

5. NEOGENE PLANKTONIC FORAMINIFERS FROM DEEP SEA DRILLING PROJECT SITES 502 AND 503¹

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ABSTRACT

Deep Sea Drilling Project Sites 502 (Colombian Basin, western Atlantic Ocean) and 503 (eastern equatorial Pacific Ocean) are well located for comparison of the late Neogene paleoceanographic history of the tropical Atlantic and Pacific oceans. Comparing the faunal and floral history at each location should reveal changes arising from the late Neogene shoaling of the Isthmus of Panama and the separation of the tropical oceans.

At each site we recovered an apparently continuous, largely undisturbed sedimentary sequence from Holocene to about 8 m.y. in age. Tropical and subtropical planktonic foraminifers occur throughout each sequence, although diversity is lower and preservation poorer in the Pacific. At each location the Miocene/Pliocene boundary is defined by the first appearance of *Globorotalia tumida*, the early-late Pliocene boundary is defined by the extinction of *Sphaeroidinellopsis*, and the Pliocene/Pleistocene boundary is defined by the first appearance of *G. truncatulinoides*.

Planktonic foraminiferal assemblages at Sites 502 and 503 are generally similar until the early Pliocene when the faunal histories diverge. Two important exceptions are the delayed first occurrence of *Pulleniatina* at the Atlantic site (4.4 Ma) relative to the Pacific site (5.5 Ma) and the common presence of sinistral *Neogloboquadrina acostaensis* and sinistral *N. pachyderma* at the Atlantic site. Sinistral *N. acostaensis* is rare at the Pacific site, and sinistral *N. pachyderma* is absent entirely. The significance of sinistral *N. pachyderma* at Site 502 is unclear. If this phenotype is due to cool water at this location, it might reflect seasonal upwelling because the fauna is otherwise tropical-subtropical.

As noted by other workers, the first planktonic foraminiferal evidence for increasing Atlantic-Pacific provinciality occurs in the early Pliocene at 4 Ma with the appearance of *Pulleniatina spectabilis* in the Pacific and its exclusion from the Atlantic. Subsequent to that, *Pulleniatina* disappeared from the Atlantic (3.3 Ma) and did not reappear until about 2.1 Ma, whereas it ranged continuously in the Pacific. The strongest biogeographic evidence based on planktonic foraminifers for the separation of the two tropical oceans by the Panama Isthmus has been the development of an endemic lineage of *Globorotalia* in the Atlantic. Members of this group become numerically important in the late Pliocene and give tropical Atlantic faunas of that age a distinctive appearance. Until recently the more advanced members of this lineage have not been recorded from Pacific sediments. At Site 503 the distinctive species *G. pertenuis* first appears at 3.3 Ma and last appears at 3.2 Ma, whereas at the Atlantic site it extends to 2.5 Ma. The short range of this species in the Pacific and the complete absence of *G. miocenica* is further evidence that by about 3 Ma the emergent Panama Isthmus was an effective barrier to the exchange of tropical surface waters between the Atlantic and Pacific.

INTRODUCTION

Deep Sea Drilling Project (DSDP) Leg 68 was conceived to test the newly developed hydraulic piston corer (HPC) in Atlantic and Pacific sediments and, if successful, to provide high-resolution stratigraphies. Comparing stratigraphic results between the two oceans would be useful in studying the late Neogene paleoceanographic effects of the closing of the Panama Isthmus, the initiation of permanent Northern Hemisphere glaciation, and the possible relation between the two. Sites 502 and 503 were cored near previously drilled Sites 154 and 83, respectively. Site 502 holes are located at 11°29.4' N and 79°22.7' W at about 3051 meters water depth, approximately 100 km east of Site 154 (Edgar, Saunders, et al., 1973). The 153-meter pelagic sequence at DSDP 154 lies on a volcanic ash turbidite, which forms a prominent reflector and was the major objective of drilling in the western Colombian Basin. The 7 to 8 m.y. old sequence at Site 502 lies on an uplifted block and does not contain the turbidite found at Site 154.

Site 503 holes are located at 4°04.04' N and 95°38.21' W at a water depth of 3672 meters. Nearby Site 83 (Hays et al., 1972) was only spot-cored in the late Miocene sequence and was thought to reach the middle Miocene, but the sediments were badly disturbed by the rotary drilling process (see Prell, Gardner, et al., 1980, fig. 2). At Site 503 the HPC recovered a largely undisturbed 234-meter sequence to within about 10 meters of basement. Based on microfossil ranges, the oldest sediment is estimated to date to 8 Ma, about the same as Site 502 (see Kent and Keigwin, this volume).

Sediment at Site 502 grades with increasing depth from a foraminiferal and nannofossil marl to a calcareous and ash-bearing clay. Planktonic foraminifers are generally common and well preserved, especially in samples above 110 to 115 meters sub-bottom. Planktonic foraminifers are generally less abundant and often show effects of calcium carbonate dissolution in the siliceous-bearing marls of Site 503.

METHODS AND RESULTS

The preliminary biostratigraphy presented in this chapter is based largely on Miocene and Pliocene core-catcher samples. Although core-catcher samples are routinely examined on board ship by biostratigraphers, we took special care to examine slices of sediment as thick as 2 cm from across the top of the core catcher when it was full. This was found to reduce the possible effects of down-core contaminants as

¹ Prell, W. L., Gardner, J. V., et al., *Init. Repts. DSDP*, 68: Washington (U.S. Govt. Printing Office).

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well as to provide large samples for analysis of biostratigraphy and stable isotopes (Keigwin, this volume).

Core-catcher samples were washed in fresh water over a 63 μm screen and then dried on the screen; that fraction greater than 175 μm was examined. Samples processed ashore were prepared following Keigwin (1976). Species abundances were estimated using the method of Poore (1978).

Ranges of taxa have been refined by analyzing one sample per core section near intervals of faunal change. Ages of first and last appearance have been determined from magnetostratigraphy (Kent and Sprioso, this volume) by interpolating between the ages and depths of magnetic reversals in each hole. Because of relatively coarse sampling, the ages of biostratigraphic datums (Table 3) are accurate to within only about 0.1 Ma. Microfossil ranges are useful in patching together a composite section from the intervals of highest recovery in each hole of each site. Results in Table 3 suggest that Hole 502C datums are about 5 meters shallower than those of the other holes at this site.

Useful zonations have been developed for the Caribbean by Bolli and Premoli-Silva (1973) and for the east equatorial Pacific by Jenkins and Orr (1972) and Kaneps (1973). The zonation of Jenkins and Orr (1972) is used in this study because it is applicable to both Atlantic and Pacific faunas. The Miocene/Pliocene boundary is based on the first appearance of *Globorotalia tumida* and the Pliocene/Pleistocene boundary (as used here) is based on the distinctive first appearance of *G. truncatulinoides* at each site. The last occurrence of *Globigerinoides obliquus*, which is also a useful marker for the Pliocene/Pleistocene boundary (Saito et al., 1975; Haq et al., 1977; Thompson and Sciarillo, 1978), occurs near the first appearance of *G. truncatulinoides* (Tables 1 and 2). Although the Pliocene is not formally divided into time-rock units, it is informally divided here into upper and lower parts based on the last appearance of *Sphaeroidinellopsis*. This extinction is a useful marker for the appearance of cooler faunal elements in low-latitude sites (Parker, 1967; Keigwin, 1976) and stable isotopic and lithologic indications of permanent Northern Hemisphere ice-sheet accumulation (Berggren, 1972; Shackleton and Opdyke, 1977; Shor and Poore, 1978; Keigwin and Thunell, 1979; Keigwin, this vol.). This datum is close to the first appearance of *G. fistulosus*, used to mark the zone of that name in the Jenkins and Orr (1972) zonation (Tables 1-3).

HISTORY OF FAUNAL CHANGE AT SITE 502

The late Neogene planktonic foraminiferal fauna in the western Caribbean is generally tropical and subtropical in character, dominated by species of keeled globorotaliids, *Globigerinoides*, *Orbulina*, and *Neogloboquadrina*. At both Sites 502 and 503 the keeled globorotaliids are largely the *Globorotalia menardii* group (Tables 1 and 2), which consists of *G. menardii*, *G. limbata*, and *G. praemiocena*. The lower part of the upper Miocene (prior to about 6 Ma) is marked by intervals of calcium carbonate dissolution. This is reflected in rare foraminifers in the bottom 20 meters of Hole 502A and the top few meters of Hole 502C. The upper part of this dissolution interval contains the upper Miocene carbon isotope shift, which, at least in the Pacific, is associated with a dissolution interval (Keller, 1980; Dunn et al., 1981). The pre-"carbon-shift" interval (below about 200 m; see discussion in Keigwin, this volume) has common *Globigerinoides quadrilobatus* and *G. obliquus*, despite the generally poorer preservation. This lower part of the upper Miocene has few to common *Neogloboquadrina acostaensis*, and these are dominantly sinistral with the exception of one sample (502A-65, CC). Remaining few-to-common foraminifers are: *Sphaeroidinellopsis subdehiscens*, *G. pleisotumida*, *Orbulina*, *Globigerina nepenthes*, and *G. bulloides*. Below 215 meters there are three occurrences of a rare spe-

cies identified as cf *Catapsydrax unicavus* (Table 1; Plate 1, Figs. 1-3). The preservation of these individuals is similar to the rest of the fauna, with no indication of other Paleogene or lower Neogene contaminants.

About 200 meters, in the upper Miocene (about 5 to 6 Ma), there is a greater abundance of keeled globorotaliids and more *G. falconensis* (Table 1). There are two more intervals where dextral *N. acostaensis* is dominant (50 and 52, CC). The preservation of CaCO_3 is generally improved over lower sediments, despite the probable shoaling of the CCD due to the Messinian "salinity crisis" (Ryan et al., 1973; Thunell (1981) and references therein). Within this uppermost Miocene interval *Globigerinoides bulloides* (Plate 2, Figs. 1-4) last appears at 183 meters (Core 52, CC; estimated age, 5.8 Ma), with a possible occurrence a little higher in the section (42, CC, Table 1). This species has a distinct last appearance high in the upper Miocene in two Panama Basin cores and is probably stratigraphically useful (Keigwin, 1976). Thompson (in press) finds *G. bulloides* with a Tortonian-Messinian range at DSDP Leg 67 sites (Middle America Trench). A related form (here identified as *G. cf bulloides*, Plate 2, Figs. 10-12) occurs in the middle Pliocene at Site 502, but has not been identified in the Pacific. *G. cf bulloides* is distinguished from *G. bulloides* by its higher spire. It resembles *Globigerina cariacensis* in the way that *Globigerinoides bulloides* resembles *Globigerina bulloides*.

By 173 meters (about 5.7 Ma) the sinistral phenotype of *N. pachyderma* (Plate 10, Figs. 4-8) is a common faunal element (estimated abundance is 30% of the planktonic foraminiferal fauna), and the sinistral form of *N. acostaensis* is abundant. These two forms are obviously related, but *N. pachyderma* may not reflect waters as cold as the modern high-latitude sinistral counterpart, because the rest of the planktonic fauna is strictly tropical and subtropical. In addition, there is evidence that the sinistral phenotype has been progressively restricted to cooler waters in the late Neogene (Kennett and Vella, 1975). Nevertheless, rare occurrences of the sinistral phenotype have been reported in the late Quaternary of DSDP Site 147 (Venezuelan Basin, Cariaco Trench) by Rögl and Bolli (1973). These workers attribute such apparently cool-water specimens to upwelling associated with the Cariaco Trench. Similar upwelling remains a possibility at Site 502.

N. humerosa (Plate 9, Figs. 9-11) first occurs at 166 meters (about 5.6 Ma) and quickly becomes a common member of the fauna (Table 1). About 2 meters below the Miocene/Pliocene boundary, typical *Globorotalia margaritae* (Plate 5, Figs. 10-12) first appear, as noted by Berggren (1977) in his study of Rio Grande Rise piston cores (South Atlantic). Associated with the typical form is a thickened variety which persists into the lower Pliocene (Table 1; Plate 6, Figs. 1-3).

The Pliocene is marked by great faunal turnover, resulting in a fauna of modern appearance by the end of the epoch. Significant biostratigraphic events before 4.6 Ma in the lower Pliocene are the last appearance of *Globigerinoides seigliei* (Plate 3, Figs. 4-6) and the first appearance of *Sphaeroidinella dehiscens* with a small sup-

plementary aperture (*forma immatura*, Plate 11, Figs. 5–6). In the temperate South Atlantic, Berggren (1977) has found the last occurrence of *G. seigliei* in the uppermost Miocene. These last occurrences are followed by the first appearance of *G. margaritae evoluta* at 126 meters and the migrational first appearance of *Pulleniatina primalis* (sinistral) and *Globorotalia crassaformis* by 4.3 Ma (123 m, Table 3). The last occurrences of *G. nepenthes*, *N. acostaensis* (sinistral), and *N. pachyderma* (sinistral) are between about 110 and 120 meters down-core (4.0 to 4.2 Ma). The nearly simultaneous disappearance of the two *Neogloboquadrina* species suggests that the *N. pachyderma* existed in a clinal relationship with *N. acostaensis*, as noted by others (Srinivasan and Kennett, 1976). It still does not explain, however, what environmental factor led to sinistral coiling. This interval (110–120 m) is probably time-equivalent to the base of the pelagic section at nearby Hole 154A, because the lowest pelagic sample examined contained *G. nepenthes* overlain by a few meters of sinistral *N. pachyderma* (Keigwin, 1978).

By about 3.9 Ma, the percent CaCO₃ in Site 502 sediments became uniformly high (Gardner, this volume) raising the possibility that both Sites 502 and 154 were uplifted together into less corrosive water and above the effects of turbidites at deeper Site 154. The timing of these events (close to 4 Ma) is close to independent evidence from stable isotopes for the beginning of restricted circulation between the Atlantic and Pacific oceans (Keigwin, this volume). At 112 meters *P. primalis* changes from dominantly sinistral to dextral coiling (3.6 to 3.7 Ma) and last appears at 91 meters, 7 meters above the extinction of *G. margaritae* (3.6 Ma). Between 90 and 95 meters, *S. dehiscentis* (*forma immatura*) is replaced by mature specimens, just after the first occurrence of *G. exilis*.

Evidence from fauna and stable isotopes shows the middle of the Pliocene to be a time of climatic deterioration. Evidence from stable isotopes is inferred to reflect the growth of permanent Northern Hemisphere ice sheets beginning about 3.2 Ma (Shackleton and Opdyke, 1977). Possible faunal evidence for cooling climate in the Colombian Basin are the first migrational appearances of *G. punctulata*, *G. inflata*, *G. hirsuta*, and *G. cariacensis*, and the last appearances of *Sphaeroidinellopsis*, *Globoquadrina altispira*, and *G. conglomerata*. In the upper Pliocene *N. pachyderma* (dextral) becomes an important faunal element in samples where the *Globorotalia menardii* group is absent. However, there are also changes which might be interpreted as evidence for warming. In the middle of the Pliocene *Globigerinoides ruber* increases in abundance and *G. cf. bulloideus* and *G. fistulosus* first occur. In addition there is the consistent presence of *Globorotalia multicamerata* and the diversification of the *G. exilis* lineage into *G. miocenica* and the exotic *G. pertenuis*. This complicated turnover of fauna is difficult to explain in terms of climatic cooling alone. Parker (1973) suggests that some Pliocene changes in fauna may be related to an ecological factor other than temperature. One possibility is salinity, which probably increased in the Caribbean during the Pliocene

(Keigwin, this volume). Useful datums in the uppermost Pliocene are the first occurrence of *N. dutertrei* (2.5 Ma) and the reappearance of *Pulleniatina* at about 2 Ma.

HISTORY OF FAUNAL CHANGE AT SITE 503

Site 503 samples are marked by fewer planktonic foraminifers and lower diversity than are those from Site 502. Nevertheless, the dominant taxa throughout the section are the same as at Site 502: the *Globorotalia menardii* group, the *Globigerinoides quadrilobatus* group, the *G. obliquus*–*G. ruber* group, the *Sphaeroidinella*–*Sphaeroidinellopsis* group, *Neogloboquadrina*, and *Globoquadrina altispira*.

As in the upper Miocene at Site 502, *Globigerinoides bulloideus* last appears and *Neogloboquadrina humerosa* first appears between the “carbon shift” (6 Ma; Keigwin, this volume) and the Miocene/Pliocene boundary. Differences between the Atlantic and Pacific sections, however, are more significant. *Pulleniatina primalis* appears (perhaps migrational, see Srinivasan and Kennett, in press) in the uppermost Miocene (5.5 Ma) compared to the lower Pliocene in the Caribbean, and *N. acostaensis* is dominantly dextral. Two intervals of sinistral coiling occur near the base of the section, just above the “carbon shift.” The higher of these intervals is probably time-equivalent with that reported from equatorial Pacific piston core RC12-66 (Saito et al., 1975) which has been used to date paleomagnetically the “carbon shift” (Keigwin and Shackleton, 1980). Even more important is the complete absence of sinistral *N. pachyderma* from Site 503. *Globoquadrina dehiscentis* is more abundant in Site 503 than Site 502 samples, and last appears in 33,CC, where *Globorotalia tumida* first appears marking the Miocene/Pliocene boundary.

Most of the lower Pliocene at the Pacific site is similar to that at the Caribbean site. Notable differences are the absence of sinistral *N. pachyderma*, sinistral *N. acostaensis*, and *G. margaritae*. A few specimens of the short-ranging *Pulleniatina spectabilis* (Plate 11, Fig. 1) were found in Sample 503B-23,CC, probably at about the same time (4 Ma) as in other locations (Parker, 1967; Keigwin, 1976). This species is not found in the Atlantic. *Globigerina nepenthes* is not common enough at this location for its last appearance to be a useful datum. Toward the end of the lower Pliocene interval (69–80 m) *Globoquadrina conglomerata* (Plate 3, Figs. 7–9) has its last occurrence and *Globorotalia crassaformis* and *Globigerinoides fistulosus* have their first occurrence. Since *Globoquadrina conglomerata* occurs in the modern Pacific (Parker, 1967; Thompson and Sciarillo, 1978), its disappearance at about 3.3 Ma at Site 503 must result from ecological change—perhaps cooling surface waters. Likewise, the middle Pliocene first occurrence of *Globorotalia crassaformis* results from ecological factors, because it appears earlier in higher latitudes (Srinivasan and Kennett, in press). Between the lower part of Core 21 and 19,CC (Hole 503B), the dominance of *P. primalis* coiling changes from sinistral to dextral. It is difficult to locate this change precisely because planktonic foraminifers are rare and sometimes absent entirely, but it occurs at about 3.7

Table 1. (Continued).

Chrono-stratigraphic Unit	Zone (Jenkins and Orr, 1972)	Approx. Depth (m)	Hole	Sample (level in cm)	<i>Globobulimina conglomerata</i>	<i>G. allispira</i>	<i>Sphaerodinellopsis subdehiscens</i>	<i>S. seminulina</i>	<i>Globobulimina venezuelana</i>	<i>Globobulimoides ballii</i>	<i>Globigerina foliata</i>	<i>Neoglobobulimina pachyderma</i> L.	<i>N. acostaensis</i> L.	<i>N. acostaensis</i> R.	<i>Globigerina druryi</i>	<i>G. nepenthes</i>	<i>Globobulimoides seigleyi</i>	<i>Globobulimina plesiotumida</i>	<i>G. merotumida</i>	<i>Globobulimoides bulloideus</i>	<i>Globobulimina dehiscens</i>	cf <i>Catapsydrax unicus</i>			
Q Upper Pliocene	<i>P. obliquiloculata</i>	45	502B 502A	11-1, 100																					
				11-2, 108																					
				11-3, 100																					
				11, CC																					
				12, CC																					
	<i>G. fistulosus</i>	50			13, CC																				
		60			14, CC																				
		70			15, CC																				
		75			16, CC																				
					17, CC																				
Lower Pliocene	<i>S. dehiscens</i>	85		18, CC																					
		90		19-1, 100																					
				19-2, 100																					
				19-3, 90																					
				19, CC																					
				20-1, 50																					
				20-1, 100																					
				20-2, 52																					
				20-2, 100																					
				20-3, 100																					
Upper Miocene	<i>G. tumida</i>	100		20, CC																					
				21, CC																					
				22-2, 100																					
				22-3, 100																					
				22, CC																					
	<i>G. plesiotumida</i>	115		23-2, 100																					
				23-3, 100																					
				23, CC																					
				24-1, 100																					
				24-2, 100																					
			24-3, 100																						
			24, CC																						
			110		25, CC																				
			115		26, CC																				
					27, CC																				
			120		28-2, 100																				
					28, CC																				
			125		29-2, 100																				
			130		29, CC																				
					30, CC																				
				32, CC																					
		135		33-3, 10																					
				33, CC																					
		140		34, CC																					
				35, CC																					
				36, CC																					
		145		37, CC																					
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		150		39, CC																					
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		170		46, CC*																					
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		185		53, CC																					
				54, CC																					
		190		55, CC																					
				56, CC*																					
				57, CC																					
		195		58, CC																					
				59, CC*																					
				$\delta^{13}C$ shift ^a																					
		200		60, CC*																					
				61, CC*																					
				62, CC*																					
		205		63, CC*																					
		210		65, CC*																					
				66, CC*																					
				67, CC*																					
		215		68, CC																					
				28, CC*																					
		215		29, CC																					
				30, CC																					
		220		31, CC																					
				32, CC*																					
				33, CC*																					
		225		34, CC																					
				35, CC																					
				36, CC																					
				37, CC																					

Table 3. Ages and depths of some DSDP Leg 68 planktonic foraminiferal datums.

Datum ^a	Hole 502			Hole 502A			Hole 502B			Hole 502C			Hole 503A			Hole 503B		
	Sample (level in cm)	Depth (m)	Age ^d (Ma)	Sample (level in cm)	Depth (m)	Age (Ma)	Sample (level in cm)	Depth (m)	Age ^e (Ma)	Sample (level in cm)	Depth (m)	Age ^f (Ma)	Sample (level in cm)	Depth (m)	Age (Ma)	Sample (level in cm)	Depth (m)	Age (Ma)
FA <i>G. truncatulinoides</i>	11,CC	41.12	1.76	11,CC	41.70	1.72	11-2, 108	43.92	1.77	1,CC	36.22	1.83	7,CC	27.68	1.40	8,CC	33.41	1.81
FA <i>P. obliquiloculata</i>	12,CC	44.40	1.88	14,CC	54.70	2.14	12,CC	48.92	2.06	3,CC	44.31	2.10	11,CC	45.46	2.35	11,CC	46.57	2.37
FA <i>N. dutertrei</i>	—	—	—	—	—	—	15,CC	60.46	2.50	—	—	—	9-1, 106	—	—	—	—	—
LA <i>G. altispira</i>	19-1, 90	76.10	2.95	19-2, 100	78.95	2.95	18-1-75	72.89	2.85	9-2, 70	71.53	3.02	14,CC	57.67	—	15-2, 106	62.21	2.88
LA <i>Sphaeroidinellopsis</i>	20-1, 100	80.56	3.08	20-2, 52	83.50	3.08	19-2, 75	78.80	3.04	10-3, 70	75.29	3.22	15,CC	62.77	—	15-3, 106	63.71	2.91
FA <i>G. miocenica</i>	21,CC	87.28	3.50	19,CC	80.45	3.00	21,CC	89.45	3.31	10-1, 60 ^(cf)	72.20	3.04	—	—	—	—	—	—
FA <i>G. fistulosus</i>	20,CC	78.75	3.02	20-1, 100	81.97	3.04	19-1, 75	77.30	3.01	10-1, 60	72.20	3.04	15-2, 106	61.56	—	16,CC	68.36	3.23
FA <i>G. hirsuta</i>	19,CC	78.75	3.02	20,CC	85.46	3.15	20-2, 75	83.20	3.15	13-1, 75	85.55	3.41	—	—	—	—	—	—
FA <i>G. puncticulata^b</i>	20,CC	83.53	3.24	21,CC	89.56	3.31	20,CC	85.30	3.21	—	—	—	—	—	—	—	—	—
LA <i>G. pertenuis</i>	17,CC	69.40	2.75	16,CC	66.84	2.54	15,CC	60.46	2.50	14,CC	59.99	2.63	—	—	—	16-3, 106	68.30	3.22
FA <i>G. pertenuis</i>	21,CC	87.28	3.50	21,CC	89.56	3.31	21,CC	89.45	3.31	14,CC	93.67	3.64	—	—	—	17-2, 106	71.27	3.34
FA <i>G. crassaformis^b</i>	27-2, 40	111.24	4.01	29,CC	122.83	4.29	—	—	—	18-2, 75 ^(cf)	108.98	4.06	—	—	—	19-2, 106	75.77	3.48
FA <i>G. exilis</i>	21-2, 60	86.08	3.42	21,CC	89.56	3.31	22-3, 75 ^(cf)	92.17	3.38	15-1, 75	94.33	3.66	—	—	—	—	—	—
LA <i>P. primalis^c</i>	23-2, 100	93.91	3.53	22-2, 100	92.41	3.41	22-2, 75	90.47	3.33	13-3, 70	88.48	3.49	—	—	—	—	—	—
FA <i>S. dehiscens</i>	—	—	—	23,CC	98.78	3.59	—	—	—	—	—	—	—	—	—	21-2, 106	88.91	3.84
<i>P. primalis</i> L. to R	24-3, 134 to	101.55	3.75	24,CC to	103.18	3.71	—	—	—	15-1, 75 to	94.33	3.66	20-2, 96 to	83.30	—	19,CC to	80.96	3.62
	24-2, 100	99.70	3.70	24-3, 100	102.72	3.70	—	—	—	15-2, 75	95.83	3.70	20-3, 106	84.90	—	21-2, 106	88.91	3.84
FA <i>P. spectabilis</i>	—	—	—	—	—	—	—	—	—	—	—	—	25,CC ^(cf)	103.00	—	23,CC	96.15	4.04
LA <i>G. margaritae</i>	23-4, 100	96.91	3.62	23-3, 100	98.38	3.58	—	—	—	14,CC	93.67	3.64	—	—	—	—	—	—
LA <i>N. acostaensis</i>	—	—	—	26,CC	111.85	3.95	—	—	—	—	—	—	—	—	—	—	—	—
LA <i>N. pachyderma</i> (L)	27-2, 40	111.24	4.01	27,CC	116.12	4.06	—	—	—	17,CC	106.50	3.99	—	—	—	—	—	—
LA <i>G. nepenthes</i>	28,CC	117.00	4.19	28,CC	119.34	4.17	—	—	—	18-2, 75	108.98	4.06	27,CC	112.65	4.50	23,CC ^(cf)	96.15	4.04
LA <i>G. seiglei</i>	32-3, 10	133.56	4.76	33-3, 10	134.27	4.68	—	—	—	24-1, 101	130.76	4.69	43,CC	185.59	—	—	—	—
FA <i>S. dehiscens</i> (L.i)	30,CC	125.76	4.46	33,CC	134.40	4.68	—	—	—	—	—	—	31,CC	133.74	5.09	—	—	—
FA <i>G. tumida</i>	35,CC	146.58	5.26	37,CC	145.14	5.26	—	—	—	26,CC	140.34	5.26	33,CC	139.27	5.24	—	—	—
FA <i>G. margaritae</i>	35-2, 100	146.20	5.25	38,CC	147.49	5.28	—	—	—	23,CC	129.54	4.66	—	—	—	—	—	—
FA <i>N. humerosa</i>	—	—	—	45,CC	166.04	5.55	—	—	—	—	—	—	36,CC	154.59	5.43	—	—	—
FA <i>P. primalis^c</i>	28,CC	117.00	4.19	29,CC	122.83	4.29	—	—	—	20,CC	119.16	4.38	38,CC	160.20	5.49	—	—	—
LA <i>G. bulloides</i>	—	—	—	52,CC	182.33	5.78	—	—	—	—	—	—	40,CC	169.90	5.60	—	—	—

^a FA = first appearance, LA = last appearance.

^b Considered nonevolutionary in tropics.

^c Site 502 only—considered nonevolutionary.

^d Ages interpolated from magnetostratigraphy (Kent and Sparisou, this volume) and assuming FA *G. tumida* = 5.26 Ma and carbon shift (502A and 503A; Keigwin, this volume) = 6.00 Ma.

^e Ages of datums deeper than 80.30 m determined by extrapolation.

^f Ages of datums extrapolated above 55.50 m and below 117.90 m for Pliocene.

Ma, in excellent agreement with the change at Site 502 (Table 3). This supports Saito's (1976) contention that this coiling change is an oceanwide isochronous marker.

The species *G. pertenuis* (Plate 7, Figs. 1-7) is present at Site 503 (Tables 2 and 3, 3.2 to 3.3 Ma), and my identification of this species has been confirmed by J. Lamb and J. Beard (J. Lamb, personal communication). This species is considered typically "Atlantic" (by Stainforth et al., 1975) and has only been recently reported by the Indo-Pacific. Thunell (1981) reports it from the uppermost lower Pliocene in DSDP 214 (Indian Ocean) and Thompson (in press) may have found the same species at DSDP Leg 67 sites (Middle America Trench). The *G. pertenuis* at Site 503 are more robust than those found in the Caribbean, perhaps indicating that more fragile members of the population have been removed by selective dissolution. The first appearance of this species (3.3 Ma) is apparently synchronous between Sites 502 and 503, but its range is truncated in the Pacific. Other synchronous datums at this location are the first occurrence of *Globigerinoides fistulosus*, the last occurrence of *Sphaeroidinellopsis*, and the appearance of few-to-common *G. ruber*.

As at the Caribbean site, the upper Pliocene is marked by the last occurrence of *Globoquadrina altispira* just above that of *Sphaeroidinellopsis* and by the simultaneous first appearances (2.4 Ma) of *P. obliquiloculata* and *N. dutertrei* higher in the section. Site 503 differs from 502 in the presence of *Pulleniatina* and the absence of *Globorotalia exilis* and *G. miocenica* through most of the upper Pliocene.

BIOGEOGRAPHIC EVIDENCE FOR ISTHMUS CLOSING

Vertebrate paleontologists studying South American land sections knew in the last century that for much of

its Cenozoic history South America was isolated from North America. The development of the Central American land bridge and its effect on fossil mammals has recently been reviewed by Simpson (1980). Recent dating of volcanic ashes associated with South American fossil beds shows the first effects of intercontinental migration at about 7 or 8 Ma (in the late Miocene), with increased interchange between 5 and 2 Ma, and an open land connection since the beginning of the Pleistocene (Marshall et al., 1977, 1979).

As terrestrial faunas of North and South America have become more similar, marine faunas of the Atlantic and Pacific have become more dissimilar. Woodring (1966) and Herm (1969) have shown increased provinciality of Atlantic and Pacific molluscs in Pliocene and Pleistocene times. Crough and Poag (1979) have reported the sporadic occurrence of the benthic foraminifer *Amphistegina gibbosa* in the California borderlands as recently as 1.8 Ma. This species is a shallow-reef dweller and is believed to have migrated from the Caribbean during warmings. Perhaps the sea level rose enough during these warmings to flood the newly emergent land bridge and permit migration of this species.

The effect of the closing Panama Isthmus on planktonic foraminifers has been discussed at length by Kaneps (1970) and Parker (1973). Both agree that by 3 to 4 Ma there was faunal evidence for increasing provinciality. In particular Kaneps (1970) cited the evolution of the *Globorotalia exilis*-*G. miocenica*-*G. pertenuis* group and its apparent restriction to the Atlantic. Parker (1973) noted the absence of *Pulleniatina spectabilis* from the Atlantic, and the Atlantic late Pliocene and Pleistocene disappearance of *Globoquadrina venezuelana* and *Globorotaloides hexagona*. Saito (1976) and Keigwin (1978) called attention to the significance of *Pulleniatina* coiling and the temporary disappearance of

this genus from the Atlantic. Increasing provinciality has continued into the late Pleistocene, affecting the ranges of *Globorotalia tosaensis*, *Globoquadrina pseudo-foliata*, and pink-colored *Globigerinoides ruber* (Thompson et al., 1979).

Interesting comparisons can be made between the planktonic foraminiferal assemblages of Sites 502 and 503. The upper 120 meters of the Site 502 (Colombian Basin) section is similar to the pelagic sequence at nearby Site 154. As noted earlier, in the Site 154 range chart of Bolli and Premoli-Silva (1973) and by Keigwin (1978), *P. primalis* ranges for about 0.2 m.y. after the early Pliocene shift from sinistral to dextral coiling. Thus, following Saito's (1976) argument, this point marks sufficient uplift of the Panama Isthmus to restrict migration of *Pulleniatina*. The short interval of sinistral *N. pachyderma* reported in the bottom of the pelagic sequence at Site 154 (Keigwin, 1978) is actually the end of a long-ranging assemblage (about 1.5 m.y.) at Site 502 which became numerically important about 5.5 Ma. This assemblage is not present in Pacific Site 503, although it ranges through a short interval in the early Pliocene of Panama Basin Site 157 (Keigwin, 1976). Curiously, related *N. acostaensis* is mostly sinistral throughout Sites 502 and dextral in Site 503. Another important difference between the sites in the late Miocene and early Pliocene is the delayed first appearance (by about 2 m.y.) of *Pulleniatina* in the Caribbean.

The most significant result of the biogeographic comparison of Sites 502 and 503 is the discovery of *Globorotalia pertenuis* in the Pacific. Its range is truncated in the Pacific sites at approximately 3.2 Ma, whereas in the Atlantic it lived until about 2.5 Ma (Table 3). As with the last early Pliocene appearance of *Pulleniatina* in the Caribbean, the emergent isthmus probably stopped the exchange of genetic information between the two oceans, isolating the less well-adapted population. If after its evolution, *G. pertenuis* migrated from the Atlantic to the Pacific then it would be expected that earlier appearing *G. exilis* would have, too. Although I have not seen *G. exilis* (*sensu stricto*) in Pacific Sites 83, 84, 157, 158, or 503, I have found a related form (*G. limbata*-*G. exilis*; Plate 5, Figs. 4-6) in the upper Miocene of Site 503. Jenkins and Orr (1972) report *G. exilis* from several DSDP Leg 9 sites, but their figured specimens differ significantly from those I have identified at Site 502 (Plate 4, Figs. 9-12). Recently, P. R. Thompson (in press) has identified *G. cf. exilis* (perhaps equivalent to *G. limbata*-*G. exilis* at Site 503) from late Miocene eastern equatorial Pacific DSDP Sites 497 and 498. He also reports a "typical" middle Pliocene first appearance, with a last appearance at the same level as *Sphaeroidinellopsis* (3.1 Ma). This Pacific last appearance is distinctly earlier than that in Site 502 (Table 1) and close to the "truncated" Pacific last appearance of *G. pertenuis*. Thus, these two "Atlantic-type" *Globorotalia* have shorter ranges in the Pacific than the Atlantic, adding further evidence that the emergent Panama Isthmus was an effective barrier to the migration of planktonic organisms by 3.0 to 3.2 Ma.

At first there appears to be a contradiction between land-mammal evidence, which suggests that the North American-South American exchange began in the late Miocene and increased in the early Pliocene, and that from planktonic foraminifers, which show that Atlantic-Pacific provinciality began about 4 Ma. In fact the two lines of evidence are easily reconciled. As Simpson (1980) has pointed out, the first exchange of vertebrates was by waif dispersal, or "island hopping," which does not preclude the exchange of planktonic organisms through relatively deep channels between the inferred islands. By about 3 Ma, populations of planktonic foraminifers from the tropical Atlantic-Pacific were completely isolated and the exchange of terrestrial vertebrates accelerated, suggesting that the land bridge between the Americas was largely completed by this time.

CONCLUSIONS

Sites 502 and 503 contain complete successions of late Neogene and Quaternary (Holocene to about 8 Ma) tropical and subtropical planktonic foraminifers. Faunal diversity is higher in the Caribbean site, and preservation has improved there since 6 Ma. Significant differences include:

1) An enigmatic and numerically important population of sinistral *Neogloboquadrina pachyderma* between about 5.5 and 4 Ma in the Caribbean. This species is always associated with warm-water faunal elements, suggesting that its presence does not indicate cold waters. It may, however, indicate seasonal upwelling.

2) The evolution of *Pulleniatina primalis* at about 5.5 Ma in the Pacific, but its exclusion from the Atlantic until approximately 4.2 Ma.

3) The gradual Pliocene divergence of Atlantic-Pacific faunal histories arising from completion of the Panama land bridge. This divergence is seen in the exclusion of *P. spectabilis* from the Atlantic, the temporary disappearance of *P. primalis* from the Atlantic at about 3.3 Ma, and the absence of the *Globorotalia exilis*-*pertenuis*-*miocenica* lineage from the Pacific since 3.0 Ma.

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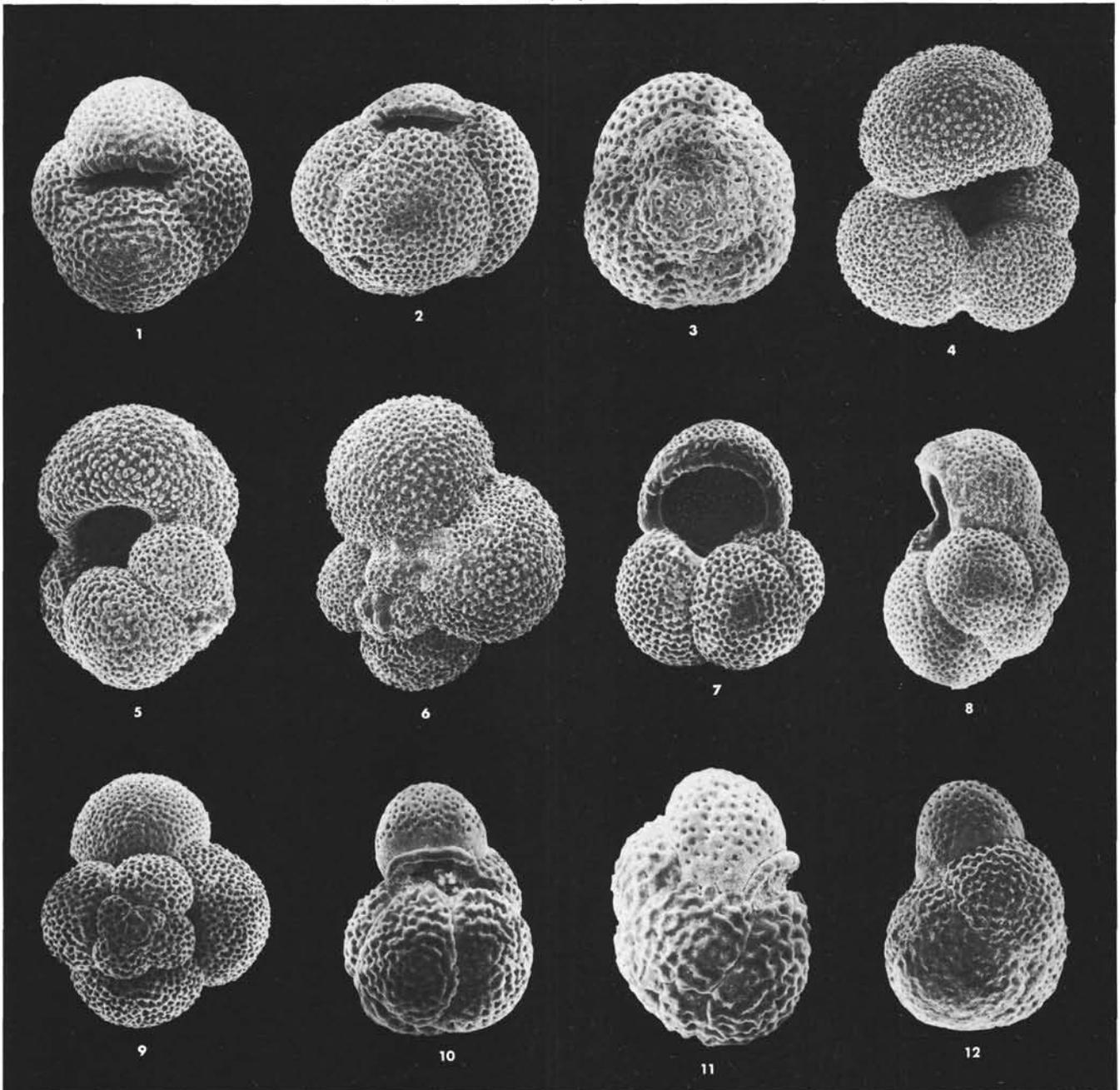


Plate 1. Neogene planktonic foraminifers. 1-3. cf *Catapsydrax unicavus*, Sample 502C-30, CC, upper Miocene, (1) ventral view $\times 110$, (2) side view $\times 115$, (3) dorsal view $\times 161$. 4-6. *Globigerina bulloides*, Sample 502C-29, CC, upper Miocene, (4) ventral view $\times 125$, (5) side view $\times 159$, (6) dorsal view $\times 143$. 7-9. *Globigerina cariacensis*, Sample 502A-23-2, 100 cm., lower Pliocene, (7) ventral view $\times 120$, (8) side view $\times 113$, (9) dorsal view $\times 115$. 10-12. *Globigerina nepenthes*, lower Pliocene, (10) Sample 502A-29, CC, ventral view $\times 133$, (11) Sample 502A-29, CC, side view $\times 178$, (12) Sample 50A-37, CC, dorsal view $\times 127$.



Plate 2. Neogene planktonic foraminifers. 1-4. *Globigerinoides bulloideus*, upper Miocene, (1) Sample 502C-32, CC, ventral view $\times 115$. 2-4. Sample 503A-46, CC, (2) ventral view $\times 106$, (3) side view $\times 122$, (4) dorsal view $\times 122$. 5-6. *Globigerinoides fistulosus*, Sample 502A-20-1, 50 cm, upper Pliocene, (5) ventral view $\times 53$, (6) dorsal view $\times 60$. 7-9. *Globigerinoides obliquus*, Sample 503A-39-1, 106 cm, upper Miocene, (7) ventral view $\times 115$, (8) side view $\times 99$, (9) dorsal view $\times 115$. 10-12. *Globigerinoides cf. bulloideus*, Sample 502A-23-2, 100 cm, lower Pliocene, (10) ventral view $\times 110$, (11) side view $\times 106$, (12) dorsal view $\times 121$.

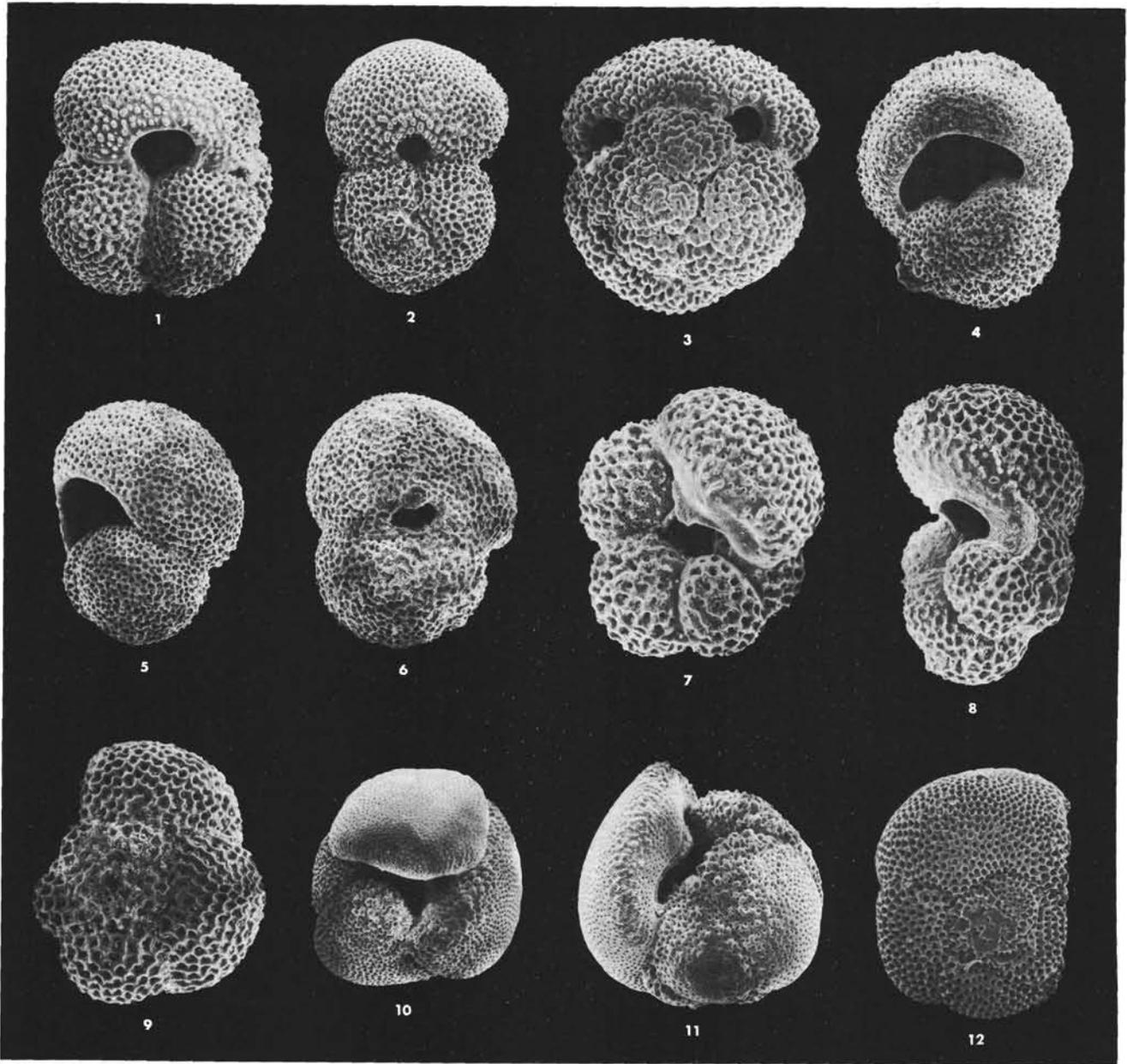


Plate 3. Neogene planktonic foraminifers. 1-3. *Globigerinoides ruber*, (1) Sample 502C-34, CC, upper Miocene, ventral view $\times 110$, (2) Sample 502C-33, CC, upper Miocene, side view $\times 126$, (3) Sample 503A-15-3, 74 cm., upper Pliocene, dorsal view $\times 92$. 4-6. *Globigerinoides seigliei*, upper Miocene, (4) Sample 502C-28, CC, ventral view $\times 100$, (5) Sample 502C-30, CC, side view $\times 115$, (6) Sample 502C-28, CC, dorsal view $\times 100$. 7-9. *Globoquadrina conglomerata*, (7) Sample 502A-47, CC, upper Miocene, ventral view $\times 166$, (8) Sample 502A-24, CC, lower Pliocene, side view $\times 150$, (9) Sample 502A-24, CC, lower Pliocene, dorsal view $\times 156$. 10-12. *Globoquadrina dehiscens*, upper Miocene, (10) Sample 503A-33, CC, ventral view $\times 88$, (11) Sample 503A-33, CC, side view $\times 94$, (12) Sample 503A-34, CC, dorsal view $\times 102$.

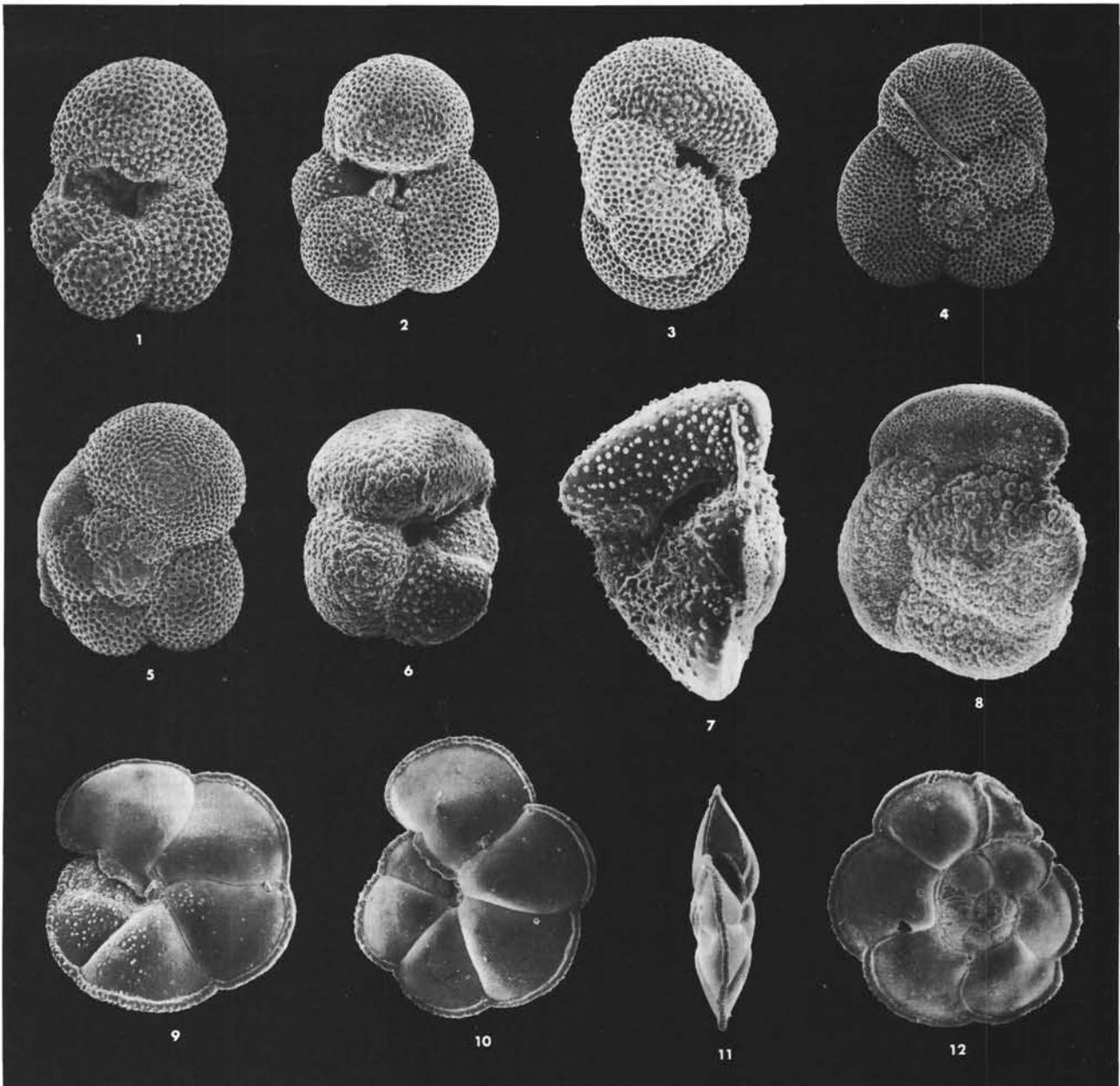


Plate 4. Neogene planktonic foraminifers. 1-5. *Globoquadrina pseudofoliata*, lower Pliocene, (1, 4) Sample 503B-22, CC, (2, 3, 5) Sample 503B-18, CC, (1) ventral view $\times 93$, (2) ventral view $\times 96$, (3) side view $\times 107$, (4) dorsal view $\times 69$, (5) dorsal view $\times 86$. 6-8. *Globorotalia crassaformis*. (6) Sample 502A-29, CC, lower Pliocene, ventral view $\times 111$, (7, 8) Sample 502B-12, CC, upper Pliocene, (7) side view $\times 166$, (8) dorsal view $\times 111$. 9-12. *Globorotalia exilis*, Sample 502B-12, CC, upper Pliocene, (9) ventral view $\times 77$, (10) ventral view $\times 73$, (11) side view $\times 58$, (12) dorsal view $\times 63$.

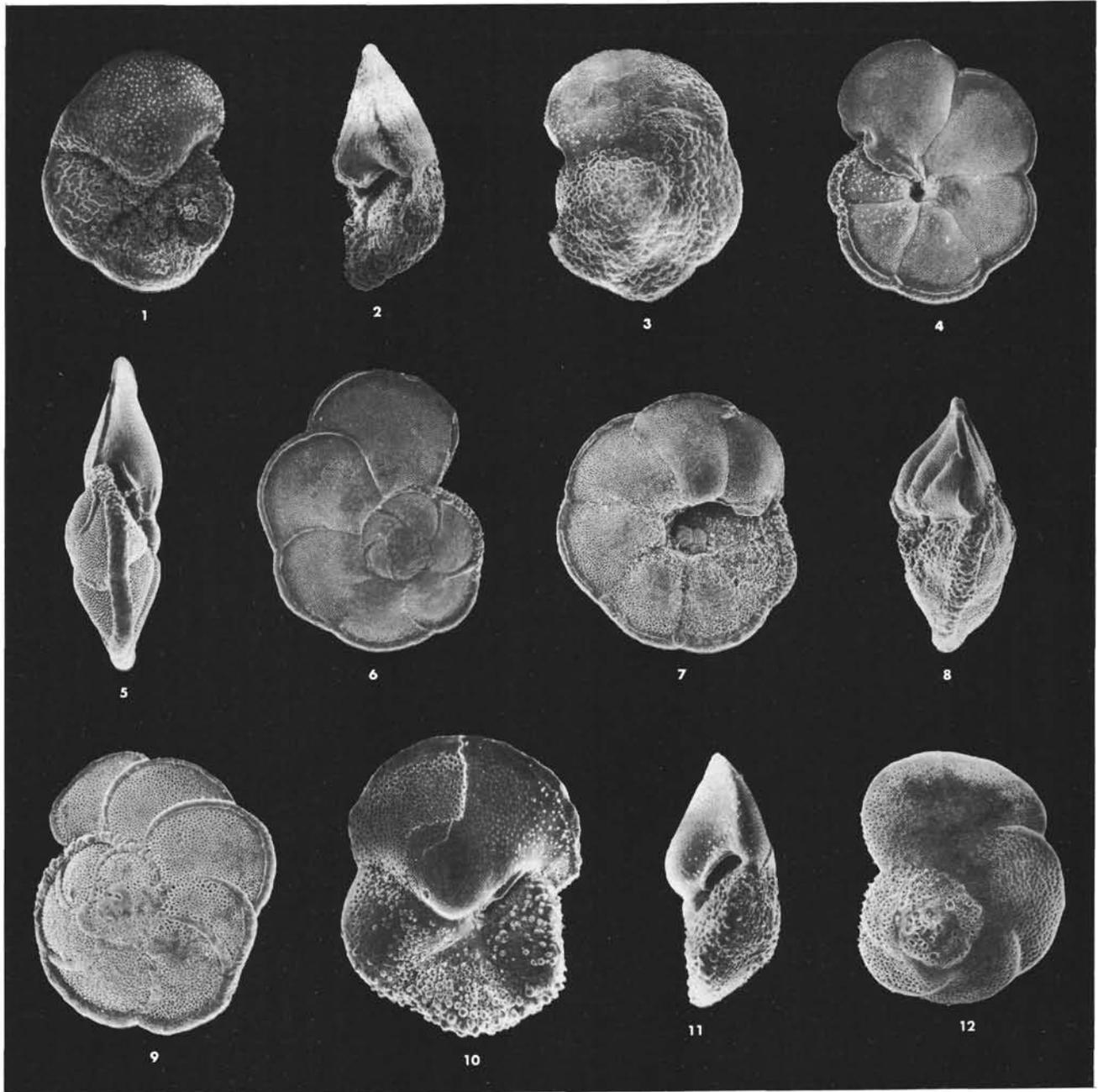


Plate 5. Neogene planktonic foraminifers. 1-3. *Globorotalia hirsuta*, Sample 502-18, CC, upper Pliocene, (1) ventral view $\times 72$, (2) side view $\times 82$, (3) dorsal view $\times 66$. 4-6. *Globorotalia limbata*-*Globorotalia exilis*, Sample 503A-39, CC, upper Miocene, (4) ventral view $\times 66$, (5) side view $\times 74$, (6) dorsal view $\times 60$. 7-9. *Globorotalia limbata*-*Globorotalia multicamerata*, Sample 502A-45, CC, upper Miocene, (7) ventral view $\times 64$, (8) side view $\times 66$, (9) dorsal view $\times 79$. 10-12. *Globorotalia margaritae*, (10, 11) Sample 502-33, CC, lower Pliocene, (12) Sample 502A-38, CC, upper Miocene, (10) ventral view $\times 110$, (11) side view $\times 110$, (12) dorsal view $\times 110$.

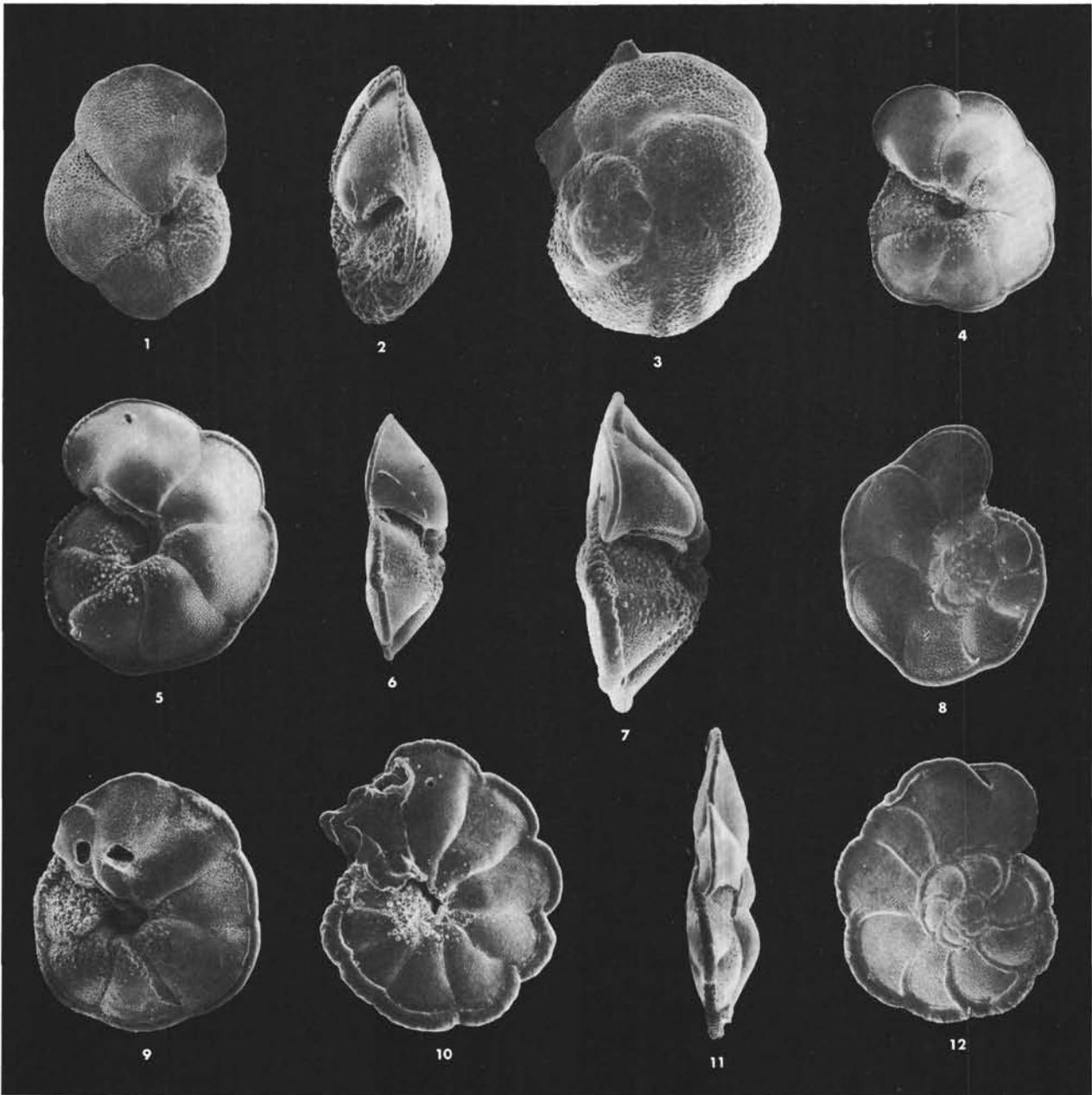


Plate 6. Neogene planktonic foraminifers. 1-3. *Globorotalia* sp. cf. *G. margaritae*, (1) Sample 502A-38, CC, upper Miocene, ventral view $\times 66$, (2) Sample 502A-37, CC, lower Pliocene, side view $\times 93$, (3) Sample 502A-38, CC, upper Miocene, dorsal view $\times 99$. 4-8. *Globorotalia miocenica*, Sample 502B-12, CC, upper Pliocene, (4) ventral view $\times 55$, (5) ventral view $\times 77$, (6) side view $\times 60$, (7) side view $\times 91$, (8) dorsal view $\times 71$. 9. *Globorotalia multicamerata*, Sample 502A-34, CC, lower Pliocene, ventral view $\times 71$. 10-12. *Globorotalia pertenuis*, (10) Sample 502A-21, CC, lower Pliocene, ventral view $\times 47$, (11) Sample 502A-18, CC, upper Pliocene, side view $\times 47$, (12) Sample 502A-21, CC, lower Pliocene, dorsal view $\times 47$.

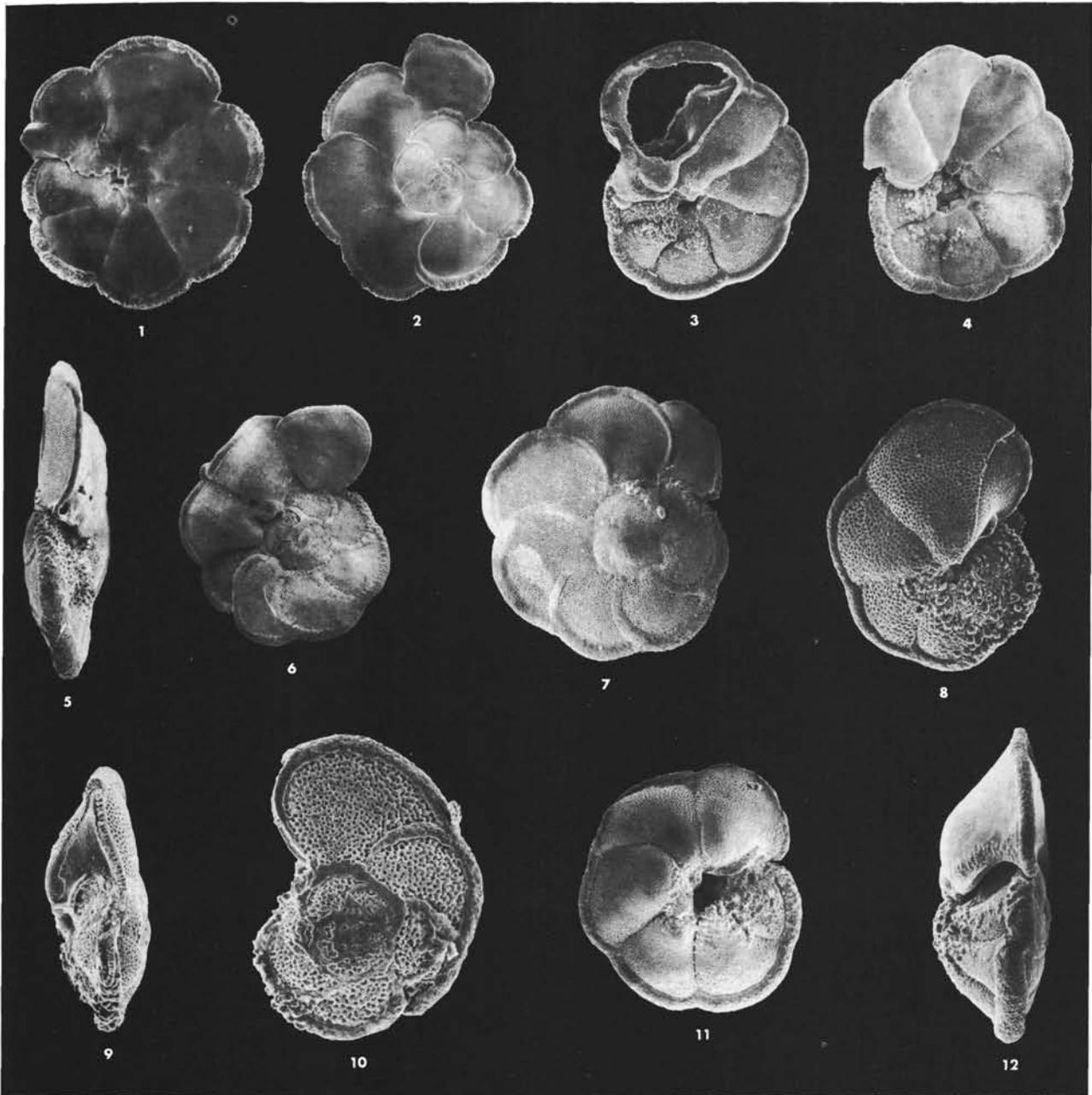


Plate 7. Neogene planktonic foraminifers. 1-7. *Globorotalia pertenuis*, (1, 2) Sample 502A-18, CC, upper Pliocene, (1) ventral view $\times 41$, (2) dorsal view $\times 47$, (3) Sample 503B-17-2, 106 cm, lower Pliocene, ventral view $\times 40$, (4-7) Sample 503B-16, CC, lower Pliocene, (4) ventral view $\times 33$, (5) side view $\times 46$, (6) dorsal view $\times 31$, (7) dorsal view $\times 42$. 8-10. *Globorotalia pleisotumida*, Sample 502C-30, CC, upper Miocene, (8) ventral view $\times 110$, (9) side view $\times 107$, (10) dorsal view $\times 132$. 11-12. *Globorotalia pseudomiocenica*, Sample 502A-39, CC, upper Miocene, (11) ventral view $\times 77$, (12) side view $\times 75$.



Plate 8. Neogene planktonic foraminifers. 1. *Globorotalia pseudomiocenica*, Sample 502A-39, CC, upper Miocene, dorsal view $\times 92$. 2-4. *Globorotalia puncticulata*, Sample 502B-20, CC, lower Pliocene, (2) ventral view $\times 155$, (3) side view $\times 121$, (4) dorsal view $\times 154$. 5-10. *Globorotalia truncatulinoides*, Pleistocene, (5-7) Sample 503B-8, CC; (8-10) Samples 502B-11-2, 108 cm, (5) ventral view $\times 154$, (6) side view $\times 190$, (7) dorsal view $\times 157$, (8) ventral view $\times 132$, (9) side view $\times 93$, (10) dorsal view $\times 99$. 11-12. *Globorotalia tumida*, Sample 503B-19-2, 106 cm., lower Pliocene, (11) ventral view $\times 48$, (12) side view $\times 46$.

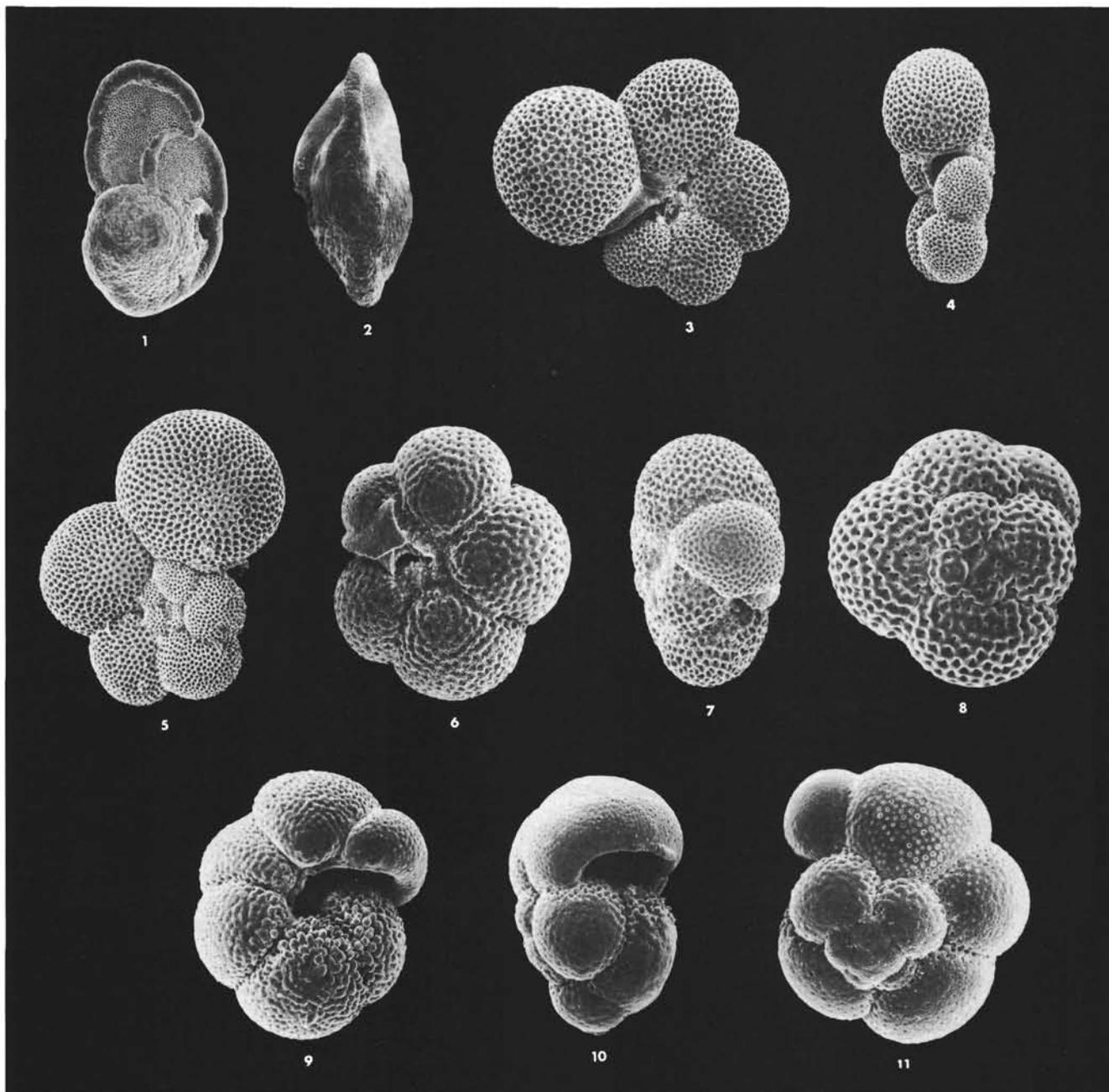


Plate 9. Neogene planktonic foraminifers. 1, 2. *Globorotalia tumida*, lower Pliocene, (1) Sample 503B-19-2, 106 cm, ventral view $\times 54$, (2) Sample 502A-37, CC, side view $\times 88$. 3-5. *Globorotaloides hexagonus*, Sample 503A-39-1, 106 cm., upper Miocene, (3) ventral view $\times 132$, (4) side view $\times 111$, (5) dorsal view $\times 110$. 6-8. *Neogloboquadrina acostaensis*, Sample 502A-26, CC, lower Pliocene, (6) ventral view $\times 132$, (7) side view $\times 134$, (8) dorsal view $\times 175$. 9-11. *Neogloboquadrina humerosa*, Sample 503A-37-1, 106 cm., upper Miocene, (9) ventral view $\times 110$, (10) side view $\times 93$, (11) dorsal view $\times 135$.

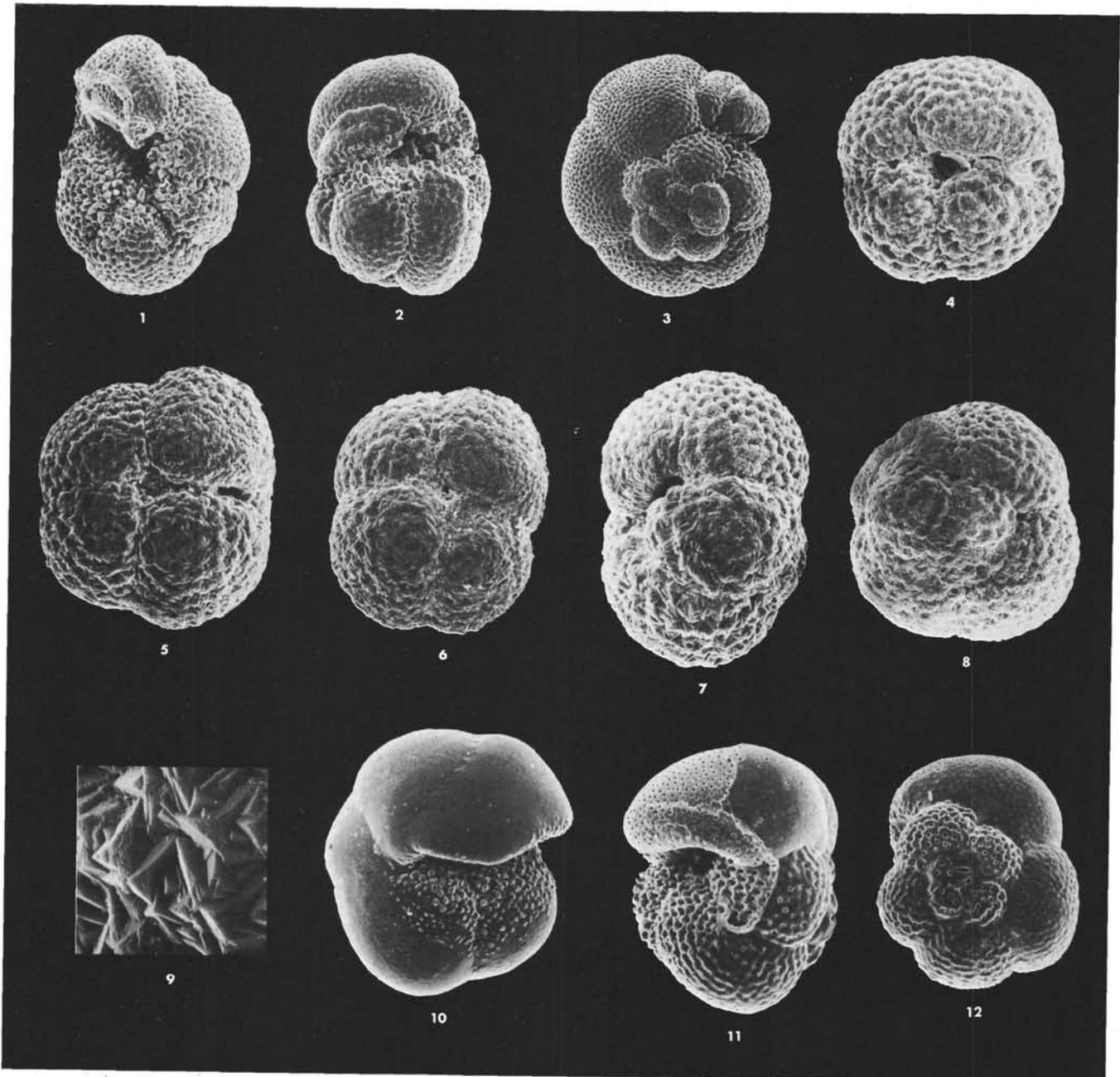


Plate 10. Neogene planktonic foraminifers. 1-3. *Neogloboquadrina dutertrei*, Sample 503A-9-1, 106 cm, upper Pliocene, (1) ventral view $\times 96$, (2) side view $\times 96$, (3) dorsal view $\times 86$. 4-8. *Neogloboquadrina pachyderma* (sinistral phenotype), (4, 5, 7, 8) Sample 502A-39, CC, upper Miocene, (6) Sample 502A-37, CC, lower Pliocene, (4) ventral view $\times 200$, (5) ventral view $\times 214$, (6) ventral view $\times 188$, (7) side view $\times 211$, (8) dorsal view $\times 198$. 9. Ultrastructure of Fig. 6, $\times 1125$. 10-12. *Pulleniatina primalis*, Sample 503B-25-2, 102, lower Pliocene, (10) ventral view $\times 126$, (11) side view $\times 154$, (12), dorsal view $\times 188$.

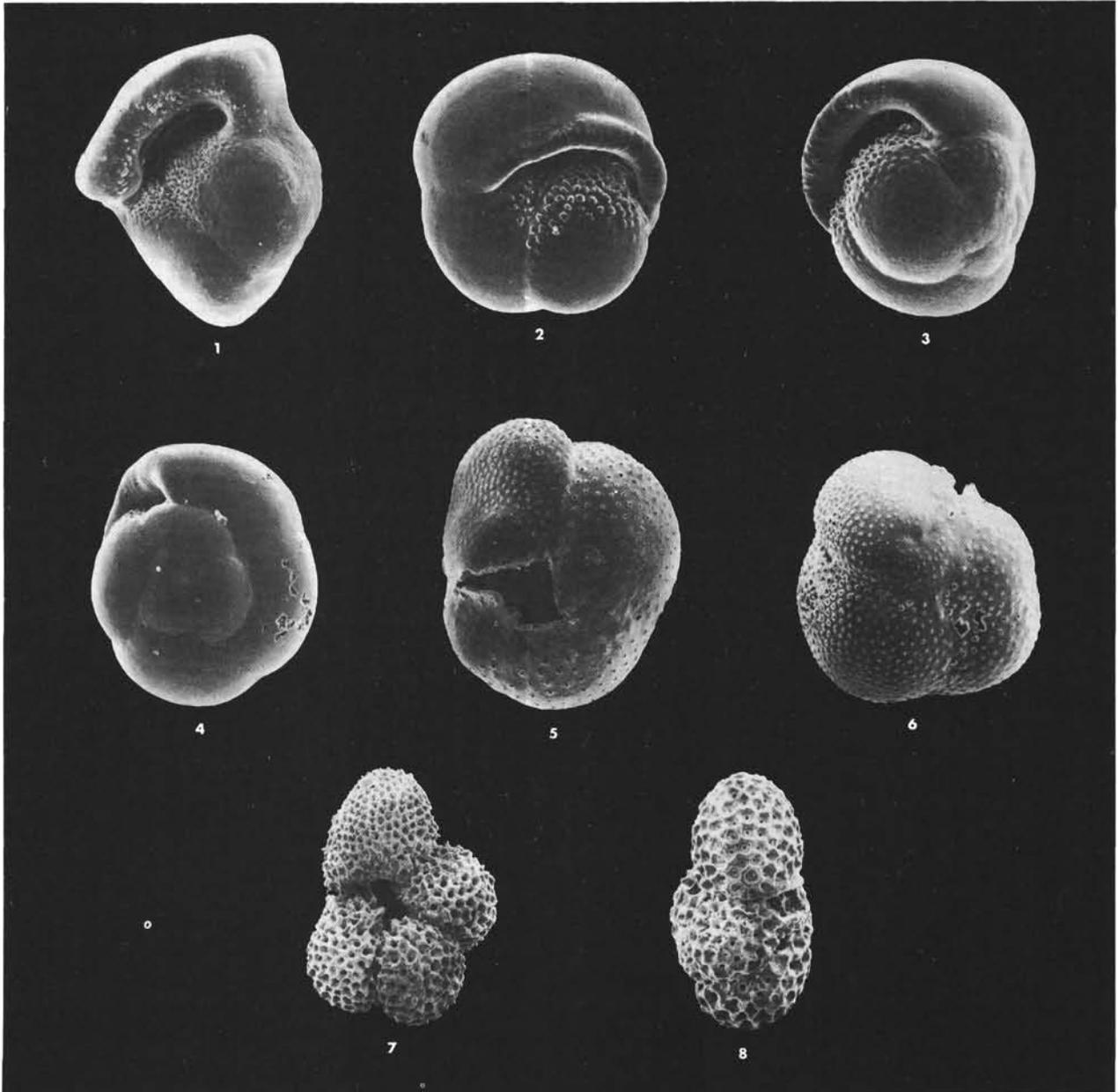


Plate 11. Neogene planktonic foraminifers. 1. *Pulleniatina spectabilis*, Sample 503B-23, CC, lower Pliocene, side view $\times 92$. 2-4. *Pulleniatina obliquiloculata*, Sample 502B-11-2, 108 cm, upper Pliocene, (2) ventral view $\times 121$, (3) side view $\times 100$, (4) dorsal view $\times 86$. 5, 6. *Sphaeroidinella dehiscens* (forma immatura), lower Pliocene, (5) Sample 503A-31, CC, ventral view $\times 82$, (6) Sample 502A-33, CC, dorsal view $\times 60$. 7, 8. *Sphaerodinellopsis seminulina*, Sample 502A-20-2, 52 cm., lower Pliocene, (7) ventral view $\times 51$, (8) side view $\times 99$.