperate regions, which its descendant *Globigerina bulloides* still maintains. *Globorotalia menardii* was a warm subtropical form upon its evolution from *G. praemenardii* 12 m.y. ago and became a tropical form about 10 Ma. Also *Globoquadrina praede-hiscens* was a tropical form, while its ancestor *G. dehiscens* is a transitional-temperate form. Nevertheless, the switching of water-mass preferences through time seems to be exceptional. Most evolutionary lineages have remained closely associated with the same water masses during the Neogene (Kennett and Srinivasan 1983).

For each of the three time-slices, distribution maps are presented for individual species as well as for five factors resulting from Q-mode factor analysis. Species were selected because of their quantitative importance in some assemblages and because of the coherent patterns displayed. Quantitatively unimportant species are not shown, although many of these also exhibit clear associations with certain water masses. Only a few species were found to exhibit irregular patterns and these are mostly quantitatively unimportant elements within the assemblages.

Earliest Miocene: 22 Ma

Earliest Miocene assemblages still contained the last rem-

nants of typical Oligocene taxa such as *Catapsydrax dissimilis*, *Globorotalia kugleri* and *Globigerina angustumbilicata*. Evolutionary radiation had already added the earliest representatives of a number of typical Neogene lineages such as *Globigerinoides*, *Globoquadrina dehiscens* and *Dentoglobigerina altispira*. For this time-slice, distribution patterns are shown for eleven taxa. Temperate-transitional assemblages were characterized by high frequencies of *Globigerinita glutinata* (Figure 5). *Catapsydrax dissimilis* clearly exhibited highest frequencies in temperate areas (Figure 6), but extended its geographic range into the transitional and eastern tropical Pacific region. This species exhibited low frequencies in the western tropical Pacific. Oxygen isotopic data (Biolzi 1983; Savin et al.; 1985) indicates that this was a deep-dwelling species.

The warm subtropical areas were marked by high frequencies of *Globigerina praebulloides* (Figure 7) and the *Globigerina woodi*-*G. woodi connecta* complex (Figure 8).

Tropical faunal distributions included two major categories; species that were distributed relatively evenly across the tropical Pacific and those that seemed to be restricted to either the western or eastern sectors.

Globorotalia kugleri (Figure 9), distinctly exhibited highest frequencies in the western tropical Pacific region. Other trans-Pacific tropical elements were *Dentoglobigerina altispira* (Figure 10) and *Globoquadrina praede-hiscens* (Figure 11).

Three forms exhibited distinctly higher frequencies in the western tropical Pacific. These include *Globigerinoides* that broadly encompassed the tropical-warm subtropical western Pacific (Figure 12); *Globigerina angustumbilicata* (Figure 13) and *Globoquadrina venezuelana* (Figure 14). Keller (1981a, b) previously recognized the western provincialism of *G. angustumbilicata*.

The eastern tropical Pacific was dominated by a single complex; *Globorotalia siakensis* and *mayeri* (Figure 15), forming a distinct biogeographic province. This species complex extended in much reduced frequencies across the tropical-warm subtropical Pacific.

The factor analysis, employing 5 factors, incorporates 96 percent of the faunal variance within the earliest Miocene (22 Ma) data set. Five distinct faunal assemblages are recognizable, as follows (Figure 16).

Factor 1. Western tropical-Subtropical Assemblage (32% of the faunal variance). This assemblage (factor) is dominated by *Globorotalia kugleri* that tended to be more dominant in the western tropics, and *Globigerina angustumbilicata* that was distributed broadly in the western subtropics and tropics but did not extend in abundance toward the eastern tropical Pacific.

Factor 2. Eastern Tropical Assemblage (23% of the faunal variance). This assemblage is dominated by the *Globorotalia siakensis*-*mayeri* complex that clearly defined a biogeographic province in the eastern tropical Pacific region.

Factor 3. Temperate Assemblage (16% of the faunal variance). This assemblage is dominated by *Globigerinita glutinata* and *Catapsydrax dissimilis* occurring in the temperate regions of

TABLE 3. DOMINANT PLANKTONIC FORAMINIFERAL SPECIES DURING SPECIFIC TIME INTERVALS OF THE MIOCENE AS RECORDED IN TROPICAL, WARM SUBTROPICAL, TRANSITIONAL-TEMPERATE, AND SUBANTARCTIC PROVINCES*

Epoch	Ma	Tropical	Warm-Subtropical	Transitional-Temperate	Subantarctic
Early Miocene	17.5-16.5	Globigerinoides spp. Gr. siakensis Gq. dehiscens D. altispira Gr. peripheroronda	Globigerinoides spp. Gq. dehiscens Gr. siakensis D. altispira Gq. praebulloides Gr. peripheroronda	Gr. peripheroronda Gq. dehiscens Globigerinoides spp. Gr. miozea Gq. woodi Gq. praebulloides	Gr. miozea Gq. woodi
	20-20.5	Gr. kugleri Gq. angustiumbilitata Gq. venezuelana Globigerinoides spp. Gr. siakensis-mayeri D. altispira Gq. praedehiscens	Gq. dehiscens Gq. praebulloides Globigerinoides spp. Gr. kugleri	Catapsydrax spp. Gq. dehiscens Gr. incognita Gq. woodi Gr. kugleri Ga. glutinata	Gq. woodi
Late Oligocene	24-25	Gr. kugleri Gq. angustiumbilitata Catapsydrax spp. Gr. siakensis Gq. venezuelana	Catapsydrax spp. Gq. praebulloides Gr. kugleri Gr. siakensis Gq. woodi	Catapsydrax spp. Gq. praebulloides Gr. kugleri Gq. venezuelana Gq. woodi	
Middle Miocene	12.5-11	Globigerinoides spp. Gr. siakensis Gr. menardii D. altispira Gq. venezuelana	Globigerinoides spp. Gr. menardii Gr. conoidea Gq. dehiscens D. altispira	Gr. conoidea Gq. dehiscens Gr. mayeri Gq. decoraperta Gq. praebulloides Gq. falconensis Gq. woodi	Gq. praebulloides Gr. challengerii N. continuosa Gr. panda Gq. woodi
	14-15.5	Globigerinoides spp. Gr. siakensis-mayeri D. altispira Gr. peripheroacuta Gq. venezuelana	Globigerinoides spp. Gr. siakensis-mayeri D. altispira Gq. dehiscens Gr. peripheroacuta	Gr. mayeri Gr. conoidea/miozea Gq. dehiscens Gq. druryi/decoraperta Gq. praebulloides Gq. woodi	Gr. mayeri/challengerii Gq. praebulloides Gr. panda Gr. conoidea Gq. woodi
Late Miocene	5-6	Globigerinoides spp. Gr. menardii Gq. dehiscens Gq. decoraperata D. altispira N. acostaensis P. primalis	Globigerinoides spp. Gr. conomiozea Gq. decoraperta Gq. woodi Gr. menardii N. acostaensis	Gr. conomiozea N. pachyderma Gq. bulloides Gq. woodi	N. pachyderma Gq. bulloides Gr. cibaoensis/crassula
	9-10	Globigerinoides spp. Gr. menardii D. altispira N. acostaensis Gq. nepenthes-druryi Gq. venezuelana	Gr. conoidea Globigerinoides spp. Gr. menardii Gq. nepenthes-druryi Gq. decoraperta D. altispira Gq. woodi	Gr. conoidea Gq. bulloides Gq. woodi N. pachyderma	N. pachyderma Gq. bulloides

*Note: Gg = Globigerina; Gr = Globorotalia; Gq = Globoquadrina; D = Dentoglobigerina; N = Neogloboquadrina; P = Pulleniatina; Ga = Globigerinita.

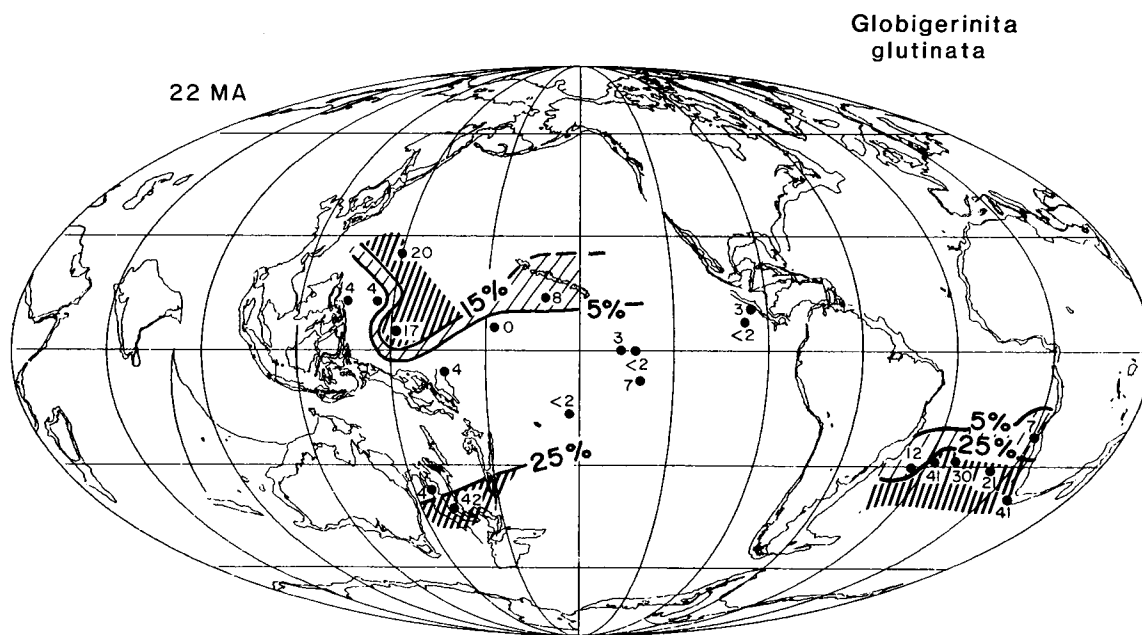


Figure 5. Percent distribution of *Globigerinita glutinata* during the earliest Miocene (22 Ma).

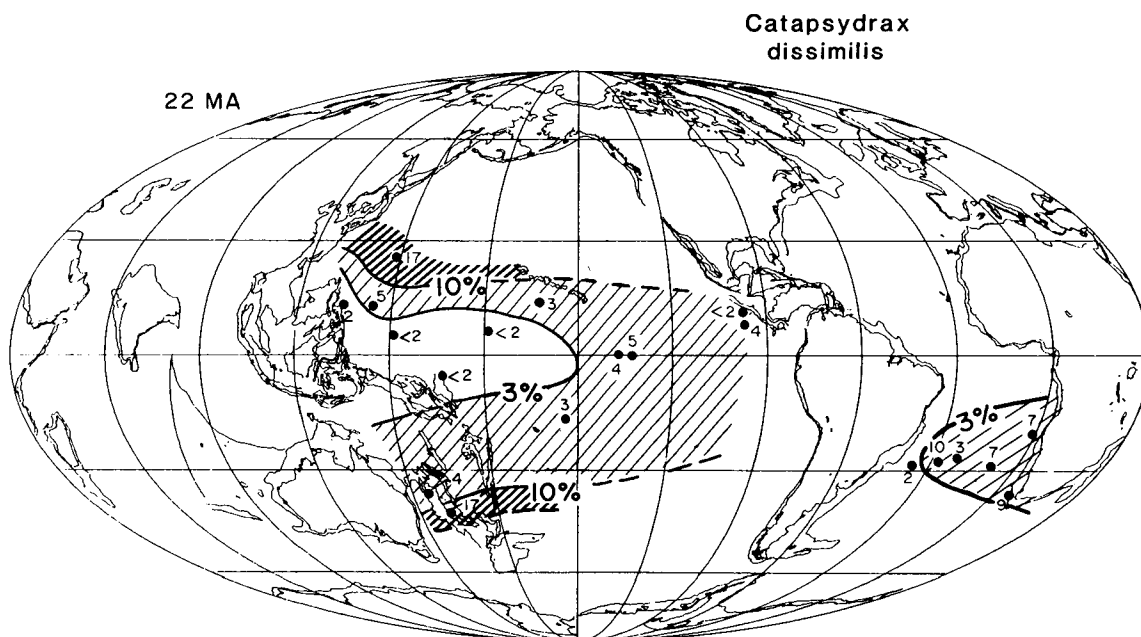


Figure 6. Percent distribution of *Catapsydrax dissimilis* during the earliest Miocene (22 Ma).

Globigerina
praebulloides

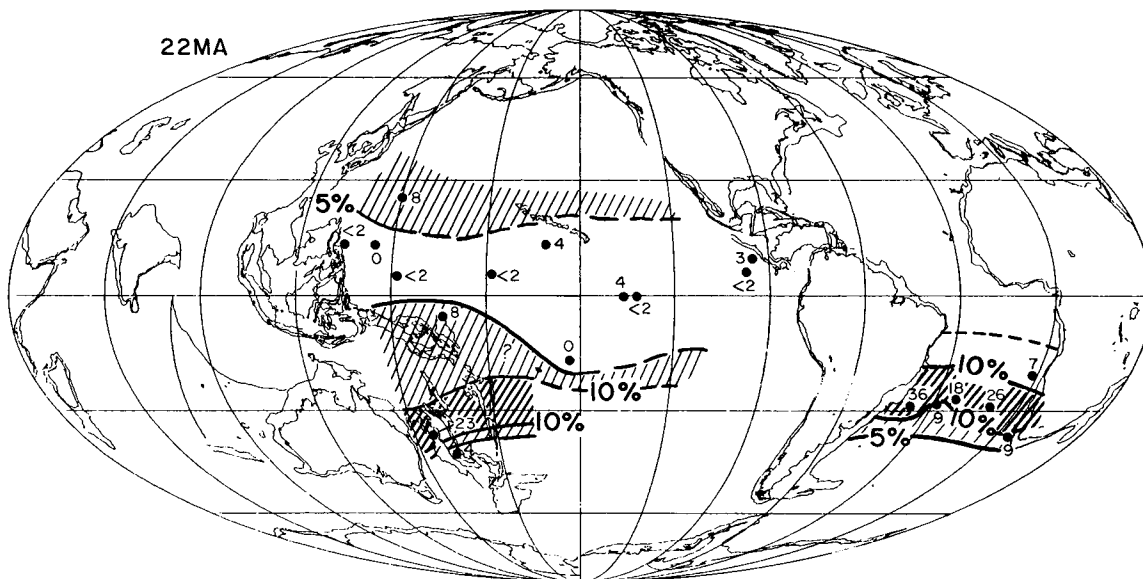


Figure 7. Percent distribution of *Globigerina praebulloides* during the earliest Miocene (22 Ma).

Globigerina
woodi and *woodi connecta*

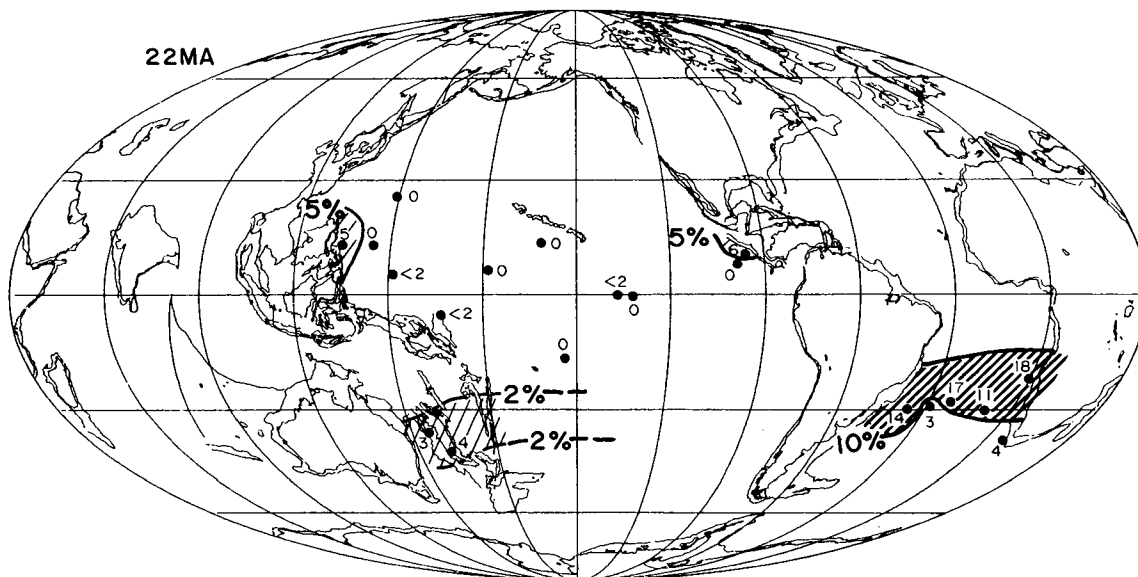


Figure 8. Percent distribution of the *Globigerina woodi*-*G. woodi connecta* complex during the earliest Miocene (22 Ma).

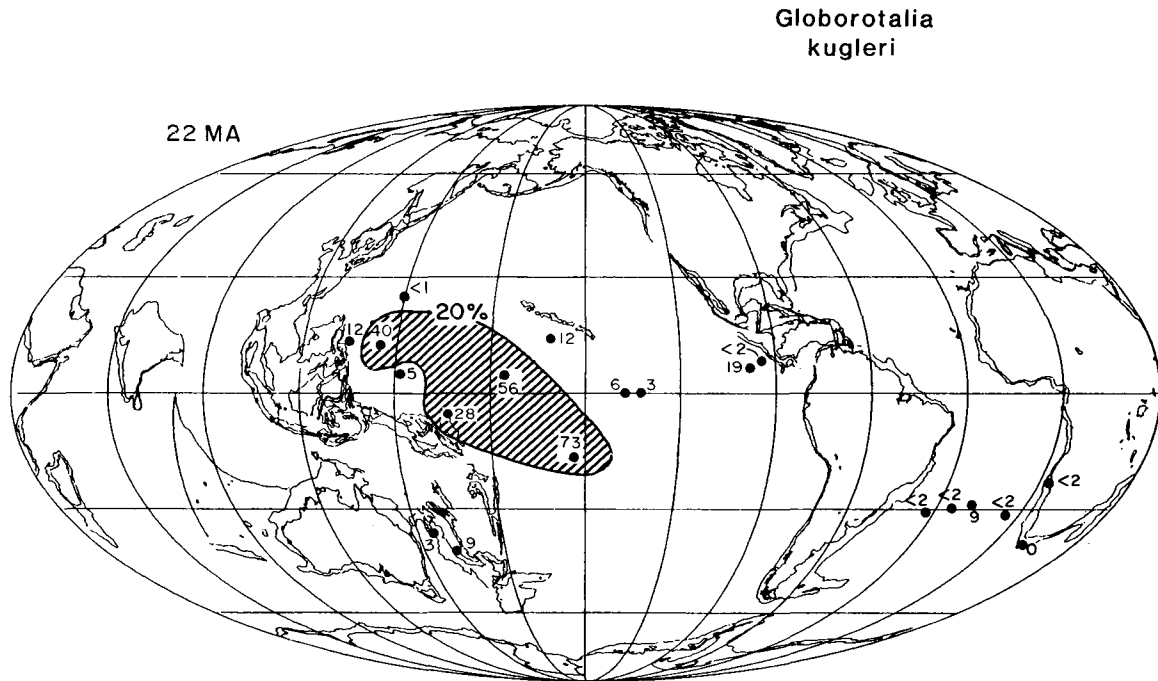


Figure 9. Percent distribution of the *Globorotalia kugleri* during the earliest Miocene (22 Ma).

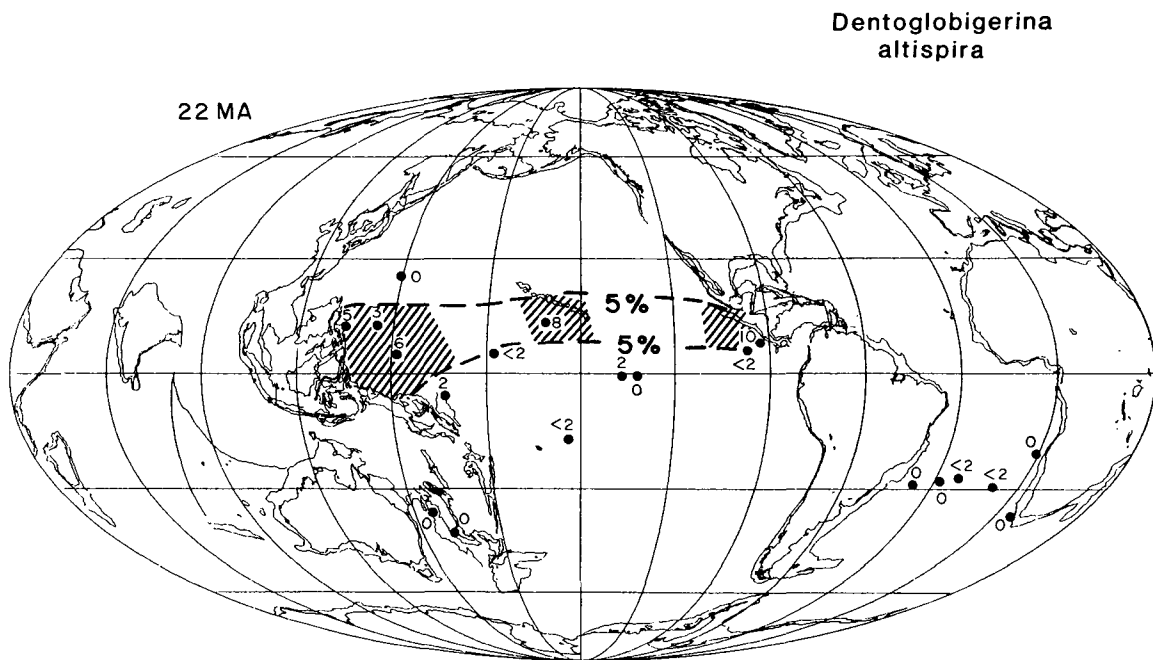


Figure 10. Percent distribution of *Dentoglobigerina altispira* during the earliest Miocene (22 Ma).

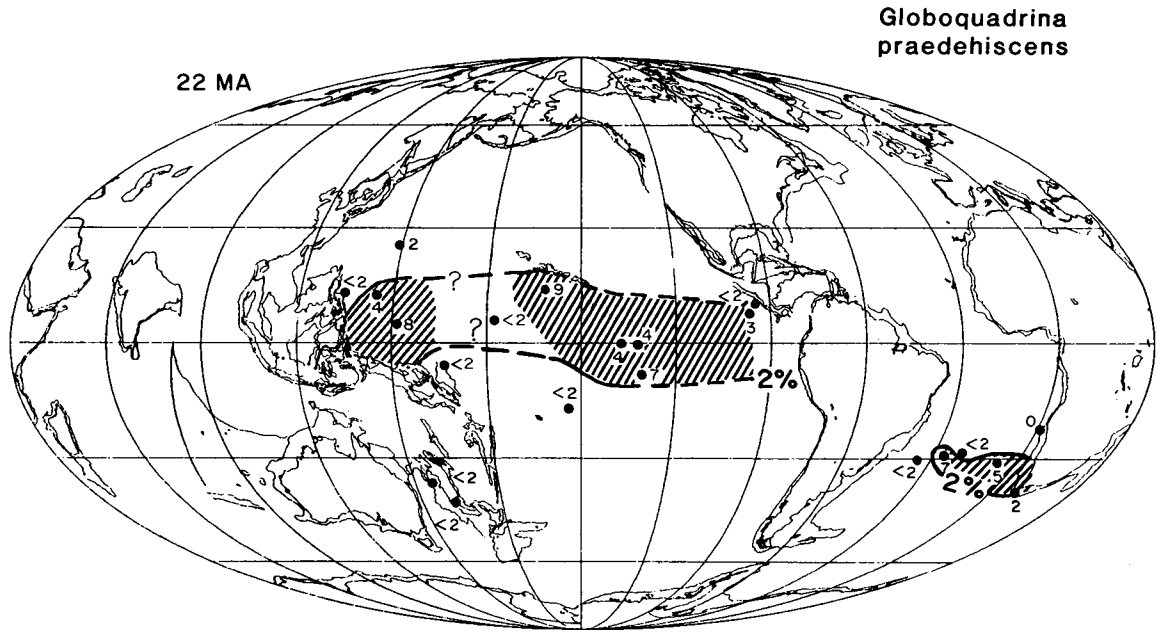


Figure 11. Percent distribution of *Globoquadrina praedehiscens* during the earliest Miocene (22 Ma).

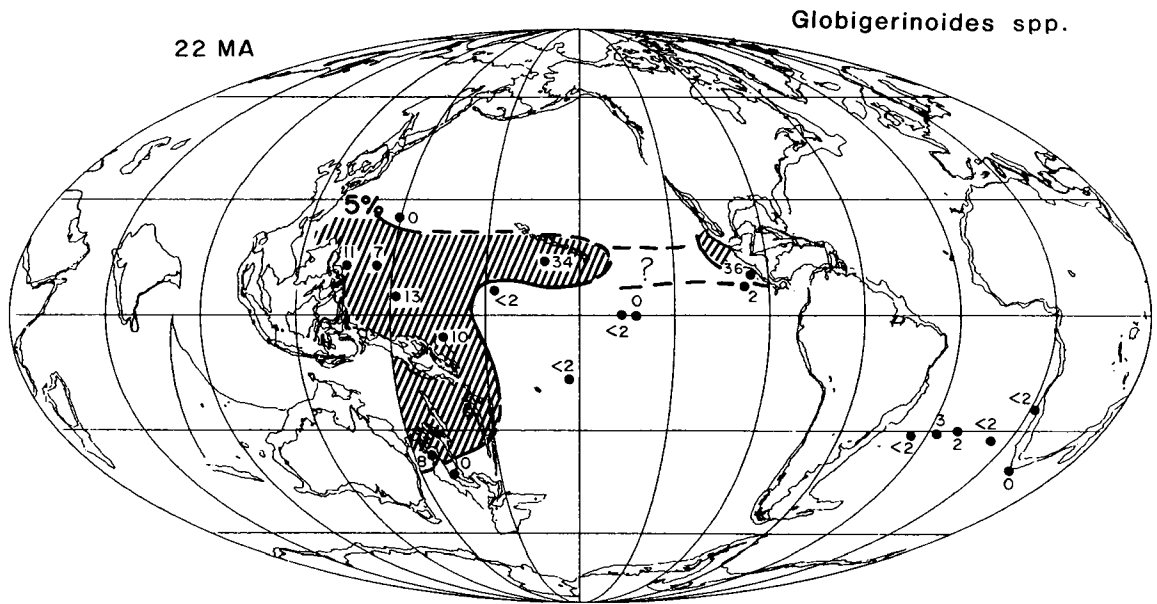


Figure 12. Percent distribution of *Globigerinoides* spp. during the earliest Miocene (22 Ma).

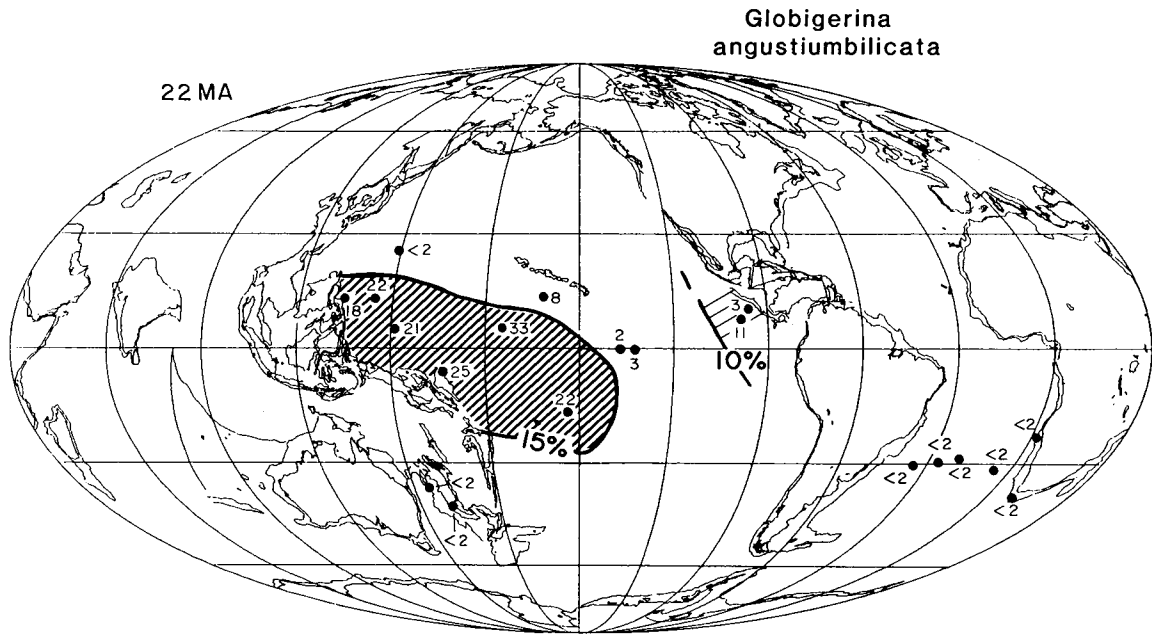


Figure 13. Percent distribution of *Globigerina angustumilicata* during the earliest Miocene (22 Ma).

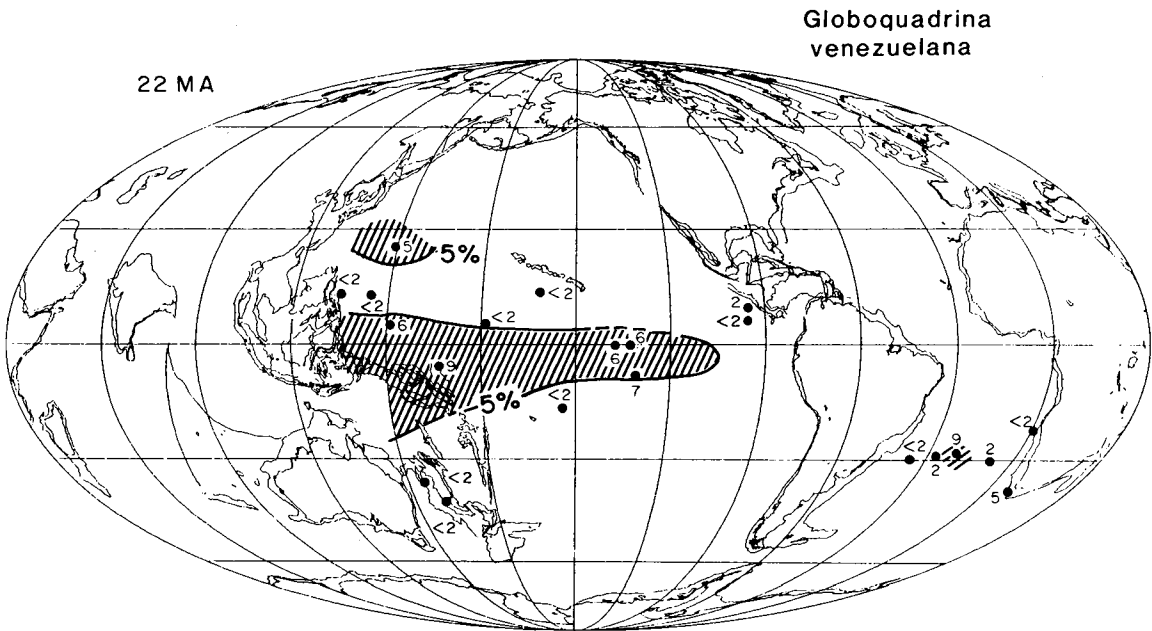


Figure 14. Percent distribution of *Globoquadrina venezuelana* during the earliest Miocene (22 Ma).

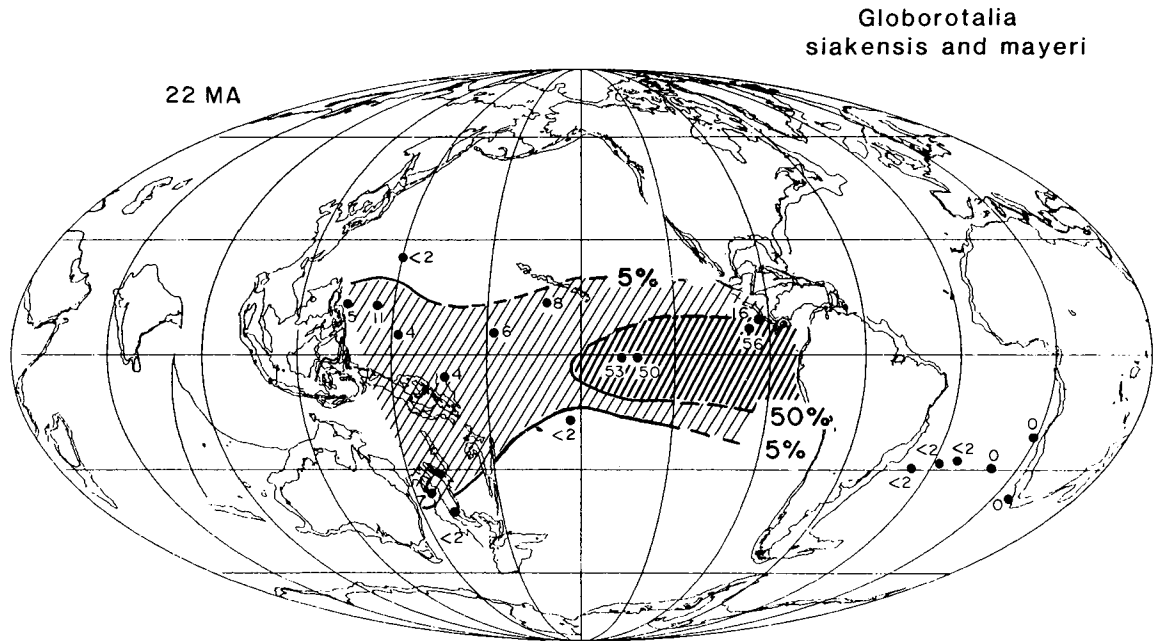


Figure 15. Percent distribution of the *Globorotalia siakensis*-*G. mayeri* complex during the earliest Miocene (22 Ma).

the Pacific. In the South Pacific this assemblage would almost certainly be latitudinally distributed across the temperate latitudes but there is insufficient sample coverage to define this pattern. It is also significant that the Temperate Assemblage occurred in relatively low latitudes in the northwestern Pacific, an area presently under the strong influence of the tropical-warm subtropical western boundary current.

Factor 4. Western Tropical (18% of the faunal variance). This assemblage is dominated by *Globigerinoides* and *Globigerina angustiumbilitata*. This factor was restricted to the low latitudes of the western Pacific. It broadly overlaps with Factor 1 but was more restricted to north central regions within the tropics.

Factor 5. Southwest warm subtropical (8% of the faunal variance). This assemblage is dominated by *Globigerina praebulloides* occurring in the warm subtropics of the southwest Pacific. This assemblage was almost certainly distributed latitudinally across the South Pacific but cannot be identified because of insufficient sample coverage.

Late Early Miocene: 16 Ma

For this time-slice, distributions are shown for eight taxa. By the late early Miocene subantarctic assemblages were dominated by *Globigerina praebulloides* (Figure 17) which also extends its range at much lower frequencies into temperate areas. During most of the early Miocene, this species was largely a warm subtropical species (Figure 7) but by the latest early to early middle Miocene it had switched its environmental tolerance to high latitudes, at least in the Pacific region.

Faunal elements clearly restricted to temperate areas were not apparent in the late early Miocene except for the *Globorotalia miozea*-*G. conoidea* complex. Species tended to exhibit broader distribution patterns and range into the warm subtropics. Important temperate-subtropical faunal elements during 16 Ma included *Globigerinita glutinata*, which also ranged into the warm subtropics and even into the tropics of the western Pacific (Figure 18); *Globoquadrina dehiscens* (Figure 19); and *Globigerina woodi* (Figure 20).

As during the earliest Miocene, tropical faunal elements tended to be distributed either in the western or eastern sectors of the Pacific. Faunal elements important in the west were *Globigerinoides* (Figure 21) which, similar to the earliest Miocene (Figure 12), were broadly distributed in both the tropics and subtropics; and *Dentoglobigerina altispira* (Figure 22). Compared with its distribution in the earliest Miocene (Figure 10), *Dentoglobigerina altispira* distinctly increased its frequencies in the western tropical Pacific, although it still extended to the east.

As in the earliest Miocene, the *Globorotalia siakensis*-*G. mayeri* complex dominated the eastern tropical Pacific (Figure 23), but higher frequencies ranged further westward than in the early Miocene. Similarly *Globoquadrina venezuelana* exhibited slightly higher frequencies in the eastern tropical Pacific (Figure 24).

Factor analysis of the 16 Ma data (5-factors; 96% of the faunal variance) shows the distribution of 5 biogeographic provinces as follows (Figure 25).

Factor 1. Western Tropical-Subtropical Assemblage (33% of the faunal variance). This assemblage, dominated by *Globige-*

22 MA

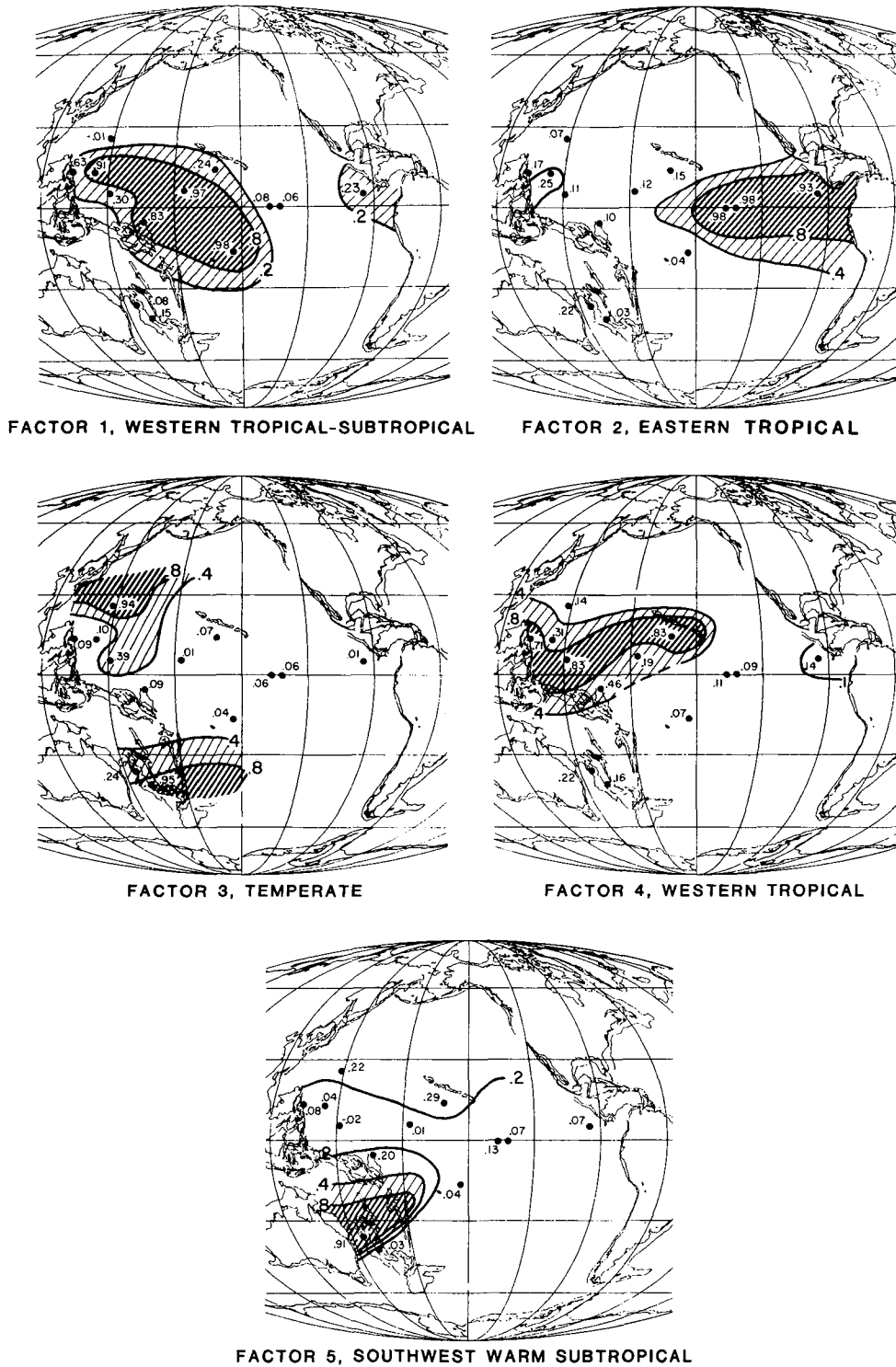


Figure 16. Distribution of planktonic foraminiferal assemblages in the Pacific at 22 Ma (earliest Miocene). Time-slice cores are plotted with indicated factor scores (from Q-mode factor analysis). Contoured and shaded areas delineate regions dominated by each assemblage: Factor 1, Western Tropical-Subtropical Assemblage; Factor 2, Eastern Tropical Assemblage; Factor 3, Temperate Assemblage; Factor 4, Western Tropical Assemblage; and Factor 5, Southwest Warm Subtropical Assemblage.

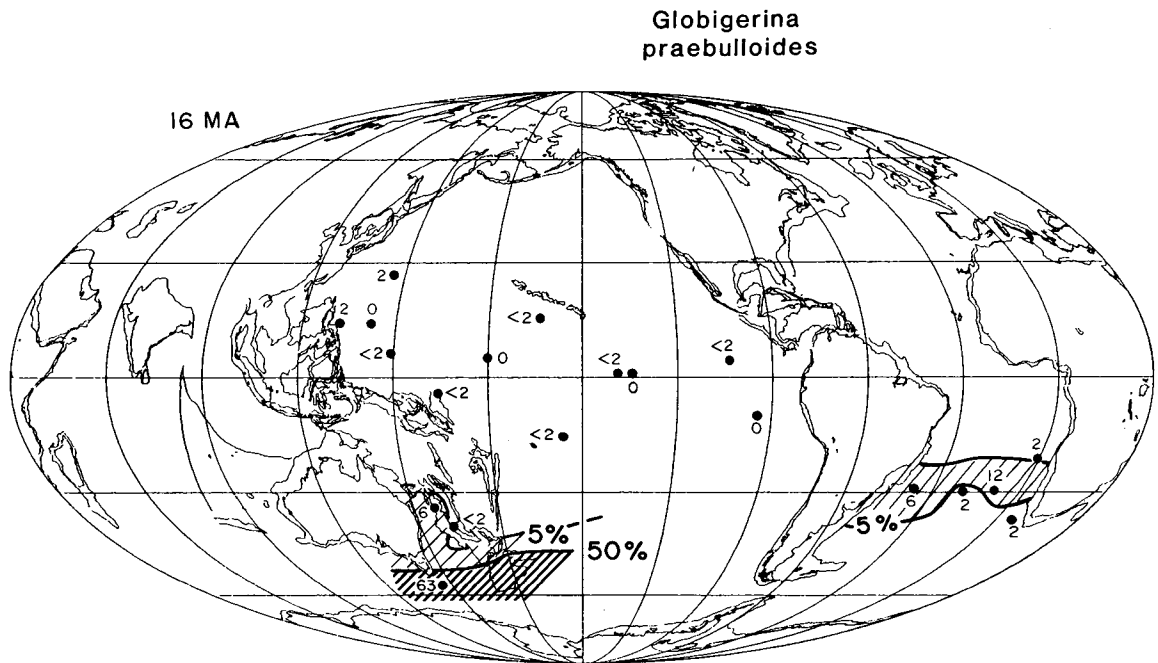


Figure 17. Percent distribution of *Globigerina praebulloides* during the latest early Miocene (16 Ma).

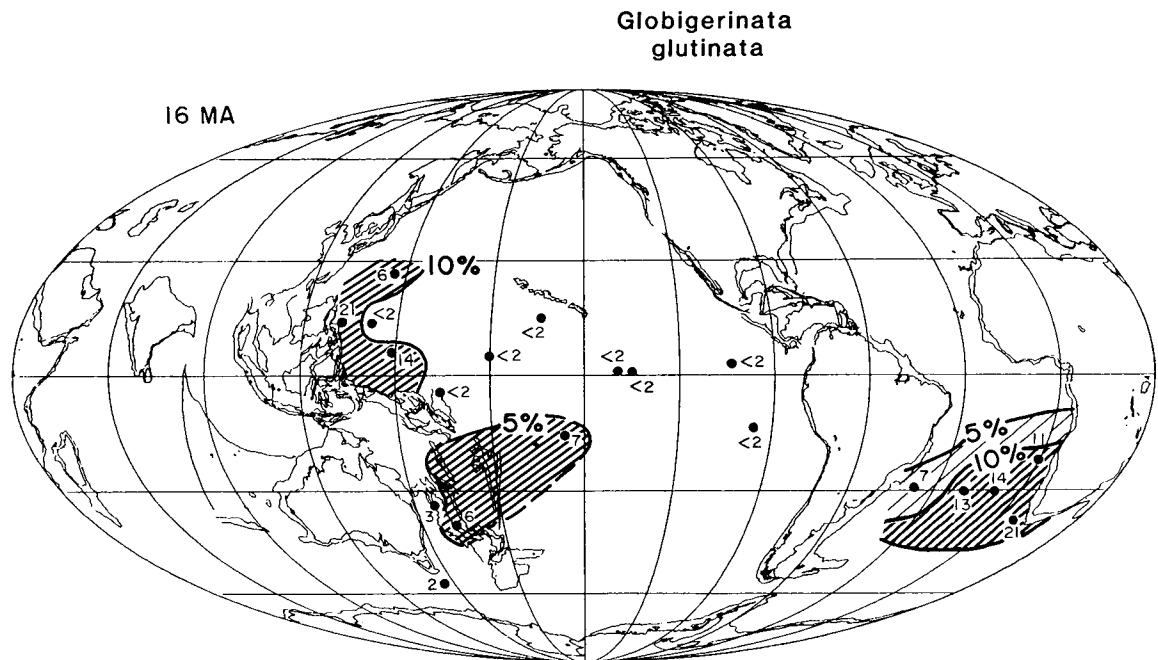


Figure 18. Percent distribution of *Globigerinina glutinata* during the latest early Miocene (16 Ma).

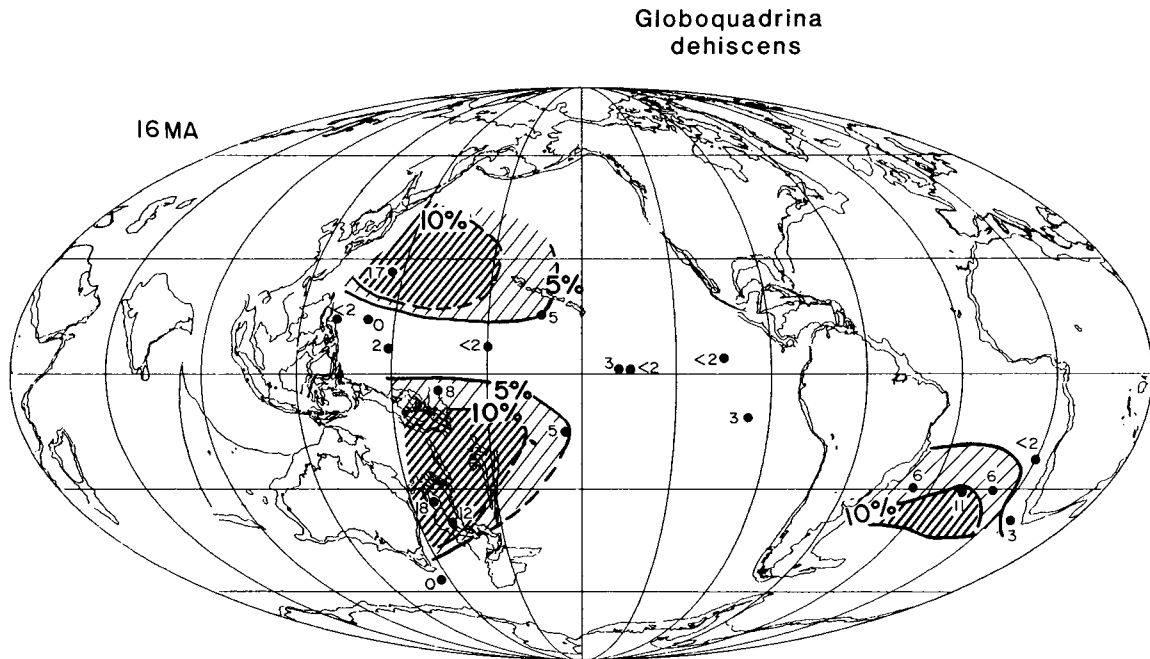


Figure 19. Percent distribution of *Globoquadrina dehiscens* during the latest early Miocene (16 Ma).

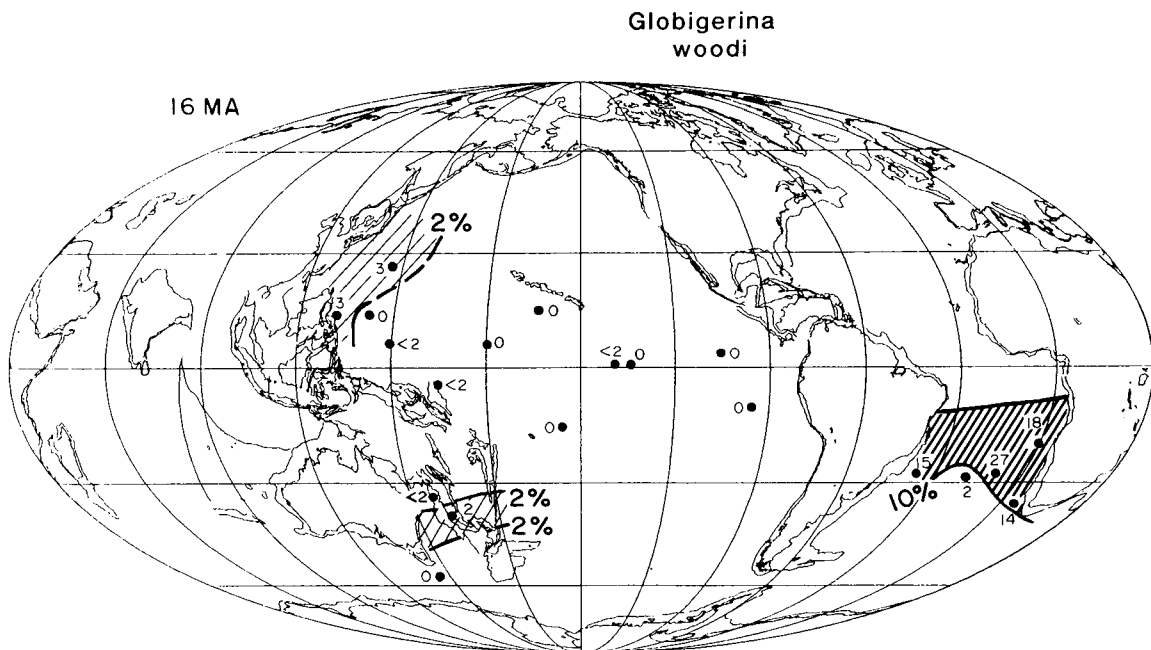


Figure 20. Percent distribution of *Globigerina woodi* during the latest early Miocene (16 Ma).

Globigerinoides spp.

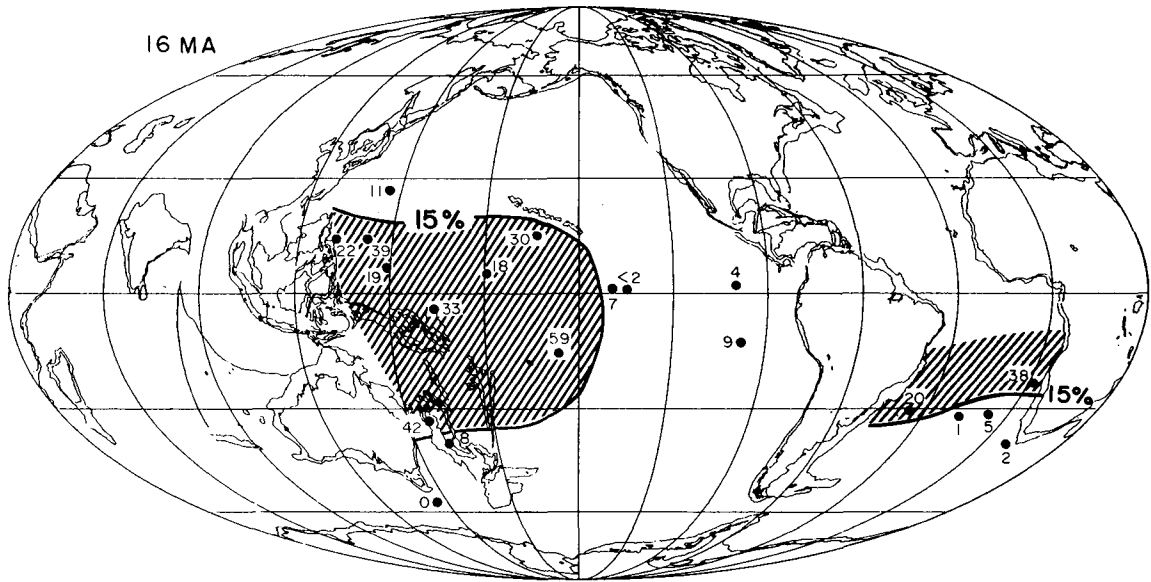


Figure 21. Percent distribution of *Globigerinoides* spp. during the latest early Miocene (16 Ma).

Dentoglobigerina
altispira

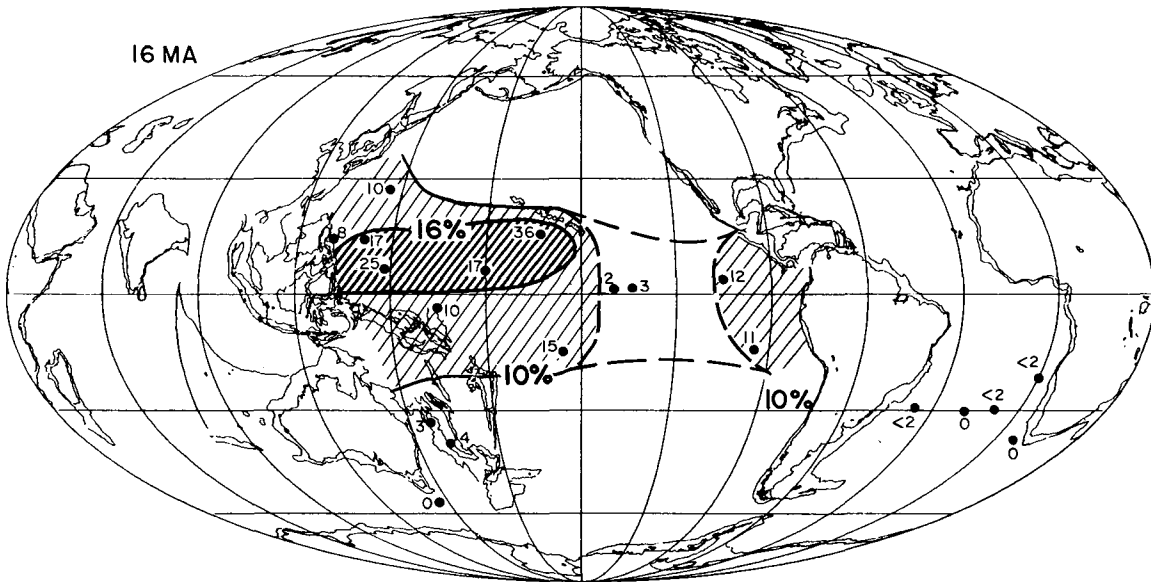


Figure 22. Percent distribution of *Dentoglobigerina altispira* during the latest early Miocene (16 Ma).

Globorotalia
siakensis and *mayeri*

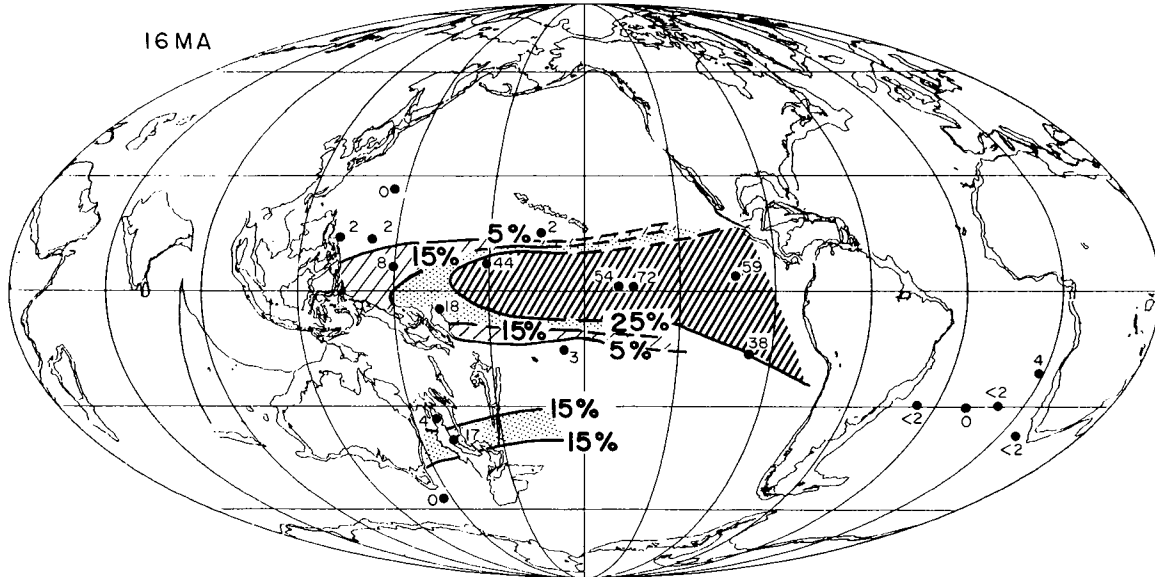


Figure 23. Percent distribution of the *Globorotalia siakensis*-*G. mayeri* complex during the latest early Miocene (16 Ma).

Globoquadrina
venezuelana

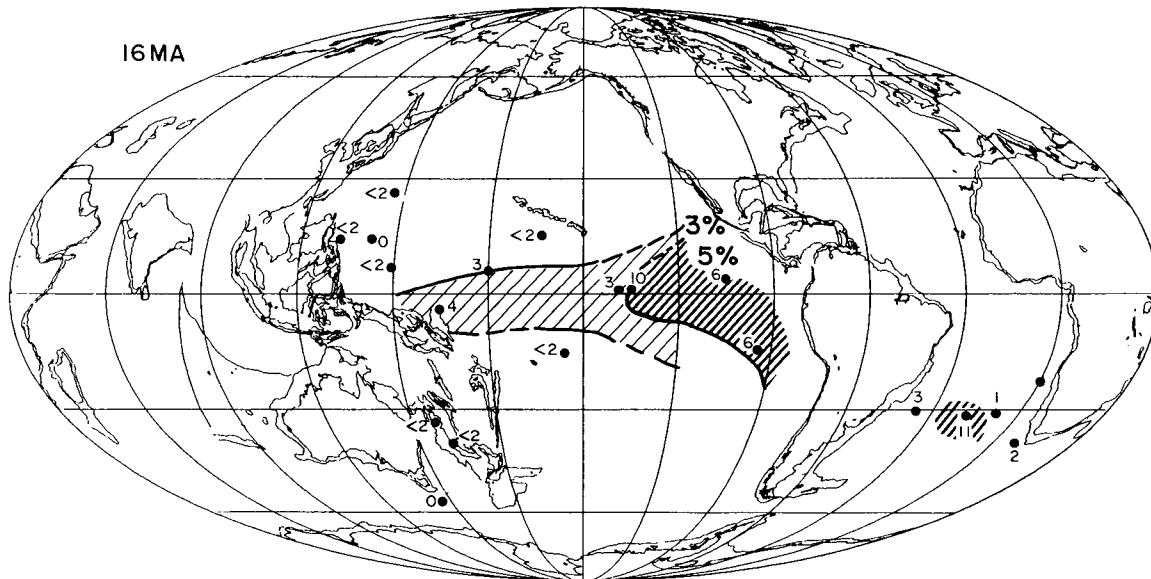


Figure 24. Percent distribution of *Globoquadrina venezuelana* during the latest early Miocene (16 Ma).

16 MA

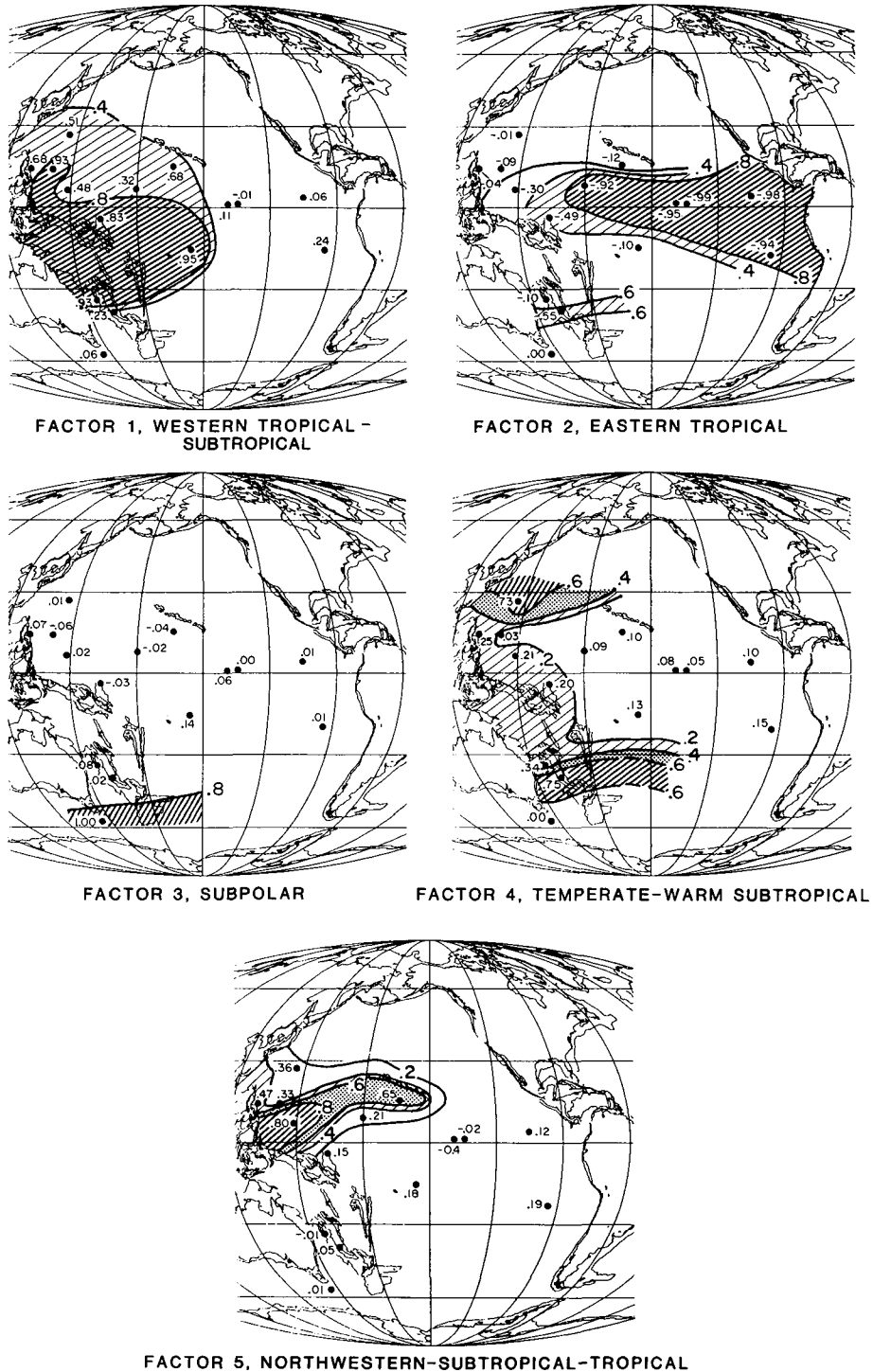


Figure 25. Distribution of planktonic foraminiferal assemblages in the Pacific at 16 Ma (latest early Miocene). Time-slice cores are plotted with indicated factor scores (from Q-mode factor analysis). Contoured and shaded areas delineate regions dominated by each assemblage: Factor 1, Western Tropical-Subtropical Assemblage; Factor 2, Eastern Tropical Assemblage; Factor 3, Subpolar Assemblage; Factor 4, Temperate-Warm Subtropical Assemblage; and Factor 5, Northwestern-Subtropical-Tropical Assemblage.

rinoides, was distributed broadly over the western tropical-subtropical Pacific, but did not extend toward the eastern tropical Pacific.

Factor 2. Eastern Tropical Assemblage (35% of the faunal variance). This assemblage is dominated, as in the earliest Miocene (Figure 16), by the *Globorotalia siakensis*-*G. mayeri* complex, that clearly defined an eastern tropical biogeographic province but extended further to the west than in the earliest Miocene (Figure 16).

Factor 3. Subpolar Assemblage (7% of the faunal variance). This assemblage is dominated by *Globigerina praebulloides* that clearly marked the subantarctic region in the South Pacific. This assemblage seems to have been latitudinally distributed around the Antarctic (including the South Atlantic), but insufficient samples were available to define this pattern.

Factor 4. Temperate-Warm Subtropical Assemblage (10% of the faunal variance). This assemblage is dominated by *Globoquadrina dehiscens* and the *Globorotalia miozea*-*G. conoidea* complex. This assemblage was most strongly developed in the temperate areas of the North and South Pacific but extended into warm subtropical and even tropical areas of the western Pacific. It was inferred that this assemblage was latitudinally distributed in temperate water masses, but not in the tropics where there was a relatively greater importance of this assemblage in the west compared to the east.

Factor 5. Northwestern Subtropical-Tropical Assemblage (11% of the faunal variance). This assemblage is dominated by *Dentoglobigerina altispira* and *Globigerinita glutinata* and was distributed in tropical-subtropical latitudes in the northwest Pacific.

Late Miocene: 8 Ma

For this time-slice, the distribution is shown for ten taxa. As with the late early Miocene time-slice, the subpolar assemblage was clearly dominated by *Globigerina bulloides* (Figure 26) (The ancestral form of *G. bulloides* is *G. praebulloides*.) This species also extended into temperate areas as an important element. It showed up clearly as the dominant element associated with the California Current; and was an important cool-water element in both hemispheres. It was also an important element in temperate latitudes of the southeast Atlantic adjacent to South Africa associated with regions of upwelling (Hodell and Kennett 1985).

The temperate regions were marked by high frequencies of *Globigerina woodi* (Figure 27) and *Globorotalia conoidea* (Figure 28), although *G. woodi* was an unimportant component of north Pacific assemblages.

In this time-slice, the distribution of most tropical taxa were unlike that of the two early Miocene time-slices. Instead of exhibiting high frequencies in the western or eastern tropics, the species were generally distributed across the tropics. The patterns are most different between the 8 and 22 Ma maps, while the 16 Ma maps tend to be intermediate in character. Such patterns are shown by the *Globorotalia menardii*-*limbata* complex that was

almost equatorial in its distribution (Figure 29); *Globigerinoides* was more broadly tropical and warm subtropical (Figure 30); the *Globigerina nepenthes*-*G. druryi* complex (Figure 31) although widespread (temperate to tropics) favored tropical to warm subtropical areas away from the equator; and *Globoquadrina venezuelana* that was closely associated with the trans-equatorial Pacific region (Figure 32).

Another important change in the distribution of planktonic foraminifera between the 8 Ma and the earlier time-slices was the strong northward distributional extension into the northwest Pacific of certain tropical taxa; in particular *Globigerinoides* and the *Globigerina nepenthes*-*G. druryi* complex (Figures 30 and 31). In the early Miocene no tropical species were found to extend their ranges so far north in such high frequencies.

There are two tropical species that may not have been distributed entirely across the tropical Pacific: *Dentoglobigerina altispira* (Figure 33) and *Neogloboquadrina acostaensis* (Figure 34). The latter, however, showed relatively high frequencies in both west and eastern sectors, separated by low frequencies in only a single mid-ocean sample (Figure 34).

The distribution of *Globigerinita glutinata* was unusually disjointed over a wide range of latitudes (Figure 35), with highest frequencies in the far eastern equatorial Pacific. Tolderlund and Bé (1971) have shown that *G. glutinata*, a surface dweller, is the most nearly ubiquitous planktonic foraminiferal species in the Modern ocean (Bé and Hamlin 1967).

Factor analysis of the 8 Ma data (5 factors; 93% of the faunal variance) shows the distribution of four distinct faunal assemblages and one less distinctive grouping as follows (Figure 36).

Factor 1. Tropical-Trans-Pacific Assemblage (23% of the faunal variance). This assemblage is dominated by the *Globigerina nepenthes*-*G. druryi* complex, which was distributed across the tropical Pacific and swept northward into the northwest Pacific as far as Japan in association with the western boundary current.

Factor 2. Subpolar-Temperate Assemblage (21% of the faunal variance). This assemblage is dominated by *Globigerina bulloides* and was distributed in polar to temperate latitudes in both hemispheres.

Factor 3. Trans-Equatorial Assemblage (18% of the faunal variance). This assemblage is dominated by the *Globorotalia menardii*-*G. limbata* complex and *Globigerinoides* and was distributed across the Pacific Ocean in close association with the equatorial and warmer tropics. High abundance of this assemblage was more closely associated with and restricted to latitudes close to the equator compared with the tropical-transpacific assemblage. Highest frequencies were closely associated with the equatorial region as in the modern ocean (Tolderlund and Bé 1971).

Factor 4. Temperate-Transitional Assemblage (20% of the faunal variance). This assemblage is dominated by *Globorotalia conoidea* and *Globigerina woodi* and almost certainly formed a latitudinally distributed zone in the Southern Hemisphere, where

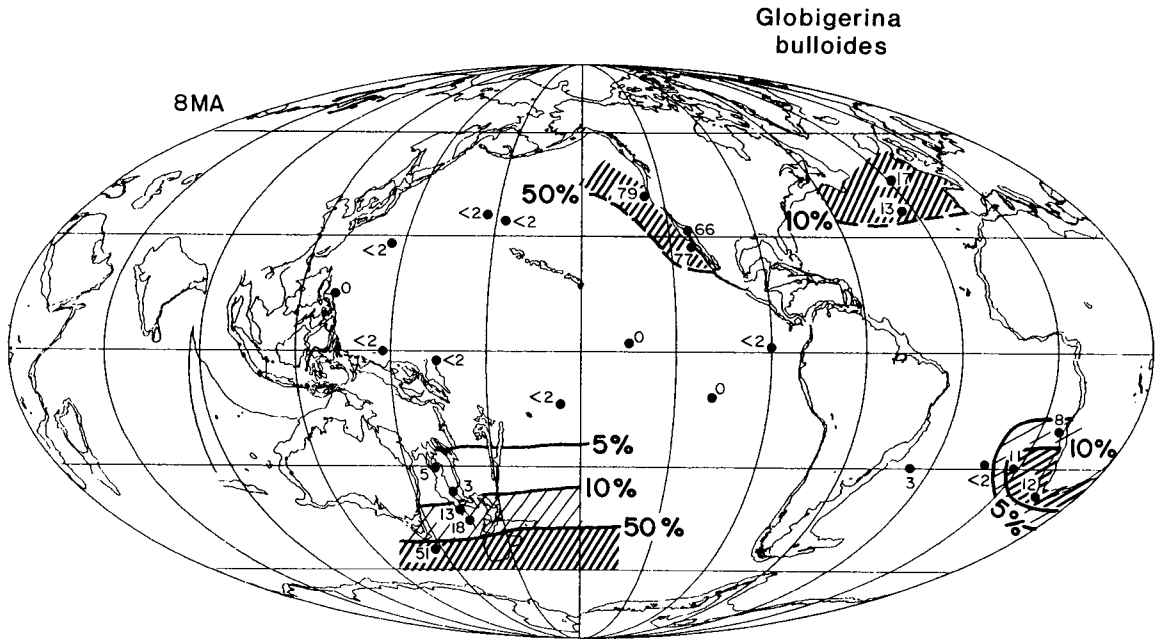


Figure 26. Percent distribution of *Globigerina bulloides* during the late Miocene (8 Ma).

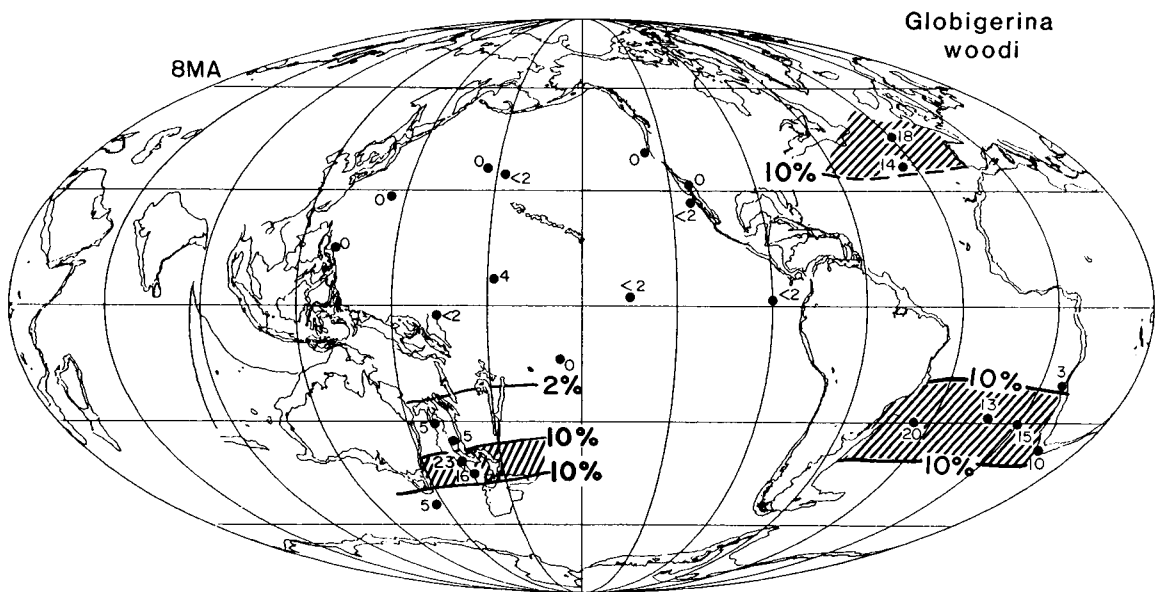


Figure 27. Percent distribution of *Globigerina woodi* during the late Miocene (8 Ma).

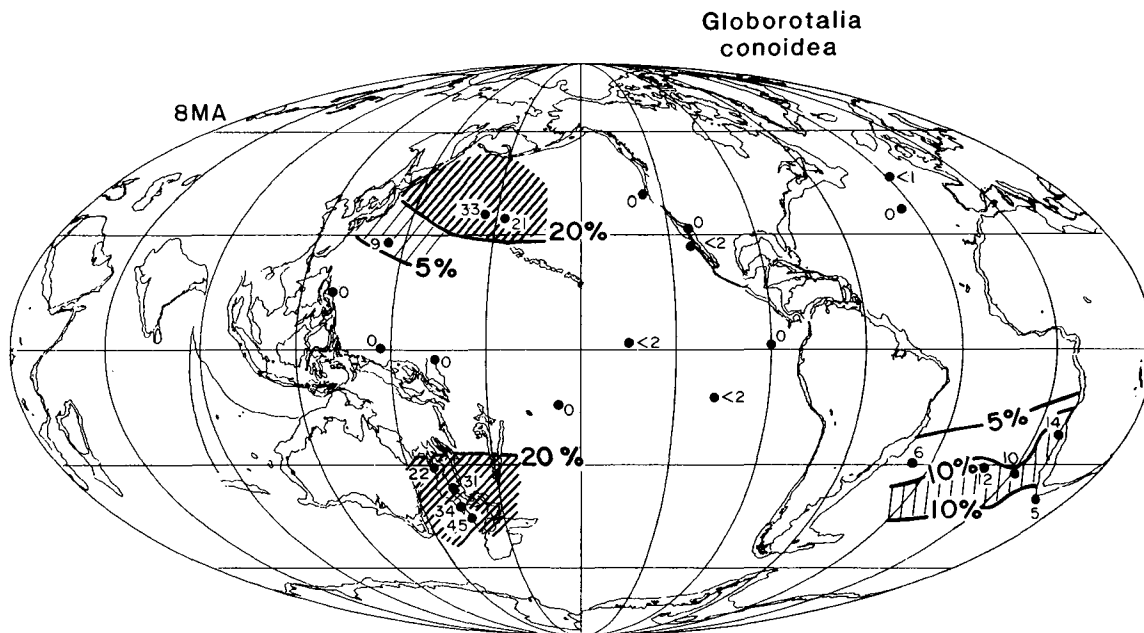


Figure 28. Percent distribution of *Globorotalia conoidea* during the late Miocene (8 Ma).

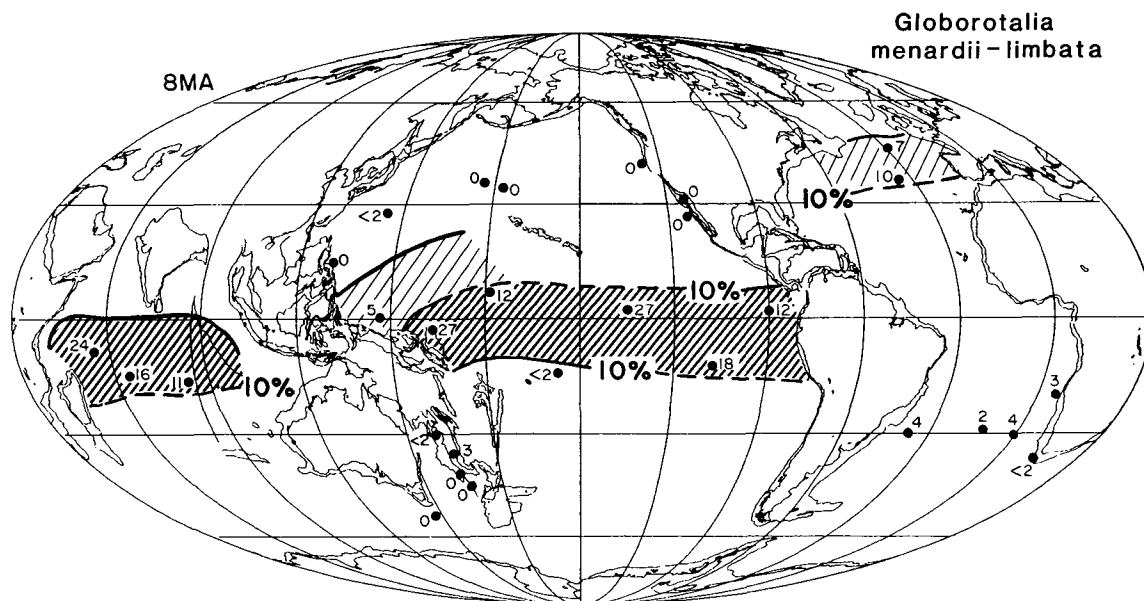


Figure 29. Percent distribution of *Globorotalia menardii*-*G. limbata* during the late Miocene (8 Ma).

Globigerinoides spp.

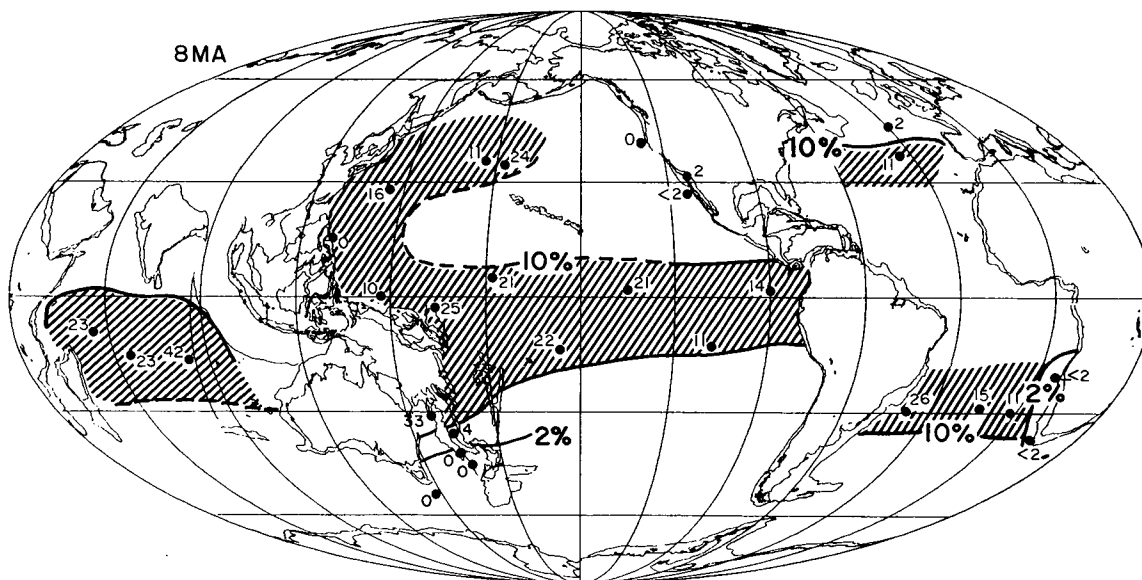


Figure 30. Percent distribution of *Globigerinoides* spp. during the late Miocene (8 Ma).

Globigerina
nepenthes and *druryi*

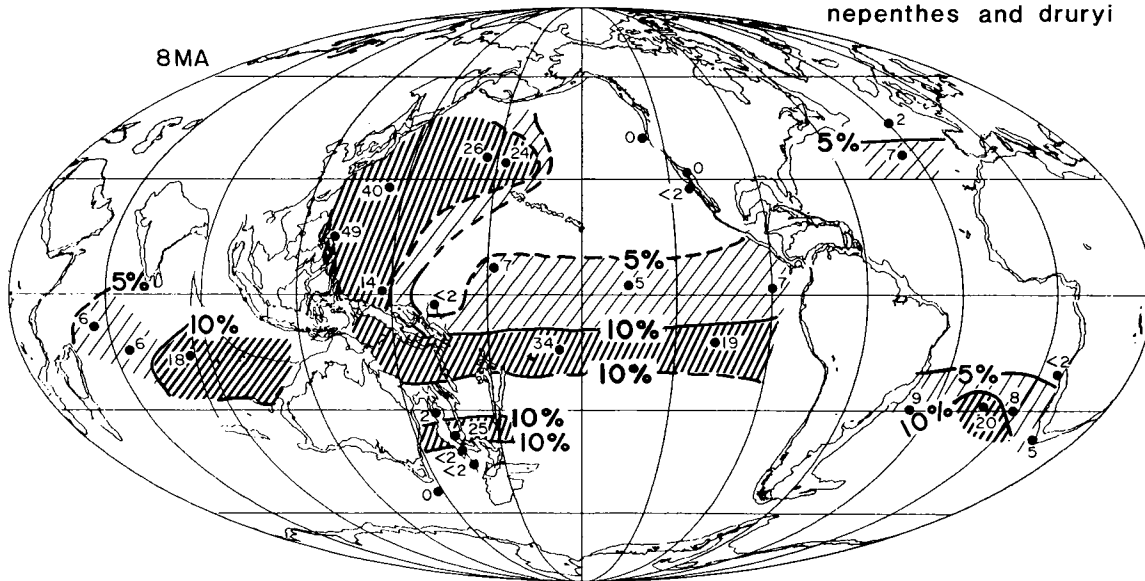


Figure 31. Percent distribution of *Globigerina nepenthes* and *druryi* during the late Miocene (8 Ma).

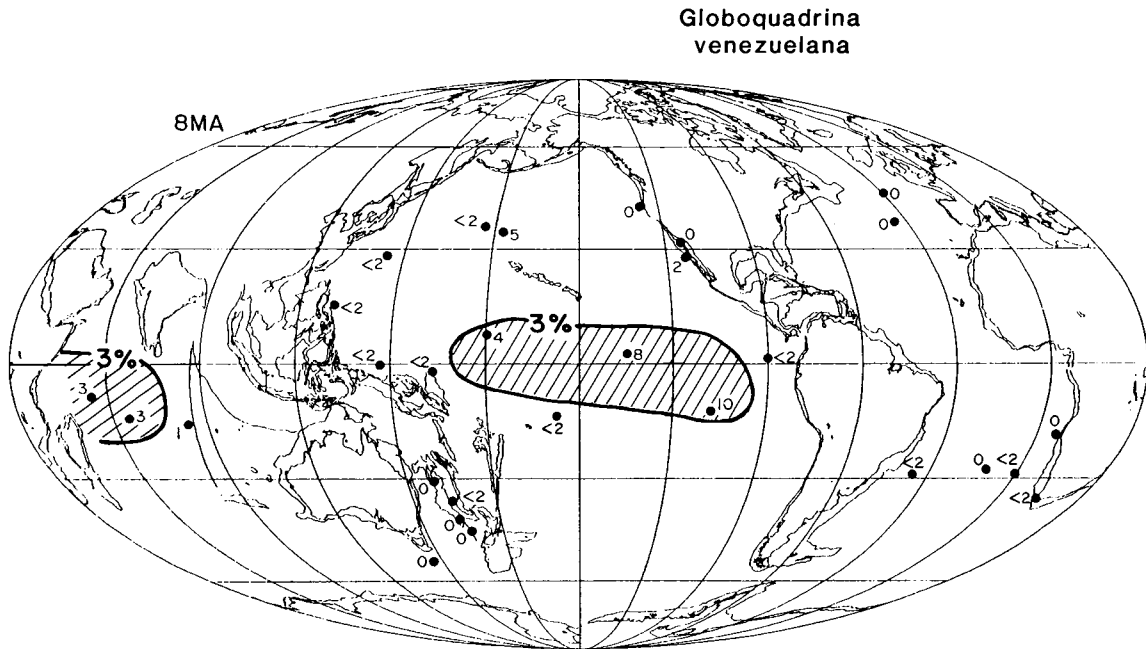


Figure 32. Percent distribution of *Globoquadrina venezuelana* during the late Miocene (8 Ma).

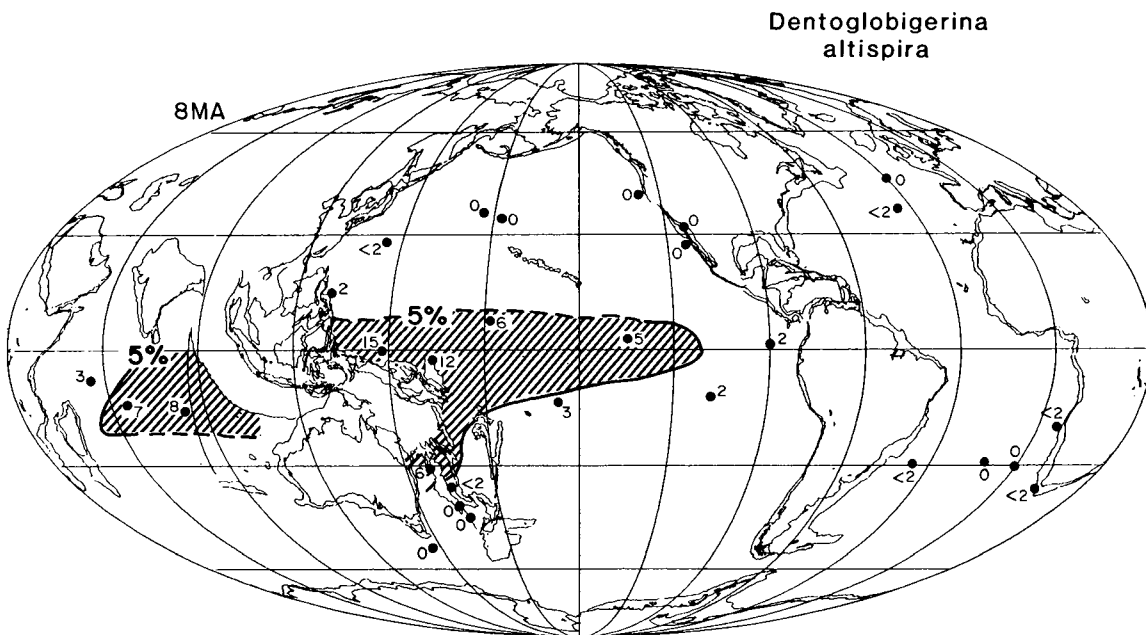


Figure 33. Percent distribution of *Dentoglobigerina altispira* during the late Miocene (8 Ma).

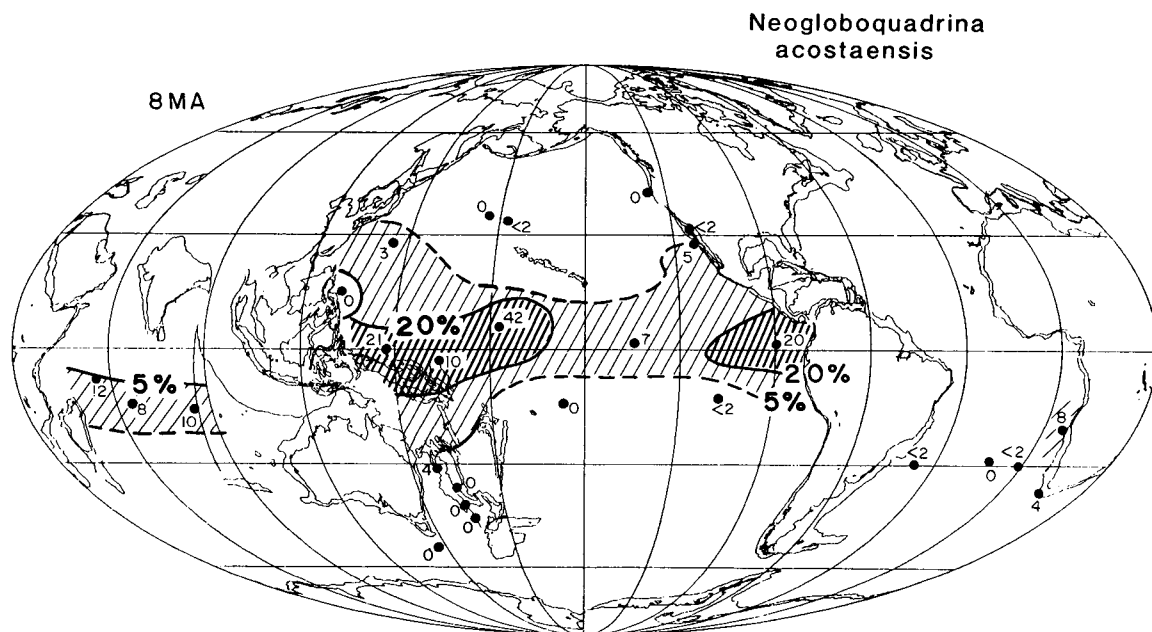


Figure 34. Percent distribution of *Neogloboquadrina acostaensis* during the late Miocene (8 Ma).

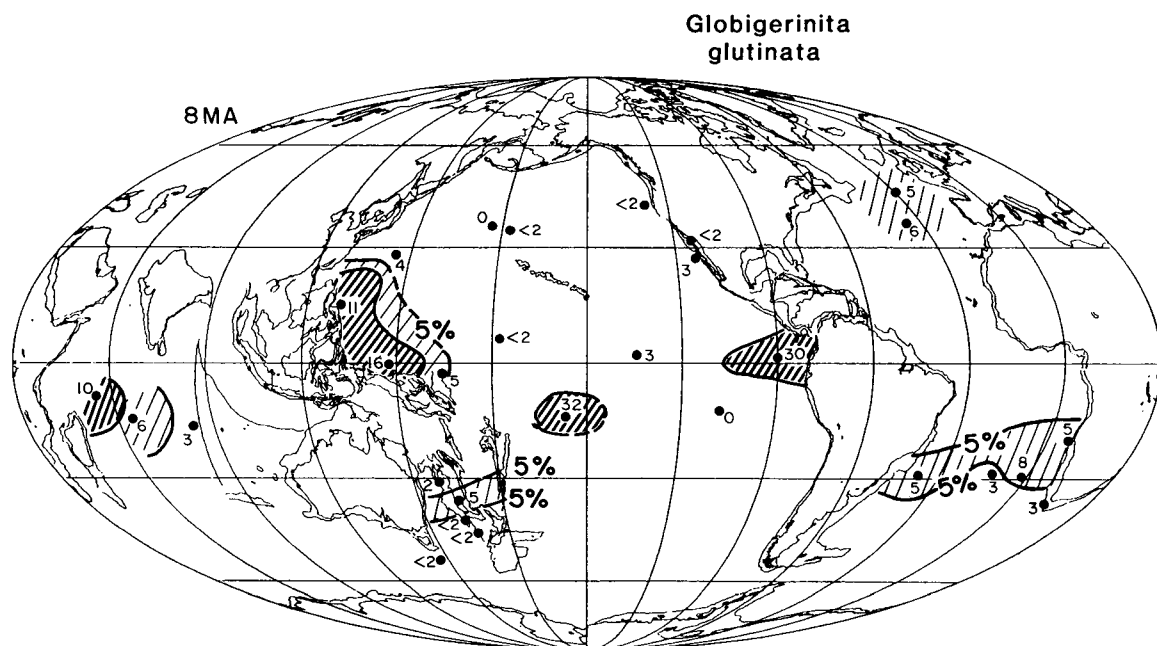


Figure 35. Percent distribution of *Globigerinita glutinata* during the late Miocene (8 Ma).

8 MA

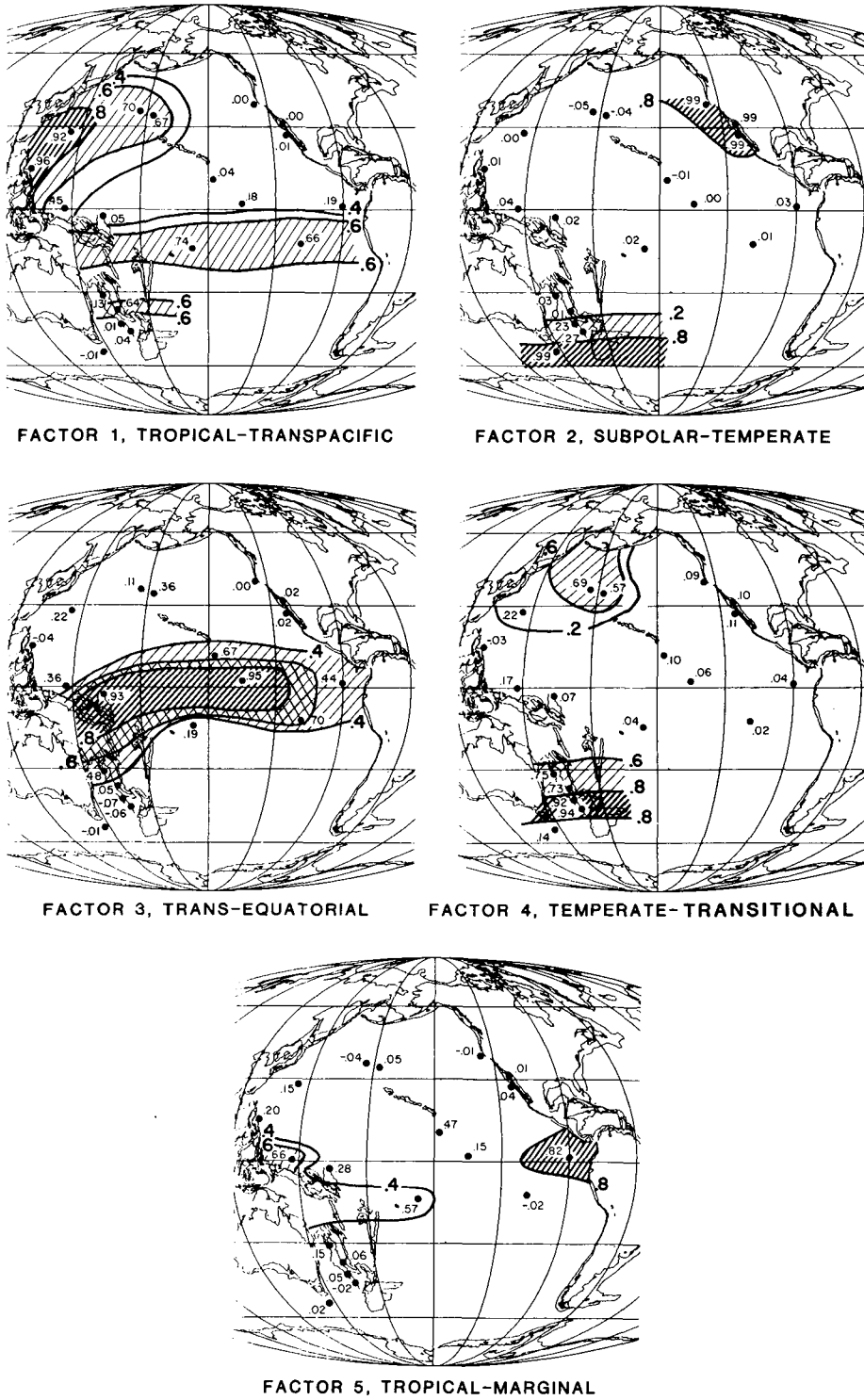


Figure 36. Distribution of planktonic foraminiferal assemblages in the Pacific at 8 Ma (late Miocene). Time-slice cores are plotted with indicated factor scores (from Q-mode factor analysis). Contoured and shaded areas delineate regions dominated by each assemblage: Factor 1, Tropical-Transpacific Assemblage; Factor 2, Subpolar-Temperate Assemblage; Factor 3, Trans-Equatorial Assemblage; Factor 4, Temperate-Transitional Assemblage; and Factor 5, Tropical-Marginal Assemblage.

it was most strongly developed. In the Northern Hemisphere it appeared to form an extension of the tongue of the warm-water assemblage represented by Factor 1.

Factor 5. Tropical-Marginal Assemblage (10% of the faunal variance). This assemblage is dominated by *Globigerinita glutinata* and *Neogloboquadrina acostaensis*. This assemblage was most strongly developed in the eastern equatorial Pacific, but occurred to a lesser extent in the western tropical Pacific, relatively close to the continental areas.

DISCUSSION

The primary objective of this mapping experiment was to determine if fundamental differences existed in the distribution patterns of planktonic foraminiferal species and assemblages between each of the three time-slice intervals. Differences might provide useful information about changes in surface-water circulation during the Miocene. Changes in Miocene biogeographic patterns should have occurred as a result of major changes in the boundary conditions of the oceans and of global climates. During each of the Miocene time-slices the Central American Seaway was open. However, during the middle to early late Miocene three fundamental changes occurred that should have affected Indo-Pacific surface-water circulation. First, continued northward expansion occurred of the Antarctic-Subantarctic water masses as Australia continued its drift northwards and as the polar glacial regime developed (Kennett 1977). This also would have contributed to the increase in temperature gradients between equator and poles. Loutit et al. (1983b) calculated that the late Miocene latitudinal temperature gradient in the Southern Hemisphere was about $\frac{3}{4}$ of the present surface ocean and that it doubled during the Miocene from about 6° to about 12°C. This was in response to the thermal isolation of Antarctica. Second, there occurred major accumulation of Antarctic ice in the form of an ice sheet from about 15 to 13 m.y. ago (Shackleton and Kennett 1975; Savin et al 1975) that resulted from the thermal isolation and cooling of the Antarctic region. The development of this ice sheet would have created positive climatic feedback and further cooling of the Antarctic region, and led to further steepening of the equator to pole temperature gradient. Third, the Indonesian Seaway became increasingly constricted, so that by the middle Miocene-early late Miocene it ceased to be an effective gateway for surface-water transportation between the tropical Pacific and Indian Oceans (van Andel et al., 1975; Edwards 1975; Kennett 1977; Sclater et al., 1985).

Our descriptions of the biogeographic maps demonstrate that important changes did occur in the biogeographic patterns of planktonic foraminifera during the Miocene and that the most important of these occurred between 16 and 8 m.y. ago (late-early and late Miocene) (See Keller 1985). Patterns are relatively similar between the two early Miocene time-slices. Thunell and Belyea (1982) have previously shown that one of the major changes in planktonic foraminiferal biogeography of the Atlantic occurred during the middle Miocene as a result of steepening of

the latitudinal temperature gradients. The primary biogeographic differences between the early and late Miocene require summary before discussion of their implications. They are as follows.

1. During the early Miocene there existed distinct faunal assemblages (provinces) in the western and eastern sectors of the tropical Pacific (Figure 37). By the late Miocene these differences had largely disappeared and trans-tropical distributions began to prevail.

2. During the early Miocene, planktonic foraminiferal patterns in the northwest and western Pacific suggest that the gyre system was more weakly developed than during the late Miocene, although greater sample coverage is needed in the North Pacific to confirm this.

3. During the early Miocene, temperate assemblages extended much further south in the northwest Pacific. By the late Miocene these were displaced northward by subtropical-tropical assemblages as the Kuroshio Current intensified.

4. During the early Miocene, there was less distinct latitudinal zonality in the South Pacific and tropical North Pacific, although this was already developed in temperate and warm subtropical areas. By the late Miocene, these zones became narrower and more distinctly latitudinal in distribution (Kennett 1983). Increased provincialism of faunas during the Miocene has been recorded previously by several workers (Berggren and Hollister 1974, 1977; Sancetta 1978; Haq 1980; Lohmann and Carlson 1981). The provincialism apparently occurred in response to changes in the thermal structure of water masses and steepening gradients.

5. During the early Miocene, there were no distinctly different equatorial and tropical assemblages. By the late Miocene, separate assemblages seemed to mark the equatorial and tropical regions, as distinct from a broader tropical assemblage.

6. During the early Miocene in the southwest Pacific, the tropical biogeographic province was broader than during the late Miocene. Keller (1981a) noted that tropical assemblages were broader during the early Miocene. From studies in the Atlantic, Thunell and Belyea (1982) described a contraction of the tropical-subtropical assemblages during the Neogene. In the early Miocene, warmer-water assemblages extended to higher latitudes in the Atlantic, with the North Atlantic warmer than the South Atlantic.

What created the changes in tropical planktonic foraminiferal distribution patterns during the middle Miocene to early late Miocene? Selective calcium carbonate dissolution of planktonic foraminiferal assemblages can potentially produce much geographic variation during any time interval. We do not consider that the major biogeographic patterns described were caused by selective foraminiferal dissolution that concentrated certain species for the following reasons.

1. Samples containing very high frequencies of *G. siakensis* and *G. mayeri* do not exhibit clear evidence of having undergone strong dissolution, as would be shown by common specimen breakage. Also the walls of *G. siakensis* and *G. mayeri* are not noticeably thickened to suggest specimen concentration as a re-

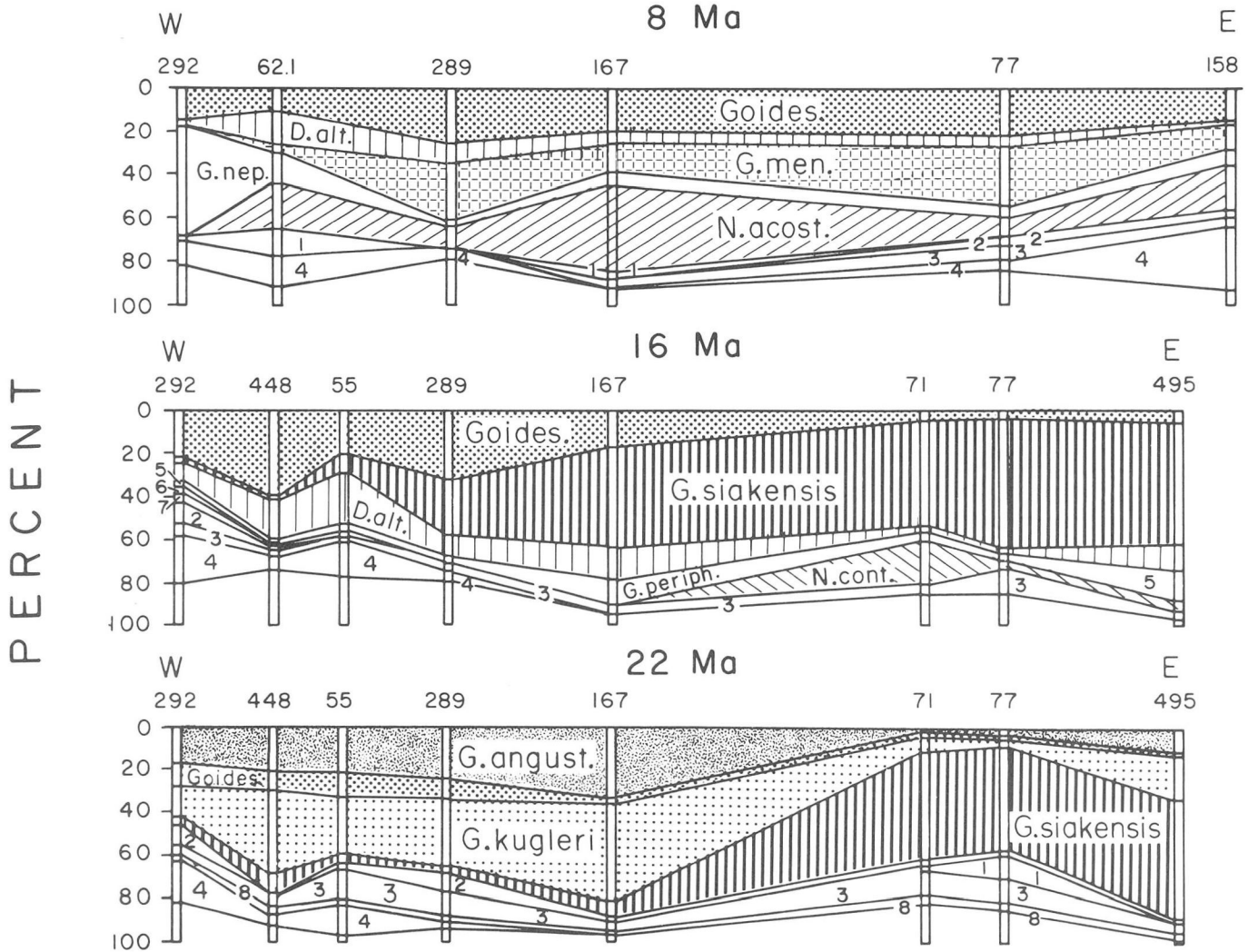


Figure 37. West to east trans-tropical Pacific traverses for three time-slices (22 Ma; 16 Ma; 8 Ma) to show changes in percent frequency distribution in planktonic foraminiferal assemblages (See Figures 1 to 3 for DSDP site locations. Abbreviations for taxa are as follows: 8 Ma: *Goides.*: *Globigerinoides*; *D. alt.*: *Dentoglobigerina altispira*; *G. men.*: *Globorotalia menardii limbata*; *G. nep.*: *Globigerina nepenthes-druryi*; *N. acost.*: *Neogloboquadrina acostaensis*; 1: *Globigerina woodi*; 2: *Globigerina bulloides*; 3: *Globoquadrina venezuelana*; 4: *Globigerinita glutinata*. 16 Ma: *Goides.*: *Globigerinoides*; *G. siakensis* also includes *Globorotalia mayeri*; *D. alt.*: *Dentoglobigerina altispira*; *G. periph.* and 5: *Globorotalia peripheroronda*; *N. cont.* and 6: *Neogloboquadrina continuosa*; 2: *Globigerina bulloides*; 3: *Globoquadrina venezuelana*; 4: *Globigerinita glutinata*. 22 Ma: *G. angust.*: *Globigerina angustumbilicata*; *Goides.*: *Globigerinoides*; *G. kugleri*: *Globorotalia kugleri*; *G. siakensis* also includes *Globorotalia mayeri*; 1: *Globigerina woodi*; 2: *Globigerina praebulloides*; 3: *Globoquadrina venezuelana*; 4: *Globigerinita glutinata*; 8: *Catapsydrax dissimilis*.

sult of severe dissolution that would be required to eliminate nearly all specimens of *Globigerinoides*. In other words, the large differences between eastern and western tropical Pacific assemblages during the early Miocene cannot be explained by differences in preservation, because there is no clear evidence for this. Such evidence would include common specimen breakage and concentration of specimens with relatively thickened tests.

2. The faunal differences between eastern and western tropical sectors (22 and 16 Ma) had largely disappeared by the late

Miocene (8 Ma) when the paleodepths of individual sites were deeper than during the early Miocene (Sclater et al. 1985). This, by itself, should have increased dissolution of assemblages, and hence exaggerated east-west differences. The calcium carbonate compensation depth (CCD) in the Pacific shallowed by about 250 m between the earliest Miocene and the late Miocene (8 Ma) (van Andel et al. 1975). This should have increased dissolution over a wider area in the late Miocene relative to the early Miocene.

Instead, unlike the early Miocene, late Miocene assemblages contain abundant (11 to 21%) *Globigerinoides* spp., a solution susceptible form, across the equatorial Pacific region. Indeed, the deepest site in the late Miocene tropical traverse (Site 77; 4127 m paleodepth) has among the highest frequencies (21%) of *Globigerinoides*. Altogether, these environmental changes would have increased dissolution during the late Miocene compared to the early Miocene and enhanced rather than decreased east-west faunal differences as the data shows.

3. In general, the deepest sites studied are in the eastern tropical Pacific, which by itself suggests a greater potential effect of dissolution upon the assemblages in this area. However, the detailed faunal-paleodepth relations do not support this. For example, in the 22 Ma time-slice, the deepest site (Site 567; 5339 m paleodepth) contains high frequencies of *Globigerinoides*. In contrast, the 16 Ma time-slice, a relatively shallow site (Site 167; 3163 m paleodepth) containing high frequencies (44%) of *G. siakensis* and *G. mayeri* also contains high frequencies (18%) of *Globigerinoides*. This association indicates that *G. siakensis* and *G. mayeri* were not concentrated by dissolution.

We believe that the faunal differences are valid biogeographic differences and that these are largely related to paleoceanographic changes. The changes were almost certainly caused, in part, by the development during the middle Miocene-early late Miocene of an effective barrier to Indo-Pacific tropical surface-water circulation. Paleoreconstructions have been made by Hamilton (1979) of the Banda Sea region between Indonesia and Australia-New Guinea (Figure 38). These show that the Indonesian Seaway would effectively have been closed during the middle Miocene, preventing any further surface-water circulation between the tropical Pacific and Indian Oceans. During the early and middle Miocene, surface-water transport would have been enhanced through the seaway (up to 1300 km wide) by the submergence of much or all of Java, Sulawesi, and Sumatra. All of these areas record regional subsidence and marine transgression during the middle Tertiary, followed by uplift, emergence, and related regression during the late Neogene, leading to the present, largely continental setting (Hamilton 1979). Audley-Charles et al. (1972) showed that the first major middle to late Cenozoic orogenic phase to affect the Banda Arc was during the middle Miocene. On the other hand, Borneo behaved more or less as a craton in middle and late Cenozoic times and had a major effect on diverting Pacific equatorial currents to the north and south. The position of Borneo relative to the equator during the early and middle Miocene is important (and not known with any accuracy; E. Silva, personal communication), since it affected the relative strengths of the western boundary current (Kuroshio Current) and the equatorial currents flowing through the Indonesian Seaway. New Guinea represents the northern leading edge of the northward moving Australian craton (Figure 38). During the early and middle Miocene, it was probably emergent enough to form the southern continental margin to the Indonesian Seaway. On the other hand, major orogeny first occurred in eastern New Guinea during the middle Miocene (Audley-Charles et al., 1972),

about 11 to 12 Ma, as a result of plate collision as Australia-New Guinea moved to the north. This resulted in initiation of turbidite deposition in the Coral Sea (Burns, et al. 1973). By the late middle to early late Miocene, the Indonesian and New Guinea land masses were sufficiently "interlocked" to prevent any further Pacific equatorial current transport into the Indian Ocean.

The development of this barrier created the Equatorial Undercurrent system that would have been previously undeveloped or nonexistent across the equatorial Pacific. The barrier would have created a pile-up of surface waters in the western equatorial Pacific and hence the development of an easterly flowing Equatorial Undercurrent (Knauss 1963). The barrier also may have helped strengthen the Equatorial Countercurrent, which results largely from the strength of winds and their differences in the equatorial region. A strong undercurrent system should have existed in the Indian Ocean because of the barrier formed by Africa to further westward surface-water transport. One of the principal effects of the modern Pacific countercurrent system is to return warm water to the eastern tropical Pacific (Figure 4). Van Andel et al. (1975) suggested that the Equatorial Undercurrent first developed about 12-11 Ma, a conclusion based upon observed large increases in biogenic sedimentation rates along the equator that they assumed resulted from increased upwelling. Leinen (1979) found no evidence of strong east-to-west gradients in opal accumulation characteristic of the Equatorial Undercurrent upwelling, before the middle Miocene. Siliceous biogenic productivity increased during the middle Miocene and peaked in the late Miocene about 8 Ma. This increase was interpreted to reflect the strengthening of the Equatorial Undercurrent system. Loutit et al., (1983b) suggest that equatorial Pacific sea-surface temperatures increased during the middle Miocene, at the time when surface waters cooled at higher latitudes.

In the late Miocene, the trans-tropical distribution pattern of *Globigerinoides*, which are warm-water, surface dwellers, is considered to record this paleocirculation change. Furthermore, the development of a distinct trans-equatorial province (as distinct from a broader, undifferentiated tropical province) marked by the *Globorotalia menardii*-*G. limbata* complex, may have been in response to the development of the Undercurrent system. These forms are non-spinose and in the Modern ocean are generally deeper-dwelling forms (except in areas of a shallow thermocline) living below 50 m and probably deeper during late ontogeny (Bé and Tolderlund 1971; Keller 1985). In the Atlantic, Jones (1967) observed that *G. menardii* in abundance is closely associated with the Equatorial Undercurrent with maximum frequencies of more than 25 percent. In the Pacific, Bradshaw (1959) showed highest abundances of *G. menardii* from plankton tows closely associated with the equator in the western Pacific but with a wider tropical distribution in the eastern Pacific. Curry et al. (1983) inferred that *G. menardii* calcifies on the thermocline in the Panama Basin. At the time of the year when *G. menardii* is most abundant in the Panama Basin, the thermocline is at a depth of only 10 m.

During the first two million years of its range, following its evolution from *G. praemenardii* 12 m.y. ago, *G. menardii* was

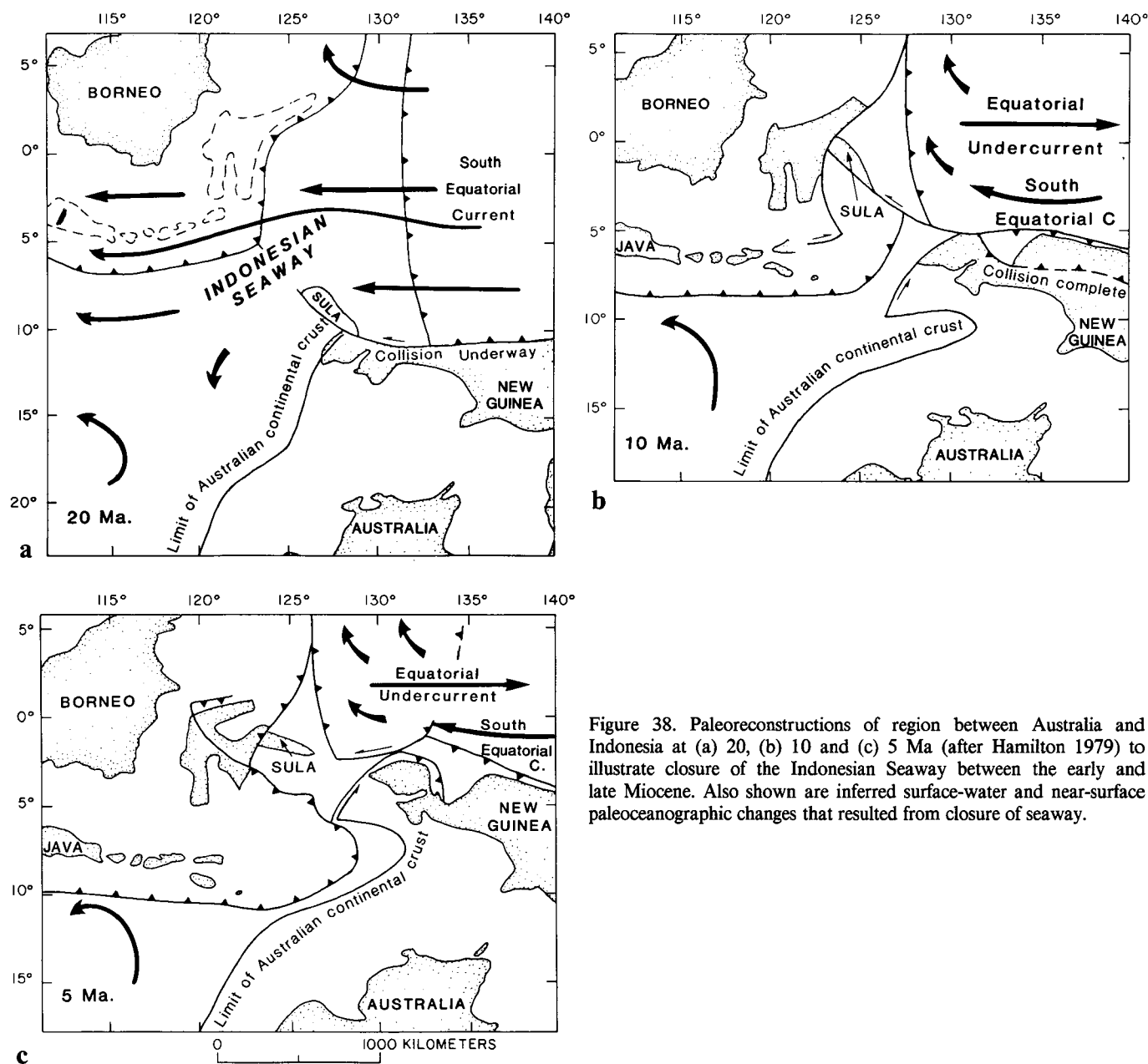


Figure 38. Paleoreconstructions of region between Australia and Indonesia at (a) 20, (b) 10 and (c) 5 Ma (after Hamilton 1979) to illustrate closure of the Indonesian Seaway between the early and late Miocene. Also shown are inferred surface-water and near-surface paleoceanographic changes that resulted from closure of seaway.

largely a warm-subtropical rather than equatorial form. However, about 10 Ma this species became more abundant close to the equator, as it is today (Tolderlund and Bé 1971), and seems to have replaced the important equatorial lineage—*Globorotalia (Fohsella)* which became extinct about 12 Ma, and perhaps even the tropical lineage *Globorotalia (Jenkinsella)* which became extinct about 11 Ma. The extinction of major Neogene lineages with no ancestral forms are unusual. These extinctions during the late middle Miocene may have been in response to the inferred large-scale paleocirculation changes in the tropical-equatorial regions.

Thus, the increased development of trans-tropical faunal distributions during or following the middle Miocene, and the con-

spicuous reduction of east-west biogeographic differences is considered to be partly in response to the development of this countercurrent system. These currents assisted in reducing inferred stronger environmental gradients that had existed between the eastern and western tropical Pacific during the early Miocene.

Another change that may have helped reduce east-west tropical biogeographic differences in the early Miocene would have been a general strengthening of the oceanic gyral systems resulting from a steepening of global latitudinal temperature gradients. An intensification of latitudinal temperature gradients almost certainly occurred during the middle Miocene when much of the east Antarctic ice sheet is believed to have accumulated (Shackleton & Kennett 1975; Savin et al. 1975). In the North Pacific,

faunal evidence indicates that such a strengthening did take place. A more sluggish oceanic circulation system might weaken east-west surface water transport in the tropics and in turn would favor the maintenance of the faunal differences that we have observed in the early Miocene. Conversely, an increase in gyre strength should help reduce the east-west faunal differences leading to a late Miocene pattern. For the Quaternary ocean, Moore (1978) observed that during the last ice age tropical radiolarian faunal distributions are much more trans-Pacific compared with the modern ocean where there are distinct west to east faunal differences. These changes were interpreted to reflect differences in strength of the circulation.

Gyral circulation in the North Pacific was intensified by the closing of the Indonesian Seaway during the middle Miocene. This should have strengthened the Kuroshio Current and led to the northward expansion of tropical assemblages into the northwest Pacific. The southeastern areas of the Japanese islands may have exhibited increased warming during the late middle Miocene (as expressed in subtropical species distributions along the marginal northwest Pacific) at a time when global climates were cooling. However, there is a widespread hiatus in Neogene sections on the Pacific coast of Japan, in the late middle Miocene (12–14 Ma) (Ujii 1984) that will make such evidence difficult to obtain. However, in the northern half of Japan, tropical faunas were replaced by temperate faunas after about 13 Ma (Saito 1963; Berggren 1984) as the Oyashio Current intensified. Thus a very large latitudinal thermal gradient developed in the ocean east of Japan.

An important corollary to these findings is that an open equatorial-tropical seaway system between several oceans does not, by itself, produce uniform surface-water paleoenvironmental conditions girdling the tropics and hence uniformity of biogeographic patterns. With the absence of a relatively strong global circulation and an absence of a strong countercurrent system, the open central American and Indonesian Seaways seemed to have had minimal effect in producing a trans-tropical faunal province. Less mixing took place between the east and western assemblages and faunas of the North Pacific gyre may have been largely isolated from the influence of tropical circulation.

It is more difficult to determine the actual environmental changes in the surface water masses that lead to the changes in Miocene biogeographic patterns. Specifically, what changes occurred in water-mass structure that led to such a dominance of the *G. siakensis*–*G. mayeri* plexus in the eastern tropical Pacific during the early Miocene (Figure 37) and different forms in the western tropical Pacific (22 Ma time-slice—*Globigerina angustiumbilitata*, *Globigerinoides* and *Globorotalia kugleri*; 16 Ma time-slice *Globigerinoides* and *Globorotalia kugleri*; 16 Ma time-slice *Globigerinoides* and *Dentoglobigerina altispira*)? If we knew the preferred depth habitat of these taxa, the problem would be easier to solve, but most of these species are now extinct and several, for example, the *G. siakensis*–*G. mayeri* plexus, do not even have modern living descendants.

The oxygen isotopic composition of the foraminiferal tests

can serve as a general guide to the depth of calcification of foraminiferal tests in the upper part of the water column (Douglas and Savin 1978); but this, by itself, can be unreliable because several modern species, especially those spinose forms with symbiotic zooxanthellae, may fractionate oxygen isotopes out of equilibrium with temperature and the oxygen isotopic composition of the sea water in which they live (Fairbanks et al. 1980; Fairbanks et al. 1982). Modern forms calcify out of oxygen isotopic equilibrium by approximately –0.3 to 0.4 per mil in δO^{18} values (Fairbanks et al. 1982; Curry et al. 1983). *Globigerinoides* are extant forms in which all species are spinose surface dwellers that prefer tropical-warm subtropical water masses. Most modern spinose species of planktonic foraminifera exhibit maximum concentrations in the upper 10 m of the water column (Bé and Tolderlund 1971). All species of *Globigerinoides* may have had symbiotic zooxanthellae (Bé 1977; Bé and Hutson 1977) and thus have calcified out of oxygen isotopic equilibrium. Oxygen isotopic measurements of Miocene *Globigerinoides* (Biolzi 1983; Savin et al. 1984; Keller 1985) show that this taxa almost always provides the lightest measured values of several taxa within an assemblage. Also, neither have the basic morphology of *Globigerinoides* species, nor have the latitudinal distribution patterns of these forms changed much during the Neogene, which suggests that they have not changed their depth preference in the uppermost part of the water column.

The preferred depth habits of other taxa are more difficult to interpret. Deeper-dwelling non-spinose, modern species may be at, or close to oxygen isotopic equilibrium (Fairbanks et al. 1982; Curry et al. 1983). Therefore, the oxygen isotopic values of inferred deeper-dwelling taxa in Miocene assemblages are probably more reliable. But what, for instance, was the preferred depth habitat of the *Globorotalia siakensis*–*G. mayeri* complex? Oxygen isotopic values of these forms are almost always relatively light compared with most species, suggesting a surface-water preference (Biolzi 1983; Keller 1985). In general, these forms have slightly heavier values than the *Globigerinoides*, (Biolzi 1983, shows heavier values of between 0.2 and 0.8 per mil in δO^{18} values), but then *Globigerinoides*, a known surface-dweller, fractionates to provide lighter values than the water in which it lives. More important is that *G. mayeri* is consistently heavier by .07 to .83 per mil in δO^{18} values than *Globoquadrina dehiscens* (Biolzi 1983), a non-spinose form that almost certainly did not live in the upper few meters of the ocean. The surface ultrastructure (Kennett and Srinivasan 1983) of the *G. siakensis*–*G. mayeri* complex indicates a lack of spines. Furthermore, general morphological considerations suggest that this plexus may have preferred a slightly deeper habitat than *Globigerinoides*. The morphology of this plexus is generally similar to *Neogloboquadrina* that includes extant, known deeper-dwelling species that calcify on the thermocline (Curry et al. 1983), but there is no close phylogenetic relationship between these forms. The morphology of *G. siakensis* is similar to *N. dutertrei* while that of *G. mayeri* is generally similar to *N. pachyderma*.

Our preferred interpretation is that the *G. siakensis*–*G.*

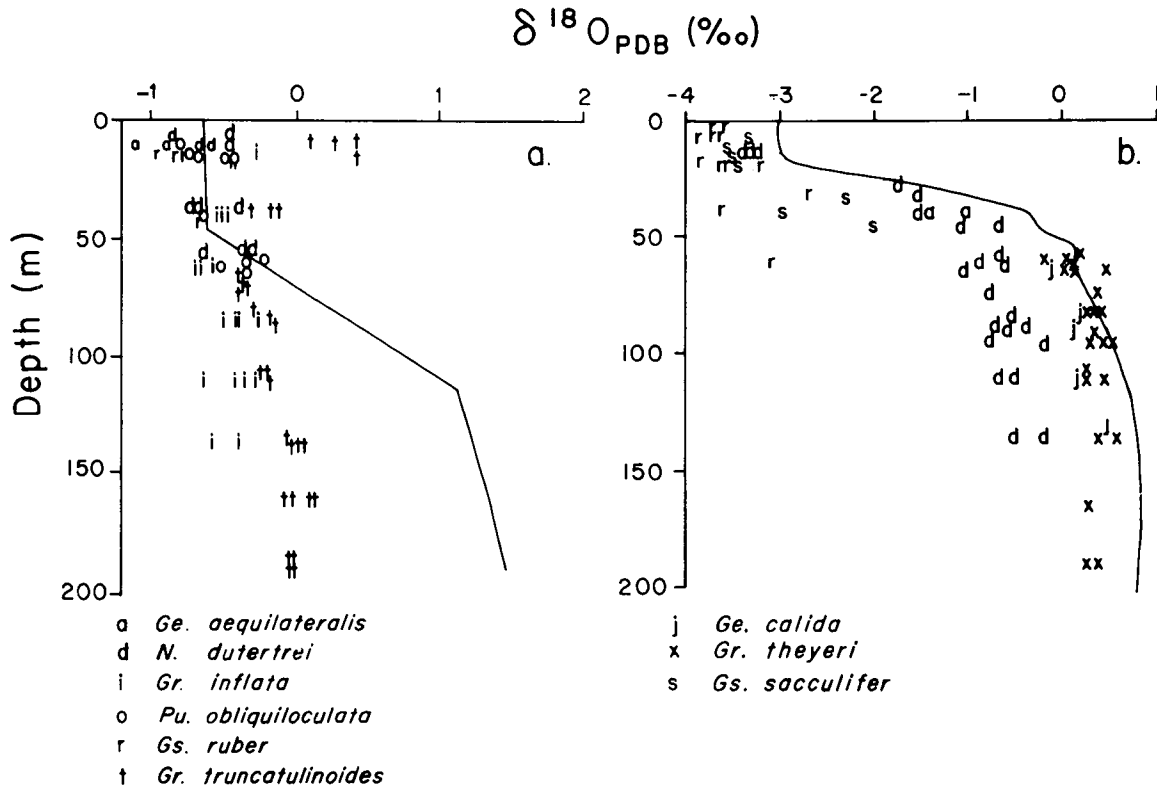


Figure 39. Oxygen isotopic composition of the tests of various living planktonic foraminiferal species and size fractions (from planktonic tows) as a function of water depth in (a) region of deep thermocline; and (b) shallow thermocline. Solid lines in (a) and (b) are the calculated equilibrium $\text{CaCO}_3\text{-}\delta^{18}\text{O}$ variation with depth. Note similarity of oxygen isotopic composition within and between species in area of deep thermocline (a) compared with changing values with increasing water depth associated with shallow thermocline (b). (a) is after Fairbanks et al. (1980) for the western North Atlantic; (b) is after Fairbanks et al. (1982) for the Panama Basin.

mayeri plexus lived at slightly deeper depths than *Globigerinoides*, closer to the thermocline. Other evidence suggests that deeper-dwelling species were quantitatively favored in early Miocene assemblages in the eastern tropics. Higher frequencies of *Catapsydrax dissimilis* occur in the eastern tropics, but not to the west (Figure 6). This taxa is heavily calcified, provides by far the heaviest $\delta^{18}\text{O}$ values and light $\delta^{13}\text{C}$ values typical of a deep pelagic habitat, and hence was a deep-dwelling form probably living below the thermocline (Biolzi 1983; Keller 1985).

The relative quantitative importance of species in assemblages may be determined by the position of the thermocline within the upper part of the photic zone where more food is available (i.e., upper 100 m of the water column). Some species prefer to live within the thermocline, some above and some below. If a species prefers to live and calcify within the thermocline, it will adjust its depth habitat to follow any movement of the thermocline. If the thermocline is shallow, deeper-water species will be quantitatively favored in the assemblage. Fairbanks et al. (1982) have found that most modern foraminiferal species precipitate most of the calcium carbonate in their tests in the upper 100 m of the water column (upper photic zone), even though a species may be found in abundance below 100 m.

Figure 39 shows two contrasting models of planktonic foraminiferal growth and oxygen isotopic composition dependent upon a deeper (Figure 39a) or shallower (Figure 39b) thermocline (Fairbanks et al. 1980; Fairbanks et al. 1982). Where the thermocline is deeper relative to the photic zone, most foraminiferal productivity and calcification occurs in the photic zone above the thermocline, and thus between-species $\delta^{18}\text{O}$ values are similar because of the relatively uniform water-mass temperatures in which calcification takes place. Where the thermocline is deep, shallower-dwelling forms such as *Globigerinoides* are quantitatively more important in assemblages (Thunell et al. 1983). In contrast, where a shallow thermocline exists within the photic zone (Figure 39b) most calcification and growth of foraminifera occurs within and below the thermocline in association with the chlorophyll maximum where food is more plentiful. This leads to greater between-species differences in $\delta^{18}\text{O}$ values and a higher quantitative importance of deeper-dwelling taxa (Thunell et al. 1983).

There seem to be two possible hypotheses to explain east-west faunal differences during the early Miocene. The first hypothesis is that surface waters were generally cooler in the eastern tropical Pacific, giving rise to the biogeographic differences

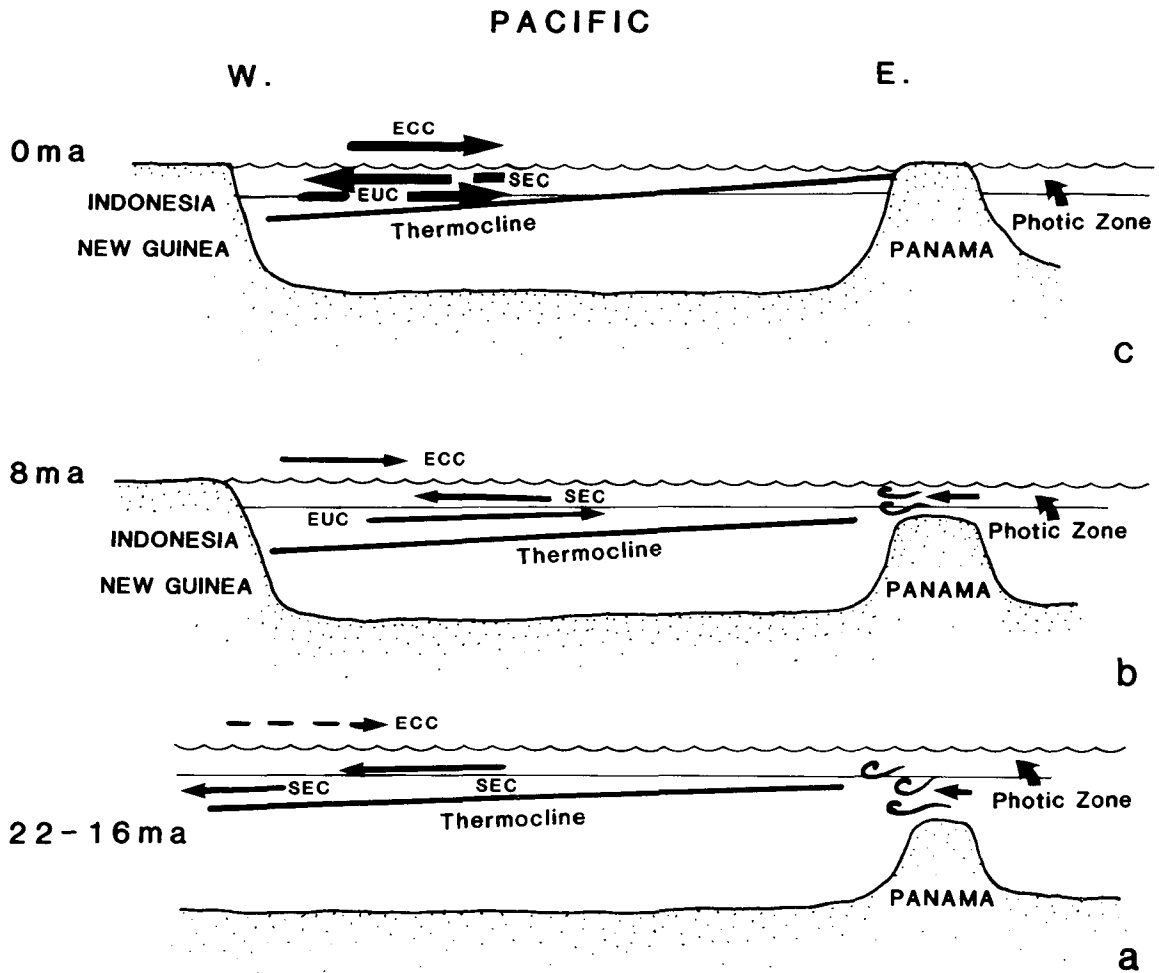


Figure 40. Suggested Neogene changes in surface water-mass structure in the equatorial Pacific Ocean between early Miocene (a); late Miocene (b); and the Modern ocean (c). Shown in each case is the position of the thermocline relative to the photic zone and current directions of major currents as follows: SEC: South Equatorial Current; ECC: Equatorial Countercurrent; EUC: Equatorial Undercurrent. a. Early Miocene—22–16 Ma. Both Indonesian and Central American Seaways open to surface waters. Thermocline is relatively deep across the equatorial Pacific in absence of an Equatorial Undercurrent. Equatorial Countercurrent (dotted line) is weak. b. Late Miocene—8 Ma. Indonesian Seaway is now closed, the barrier forming the Equatorial Undercurrent. Thermocline is shallower in the photic zone. Equatorial Countercurrent is moderately strong. c. Modern Ocean—0 Ma. Central American Seaway is now closed. All surface water circulation is more vigorous. Stronger Equatorial Undercurrent further raises thermocline within photic zone especially in eastern Pacific. Equatorial Countercurrent is more vigorous transporting warm water to east.

among surface or near-surface forms. In the western tropical Pacific, surface waters were not only distinctly warmer, but tropical conditions were also broader in the South Pacific. The relatively sluggish equatorial circulation, the absence of an Equatorial Undercurrent, and a weak Equatorial Countercurrent allowed distinct biogeographic differences to develop between the east and the west.

The alternate hypothesis states that the east-west differences resulted from a relatively shallow thermocline over broad areas of the eastern tropical Pacific, and a deeper thermocline in the western tropical Pacific (Figure 40). Nevertheless, the thermocline

across the tropical Pacific was somewhat deeper perhaps than that of the modern ocean and located everywhere in the deeper part of, or below the photic zone (Figure 40a). Shallow-water warmer taxa (such as *Globigerinoides* spp.) were favored in the west and slightly deeper, cooler species (especially *G. siakensis*–*G. mayeri*) were favored in the east.

With a strengthening of the Equatorial Countercurrent by the late Miocene (Figure 40b), warm, shallow-water dwellers such as *Globigerinoides* spread across almost the entire tropical Pacific. Also, the development of the Equatorial Undercurrent system (Figure 40b) returned relatively warmer, deeper waters to

the eastern tropics. Deeper-dwelling forms such as the *Globorotalia menardii*-*G. limbata* plexus and *N. acostaensis* were able to exploit this water mass across much of the tropical-equatorial Pacific (Figure 37). Thus, by the late Miocene, both shallow (*Globigerinoides*) and deeper forms (*G. menardii*-*G. limbata*; *N. acostaensis*) occurred in faunas across the equatorial Pacific as a result of seasonal changes in the depth of the thermocline and of upwelling that must have been much stronger than during the early Miocene.

Late Miocene equatorial patterns of planktonic foraminiferal distributions did not persist into the Modern ocean. As in the early Miocene, modern assemblages again exhibit important east-west differences across the tropical Pacific. These differences, however, are largely restricted to taxa that normally live deeper within the water column. The eastern province, marked by strong seasonal upwelling, is dominated by *N. dutertrei*, followed by *G. tumida* and then *P. obliquiloculata* along a westward path (Parker and Berger 1971). The Panama Basin exhibits a strong dominance of *N. dutertrei* and *Globorotalia theyeri* as a result of strong seasonal upwelling (Thunell et al. 1983). In contrast, typically shallow-dwelling forms (such as *G. ruber* and *G. sacculifer*) occur at important elements from west to east across the equatorial region (Parker 1960; Bé 1977; Bradshaw 1959; Coulbourn et al. 1980; Thompson 1981), as in the late Miocene, but unlike the early Miocene. Also, *G. menardii* is distributed across the tropical Pacific with highest frequencies occurring in close association with the equator.

The modern pattern is thus different from both early and late Miocene patterns, by exhibiting east-west differences in deeper-dwelling forms but at the same time maintaining important populations of shallow-water taxa across the region. The pattern is promoted by a relatively shallow thermocline (which seasonally becomes extremely shallow in the east) maintained by a strong Equatorial Undercurrent. This favors production of the "deeper-dwelling" taxa (*N. dutertrei*, *G. tumida* and *P. obliquiloculata*). There is also a strong Equatorial Countercurrent that returns warmer waters to the east and favors seasonal production of "surface-dwelling" taxa (*G. ruber*, *G. sacculifera* and *G. aequilateralis*). It seems that the Modern equatorial Pacific differs from the early Miocene (Figure 40A) in having a shallower thermocline located well within the photic zone (Figure 40C), especially in the east due to more vigorous circulation and a strong Equatorial Undercurrent, and a strong return flow of warm surface waters and associated faunas as a result of a stronger Equatorial Countercurrent.

CONCLUSIONS

1. Biogeographic patterns of Pacific planktonic foraminifera have been quantitatively mapped for two time-slices in the early Miocene (22 Ma and 16 Ma) and one in the late Miocene (8 Ma).

2. Important changes occurred in the biogeographic patterns of planktonic foraminifera, especially between the early (16 Ma) and late Miocene (8 Ma), which are interpreted as

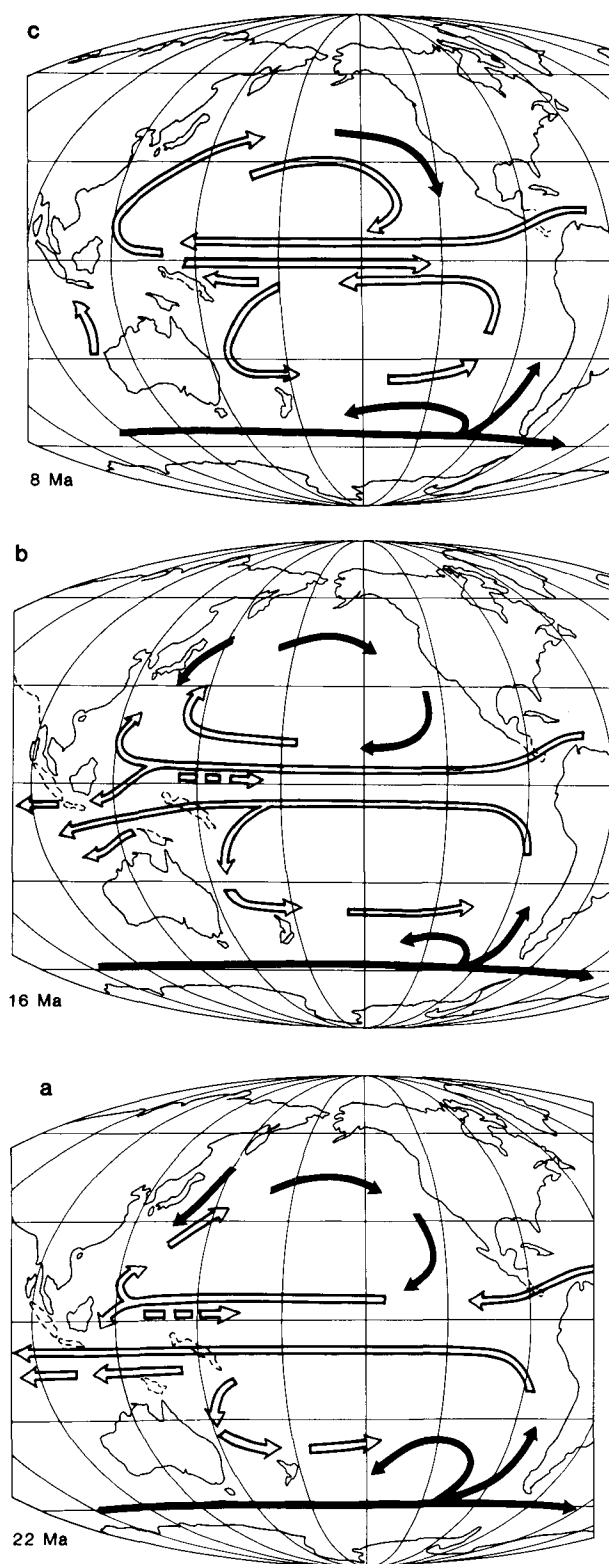


Figure 41. Inferred circulation patterns of surface and near surface waters in the Pacific Ocean at (a) 22 Ma, (b) 16 Ma, and (c) 8 Ma. Closed arrows indicate cold currents; open arrows indicate warm currents. Paleoreconstructions after Sclater et al. (1985).

reflecting major changes in surface-water circulation of the Indo-Pacific region (Figure 41).

3. In the tropical Pacific during the early Miocene, the planktonic foraminiferal assemblages were dominated by different taxa in the eastern and western areas. This changed by the late Miocene when the assemblages became more similar across the entire expanse of the tropical Pacific. These changes are interpreted to reflect both the development, during the middle Miocene, of the Equatorial Undercurrent system when the Indonesian Seaway effectively closed and the general intensification of tropical and gyral surface-water circulation, including a strengthening of the Equatorial Countercurrent, that resulted from a steepening of latitudinal temperature gradients.

4. The east to west faunal differences across the tropical Pacific in the early Miocene were due to differences in the surficial water-mass structure. Either generally warmer surface waters or the presence of a deeper thermocline in the west quantitatively favored shallow-water dwellers such as *Globigerinoides*, while a shallower thermocline in the east favored slightly "deeper-dwelling" forms. These differences across the equatorial Pacific were maintained because the Equatorial Countercurrent system was only weakly developed (Figure 41a, b).

5. A separate equatorially distributed assemblage (*Globorotalia menardii*-*G. limbata* and *Globigerinoides*) had developed by the late Miocene, perhaps in response to the development of the Equatorial Undercurrent system and the strengthening of the Equatorial Countercurrent (Figure 41c). Two important tropical Neogene lineages became entirely extinct about this time, perhaps in response to these water-mass changes.

6. Modern distribution patterns in the equatorial Pacific differ from those of both the early and late Miocene. East-west differences occur in "deeper-dwelling" forms while "shallow-dwelling" forms occur in seasonal abundance across the region. This pattern resulted from the intensification of the Countercurrent system that had developed by the late Miocene. This had the effect of shallowing the thermocline in the equatorial Pacific and strengthening the return flow of warm waters to the east within the Equatorial Countercurrent.

7. In the northwest and western Pacific, the distribution of faunas indicates that the gyral circulation system was only weakly developed in the early Miocene, but was strong by the late Mio-

cene. This resulted from the closure of the Indonesian Seaway during the middle Miocene and the general intensification of ocean circulation as the latitudinal temperature gradient steepened.

8. Other changes that occurred between the early and late Miocene were the northward displacement of temperate faunas in the northwest Pacific as the Kuroshio Current intensified; the development of more distinct latitudinally distributed, narrower provinces in the south and tropical Pacific; and in the south Pacific, the northward expansion of the polar-subpolar province and the latitudinal contraction of the tropical provinces. These changes resulted from the continued areal expansion of the polar and subpolar water masses as Australia drifted northward from Antarctica and from the steepening of pole to equator thermal gradients related to increased Antarctic glaciation.

9. The early Miocene tropical distribution patterns indicate that an open equatorial-tropical seaway system between several oceans has not, by itself, led to the development of uniform surface-water paleoenvironmental conditions girdling the tropical regions and producing a uniform biogeographic province.

10. Several planktonic foraminiferal lineages and species changed their surface-water preferences during the Miocene, although most lineages remain closely associated with particular water masses.

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