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# Planktonic Foraminifera<sup>1</sup> Allan W. H. Bé<sup>2</sup>

## INTRODUCTION

There are about 30 species of planktonic Foraminifera, as contrasted with the more than 4200 benthic species in the oceans of the world. Most of the planktonic species belong to the families Globigerinidae and Globorotaliidae. Of the 30 species, 9 occur in Antarctic<sup>3</sup> and Subantarctic<sup>4</sup> waters; however, none of these cold-water species are restricted to the 'Southern Ocean,'<sup>5</sup> except possibly the newly recognized *Globorotalia cavernula* (Bé, 1967b). These species are distributed in broad zones of similar temperature in both the Northern and Southern Hemispheres. Hence, it is not possible to refer to these species as endemic to the Antarctic or Subantarctic, although some of them do appear in very high concentrations of 10 specimens/m<sup>3</sup> or more in the Antarctic regions. The species inhabiting the major distributional zones in the world's oceans (Figure 1) are listed in Table 1. It is noteworthy that the highest species diversity occurs between latitudes 40°N and 40°S in regions where surface temperatures are greater than 18°C.

Most planktonic Foraminifera live in the euphotic zone during their early stages; they descend to deeper water as adults and secrete thick, calcite tests. Other species prefer to live in deep water; for example, *Globorotalia scitula* is most commonly encountered between depths of 500 m and 1000 m. Spinose *Globigerinoides* and *Globigerina* are generally epipelagic, whereas the nonspinose *Globorotalia* and *Globoquadrina* have a greater range of depth habitats.

The plankton samples upon which the accompanying maps are based were collected between 1960 and 1965 on the research vessels *Eltanin* of the National Science Foundation (U.S. Antarctic Research Program), and *Vema* and *Conrad* of the Lamont Geological Observatory (Table 2). All surface (0 m to 10 m) and vertical (0 m to 300 m) tows were obtained with plankton nets of uniform mesh size and material (NITEX 202 =  $202 \mu$  mesh-aperture width) and were provided with flowmeters for quantitative readings of amounts of water filtered. The locations of the stations from which plankton samples have been examined are shown in Map 1, Plate 1.

Investigations of living planktonic Foraminifera in the Antarctic and Subantarctic are comparatively few. Boltovskoy (1959a, 1959b, 1959c, 1961, 1962, 1966a) has studied the distribution of modern species in the western South Atlantic between Cape Horn and Porto Alegre. Using Foraminifera as indicator species for differentiating between the Malvin (Falkland) Current and the Brazilian Current, he was able to locate the 'Subtropical–Subantarctic Convergence Zone'<sup>6</sup> off Argentina. Its southern and northern boundaries are located, respectively, at 47°45'S and 29°30'S in winter and at 49°S and 35°30'S in summer (Boltovskoy, 1966a).

Parker (1960) has delineated the distribution patterns of planktonic Foraminifera from the equatorial and southeast Pacific as far south as 46°S latitude using 81 plankton samples collected between October 1957 and February 1958. Her tows were obtained with considerably coarser nets (mesh-aperture width of 650  $\mu$ ) than those used in our study, and they consequently allowed the escape of a large fraction of Foraminifera. Comparison of Parker's results with ours is possible for the larger species only. Bradshaw's (1959) comprehensive work in the North and equatorial Pacific does not consider distribution south of 20°S. Boltovskoy's (1966b) distributional study, based on three *Eltanin* cruises in the South Pacific sector of the Antarctic waters, agrees generally with our results.

<sup>a</sup>Waters south of the Antarctic Convergence (sometimes called Antarctic Polar Front) <sup>4</sup>Waters between the Antarctic Convergence and the Subtropical Convergence <sup>5</sup>Roughly, all oceans south of the Subtropical Convergence

"Roughly equivalent to the region of the Subtropical Convergence

Uchio (1960) described the planktonic Foraminifera in two plankton tows and eleven bottom samples from the southern Indian Ocean. Belyaeva (1964) has made an extensive comparison of the distribution of living and dead assemblages of planktonic Foraminifera in 400 plankton and 286 bottom samples in the Indian Ocean. Her observations on the fossil distributions covered the entire Indian Ocean to Antarctica, but her study of living species was limited to the region north of 40°S latitude.

The dead assemblages of planktonic Foraminifera in South Pacific sediments have been studied by Parker (1962), whose definitive taxonomic survey of 34 species included their gross geographic distributions. Blackman (1966) also investigated planktonic foraminiferal assemblages in sediment cores from the southeastern Pacific, including the Albatross Cordillera. Kustanowich (1963) recorded the distributions of 26 species in sediments from the New Zealand region between 18°S and 54°S latitude. Blair's (1965) and Kennett's (1968) investigations of planktonic foraminiferal assemblages in sediments of the Scotia Sea and the South Pacific are particularly pertinent, and correlatable to our study, because their core samples and our plankton tows were obtained on the same expeditions (*Eltanin* Cruises 3 to 15).

## DISTRIBUTION IN THE UPPER 300 M (PLATES 1 AND 2) MAPS 2 AND 3: Globigerina quinqueloba Natland

This species occurs commonly along both sides of the Antarctic Convergence but is perhaps more abundant south of it. The typical form has a final chamber that extends as a lobe over the umbilicus and constricts the aperture. Unfortunately, this prominent feature is lacking in the earlier stages, and they are then difficult to distinguish from juvenile *Globigerina pachyderma*. Since the latter species lacks spines in the adult stages and probably also in earlier ontogeny, we consider the possession of spines by *G. quinqueloba* and the absence thereof on *G. pachyderma* as the major distinguishing criterion. This is not always as obvious as it seems because the very delicate spines of *G. quinqueloba* can be readily rubbed off by abrasion while in the plankton net or sample jar or dissolved by inadequately buffered preservative.

The regions and seasons of maximum abundance of *Globigerina quinqueloba* coincide with those of *Globigerina pachyderma* (Maps 4 and 5), but the former decreases toward the pole and is absent in the southernmost stations (Maps 2 and 3). It occurs less abundantly in Subantarc: waters and has a northern limit in the Southern Hemisphere at approximately 40°S latitude.

Blair (1965) noted that G. quinqueloba constitutes less than 10% of the total planktonic Foraminifera in Recent sediments in the Drake Passage and the South Pacific and that it appeared in larger numbers and at more stations north of the Antarctic Convergence than south of it. Kustanowich (1963) found it a rare but widespread species in the surface sediments around New Zealand and south of it.

Globigerina quinqueloba occurs predominantly in waters colder than  $12^{\circ}$ C, and in the Antarctic region it is most frequently found in water temperatures between  $1^{\circ}$ C and  $6^{\circ}$ C.

# MAPS 4, 5, AND 6: Globigerina pachyderma (Ehrenberg)

This species, particularly the left-coiling variety, is the most cold-tolerant of the planktonic Foraminifera and is abundant in Antarctic and Subantarctic as well as in Arctic and Subarctic waters. In Subantarctic waters it is especially common over the Argentine continental shelf. The species is very rare, or absent, in subtropical waters.

Juveniles of G. pachyderma have 4.5 to 5 hemispherical chambers per whorl, a large aperture, an open umbilicus, and a thin-walled test that looks considerably different from the compact, thick-walled adult test

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whorl, a large aperture, an open umbilicus, and a thin-walled test that looks considerably different from the compact, thick-walled adult test with 4 coalescing chambers per whorl, a reduced final chamber, and a constricted aperture. The typical adult form of G. pachyderma is attained by crystalline thickening (Bé, 1960b).

The young forms of Globigerina pachyderma are difficult to separate from G. quinqueloba Natland, as we have discussed previously. Spinosity may or may not prove to be a real distinguishing characteristic, since it has not yet been established whether G. pachyderma truly lacks spines in its earlier stages.

There are several regions where either the right-coiling or the leftcoiling variety is predominant (Map 6). One area where right-coiling specimens predominate is located over the Argentine continental shelf north of the Falkland Islands, where concentrations of G. pachyderma are exceptionally high for a region so far north of the Antarctic Convergence. Our plankton collections and those of Boltovskoy (1966a) both indicate a sharply defined boundary between predominantly left-coiling and right-coiling populations north of the Falkland Islands. Another region of mostly right-coiling forms is east and west of New Zealand (Jenkins, 1967). Because of the generally rapid decrease of G. pachyderma northwards and the lack of sample coverage in certain parts of the ocean, the actual extent of these regions cannot be readily ascertained. It should be



Fig. 1. World distributional zones of planktonic Foraminifera. Species that inhabit each zone are listed in Table 1.

noted, however, that the water is warmer in these areas than in regions inhabited by left-coiling forms. It may well be that dextral populations of G. pachyderma are distributed in a continuous belt north of their sinistral relatives in a manner reciprocal to that observed by Ericson (1959) in the North Atlantic. It is also possible that a gradual and nearly continuous genetic gradient exists from left-coiling to right-coiling populations of G. pachyderma and that the latter, in turn, grade into Globoquadrina dutertrei. Cifelli (1961), Parker (1962) and Zobel (1968) have noted strong morphological similarities between the two species.

The left-coiling variety occurs preponderantly in the colder Subantarctic and Antarctic waters. The percentage of sinistral forms increases southward as water temperature decreases. Ninety percent or more of G. pachyderma tests are sinistral south of the Antarctic Convergence. This agrees closely with Blair's (1965) and Kennett's (1968) observations of coiling ratios of G. pachyderma in Antarctic Recent bottom sediments. The 90% left-coiling isopleth of both investigators is based on fossil populations and runs north of the Antarctic Convergence, while our relative abundances of 90% for living forms generally follow the Antarctic Convergence or are located to the south of it. We believe this indicates that a southward shift of predominantly sinistral populations has taken place in the recent past.

TABLE 1. Species Composition of World Distributional Zones Shown in Figure 1

Zone	Species
NORTHERN AND SOUTH	IERN COLD-WATER REGIONS
Arctic and Antarctic zones	Globigerina pachyderma
	(left-coiling variety)
Subarctic and Subantarctic zones	Globigerina pachyderma
	(right-coiling variety)
	Globigerina quinqueloba
	Globigerina bulloides
	Globigerinita uvula
	Globorotalia scitula
	Globorotalia cavernula⁴
TRANSIT	TION ZONES
Northern and southern zones	Globorotalia inflata
of transition between cold-	Also, mixed occurrences
water and warm-water regions	of subpolar and tropical-
	subtropical species
WARM-WA	TER REGIONS
Northern and southern	Globigerinoides ruber
subtropical zones	(pink variety in
	Atlantic Ocean only)
	Globigerinoides conglobatus
	(fall species)
	Hastigerina pelagica
	Globigerinita glutinata
	Globorotalia truncatulinoides
	(winter species)
	Globorotalia hirsuta
	(winter species)
	Globigerina rubescens
	Globigerinalla aquilateralis <sup>2</sup>
	Orbulina universa <sup>2</sup>
	Globoquadrina dutertrei <sup>2</sup>
	Globorotalia crassaformis
Tropical zones	Globigerinoides sacculifer
	[incl. "Sphaeroidinella
	dehiscens" (Parker and Jones)
	Globorotalia menardii
	Globorotalia tumida
	Pulleniatina obliquiloculata
	Candeina nitida
	Hastigerinella digitata
	Globigerinella adams <sup>a</sup>
	Globoquadrina hexagona <sup>3</sup>
	Most species from subtropical
	zones are also common in troni
	20100 010 0100 00111101111 0001

Restricted to the Indo-Pacific. \*Restricted to the Subantarctic TABLE 2. Plankton Collections Used in This Study

Ship and Cruise Number	Date of Collection	Number of Samples	Number of Stations
Eltanin			
8	April 14-June 12, '63	66	21
9	Aug. 12-Sept. 13, '63	63	16
10	Oct. 13- Nov. 29, '63	101	30
11	Dec. 28, '63-Feb. 13, '64	117	29
12	Mar. 13-April 18, '64	95	9
13	May 19-June 29, '64	127	16
14	Aug. 2-Sept. 5, '64	158	19
15	Oct. 11-Nov. 21, '64	175	24
16	Feb. 4-Feb. 18, '65	45	.9
17	Mar. 25-April 30, '65	204	23
18	June 5–10, '65	26	3
19	July 13-Aug. 24, '65	147	11
Vema			
14	Jan. 8-April 5, '58	21	21
15	Feb. 24, '59	1	1
16	March 30-Apr. 16, '60	3	3
18	Feb. 28-May 15, '62	29	29
18	July 28–Aug. 7, '62	3	3
Conrad			
8	Feb. 18-April 1, '64	19	19
9	Mar. 8-April 14, '65	15	15

Globigerina pachyderma occurs most abundantly during spring, summer and early fall (early October to late April); this coincides with the period of high phytoplankton production. The region of highest abundance, where *G. pachyderma* exceeds 10 specimens/m<sup>3</sup>, lies between 60°W and 155°W and south of the Antarctic Convergence; a secondary area of high concentration is located off the Argentine shelf (Map 4). Low concentrations of *G. pachyderma* prevail during late fall and winter (May to September). The left-coiling populations are encountered at water temperatures between  $-1^{\circ}$ C to 8°C, and reach highest concentrations at temperatures below 2°C. Dextral populations are found primarily between 9°C and 15°C.

### MAPS 7 AND 8: Globigerina bulloides d'Orbigny

This is the most abundant species in Subantarctic waters, often reaching 80% to 90% of the total planktonic foraminiferal populations. It is next in importance to *G. pachyderma* as a cold-water indicator. The species occurs in a broad belt roughly between  $40^{\circ}$ S latitude and the Antarctic Convergence. Highest concentrations are generally observed during spring and summer, while sparse populations are usual in winter.

Globigerina bulloides is found to about 480 km south of the Antarctic Convergence, but the main decrease in numbers occurs within the first 160 km or so south of the Convergence. In addition, seasonal fluctuations of G. bulloides are responsible for southward invasions beyond the Convergence during summer and spring and northward retreats during late fall and winter.

The northern limit of abundant G. bulloides in the Southern Hemisphere is at approximately 40°S latitude coinciding roughly with the 18°C surface isotherm. Globigerina bulloides grades morphologically and zoogeographically into G. falconensis Blow. The latter inhabits the cooler edges of subtropical regions and differs from G. bulloides in having a smaller test, a more constricted low-arched aperture with a lip, and more elongate chambers (Bé, 1967a). We believe that the two forms belong to a cline.

Blair (1965) found that the 20% isopleth of fossil G. bulloides in Recent bottom sediments of the South Pacific is situated north of the Antarctic Convergence, whereas relative abundances of 20% for living G. bulloides are located about 160 km south of the Convergence. As is true in the comparison of fossil with living G. pachyderma populations, we infer that the present-day extension of G. bulloides south of the Convergence is due to a warming trend of waters in the recent geologic past.

Blackman (1966) observed that G. bulloides constituted from 39% to 73% of the total planktonic Foraminifera in Recent sediments of the Albatross Cordillera south of 40°S latitude. Kustanowich (1963) also observed the dominance of G. bulloides in Subantarctic sediments south of New Zealand. The species made up more than 40% of the total planktonic Foraminifera south of 40°S latitude.

Globigerina bulloides is encountered primarily in near-surface waters and decreases in number with depth. Its optimum temperature range lies between  $2^{\circ}C$  and  $10^{\circ}C$ .

## MAPS 9 AND 10: Globorotalia truncatulinoides (d'Orbigny)

This species flourishes in Subantarctic waters during late fall and winter (May to October), but is rare during the remaining months of the year (Figure 2). The seasonal factor explains why this species is sparsely distributed during summer and early fall. If only late fall and winter samples are considered, the high densities found in the Subantarctic region may well be part of an extensive bloom of G. truncatulinoides over the middle latitudes of the southeastern Pacific. The northern extent of such a fall-winter bloom cannot be ascertained because of the paucity of samples in the southeastern Pacific.

Parker (1960) did not report any *G. truncatulinoides* south of 40°S latitude. However, on the Albatross Cordillera between  $25^{\circ}$ S and  $45^{\circ}$ S latitude, in Recent sediments, it is one of the dominant species, constituting more than 20% of the planktonic foraminiferal assemblages (Blackman, 1966). The absence of *G. truncatulinoides* in Parker's southern stations may be due to its very low concentration between October and February and is a further indication that it is a mid-latitude species which occurs most abundantly in late fall and winter in subtropical, transitional, and Subantarctic waters of the South Pacific.

In the North and South Atlantic G. truncatulinoides is also a winter species, occurring primarily between December and April in the Sargasso Sea and in July and August in the central South Atlantic (Bé, 1960a, and unpublished data). However, while it is restricted to subtropical waters in the Northern Hemisphere (Bradshaw, 1959; Bé, and Hamlin, 1967), G. truncatulinoides appears to have a wider temperature tolerance in the Southern Hemisphere, where it flourishes in Subantarctic as well as subtropical waters. In the Northern Hemisphere it does not occur in regions with surface temperatures below  $14^{\circ}$ C, but in the Southern Hemisphere this species is common in Subantarctic waters with temperatures as low as  $4^{\circ}$ C.

Blair (1965) reported that in bottom sediments the relative abundance of *G. truncatulinoides* tests are about 1% and 2% along the Antarctic Convergence in the South Pacific and about 1% to 5% in the Scotia Sea north of the Convergence. Although this seems considerably lower than the high percentages of living *G. truncatulinoides* along or north of the Convergence (Map 10), the lower frequencies in the sediments may reflect either the averaging effect of the strongly seasonal productivity of this species or the recency of the incursion of greater concentrations of *G. truncatulinoides* in the Subantarctic region.

Left-coiling tests of *G. truncatulinoides* greatly outnumber the rightcoiling ones in Subantarctic waters.

## MAPS 11 AND 12: Globorotalia inflata (d'Orbigny)

This is a good indicator species of transitional waters between the subtropical and Subantarctic regions in the South Atlantic, but in the South Pacific highest frequencies are found mainly in Subantarctic waters (Map 12). Whereas in the Atlantic highest relative abundances are encountered in regions where surface isotherms are between  $13^{\circ}$ C and  $19^{\circ}$ C, in the Pacific it is one of the dominant species of Subantarctic waters having surface temperatures between  $2^{\circ}$ C and  $6^{\circ}$ C.

Globorotalia inflata occurs predominantly during winter and spring (early August to early January) reaching a climax in October and November, when relative abundances up to 70% of the total population and absolute abundances of 10 specimens/m<sup>3</sup> or more are recorded. The seasonal distribution of *G. inflata* (Figure 2) shows its spring preference even more distinctly if *Conrad* Cruises 8 and 9 are disregarded, because they are mostly north of 50°S latitude. The high concentrations in the New Zealand region contrast with the relatively low densities to the south near the Antarctic Convergence; this difference can probably be attributed to the seasonal factor.



Fig. 2. Seasonal distributions of *Globorotalia truncatulinoides* and *G. inflata* according to various cruises.

Rare (samples from north of the Antarctic Convergence)

Abundant

G. inflata is not common over the Argentine continental shelf, although the temperature-salinity conditions appear favorable for its development. Here right-coiling Globigerina pachyderma and G. bulloides are predominant among the planktonic Foraminifera.

Whether G. inflata is also abundant in the southeastern Pacific to the north of our present area of study is a matter of conjecture. Parker (1960) noted low relative abundances (<10%) in 2 out of 11 stations in this area, but her plankton samples were collected with coarse-meshed nets (0.65 mm mesh aperture) which in all likelihood allowed the escape of many Foraminifera. Blackman (1966) observed that G. inflata constituted more than 20% of the planktonic foraminiferal thanatocoenosis in the sediments south of 45°S latitude of this same area.

Blair (1965) reported relative abundances of G. inflata as high as 30% in the southeastern Pacific floor and up to 20% in the Drake Passage sediments north of the Antarctic Convergence. His 10% isopleth is also located north of the Convergence, whereas equivalent relative abundances for living G. inflata are generally south of the Convergence. This is interpreted as the result of a southward migration during the warming trend of the recent geological past. Blair's high relative abundances in the Scotia Sea are also reflected in the living populations which are transported eastward from the Pacific into the Scotia Sea.

MAPS 13 AND 14: Globigerinita glutinata (Egger)

This is a ubiquitous species that is found commonly in small numbers in Subantarctic waters. Its frequency is usually less than 5% of the total planktonic Foraminifera, although it sporadically increases to 10% or higher, as in the region west of the Drake Passage (Map 14). In the southeastern Pacific and the Atlantic sectors, reduced numbers of this species are able to cross the Antarctic Convergence. The species is absent in the southernmost stations, where surface temperatures drop below 1°C.

Globigerinita glutinata is an enigmatic species among planktonic Foraminifera. It ranges from Subarctic to tropical to Subantarctic waters, but it does not appear to have any distinct patterns or centers of maximum concentration. Bradshaw (1959) observed that it is more abundant in tropical than in Subarctic regions of the Pacific Ocean. Boltovskoy (1966a) considered it useless as an indicator species, because it inhabits Subantarctic as well as subtropical waters of the South Atlantic off Argentina. The general lack of diagnostic morphological features and the usual absence of the distinctive bulla in specimens from plankton tows make it difficult to determine whether cold-water Subantarctic or Subarctic populations belong to the same species complex as those from the tropicalsubtropical regions.

Blair (1965) noted that this species is randomly distributed in frequencies up to 9% in the bottom sediments of the South Pacific and Scotia Sea north of the Antarctic Convergence.

UNMAPPED SPECIES

Globigerinita uvula (Ehrenberg)

This species is more frequent and abundant in Antarctic than in Subantarctic regions. It was present at 23 stations south of the Antarctic Convergence and at 18 stations north of it. Globigerinita bradyi Wiesner and Globigerinoides cf. G. minuta Natland of Bradshaw (1959) are considered conspecific with Globigerinita uvula. The tightly coiled, highspired, nonspinose test frequently possesses a diagnostic bulla with infralaminal apertures. Because its maximum dimension is 190  $\mu$  or less, most specimens probably escape through the meshes of the plankton nets and our quantitative estimates are therefore unreliable. Blair (1965) reported a random distribution of G. uvula in bottom sediments from both sides of the Convergence and noted that its frequency rarely exceeded 1%.

Globorotalia scitula (Brady)

This is a Subantarctic, deepwater species which very rarely occurs in the epipelagic zone (0 m to 300 m). It appeared in the 500 m to 1000 m depth range at 4 Eltanin stations during the period August 12 to 21, 1963, north of South Georgia and the Antarctic Convergence. During October and November 1963, it was again encountered between 500 m and 1000 m at 3 stations north and 1 station south of the Convergence. Blair (1965) reported that G. scitula is rare or absent in the Antarctic sediments of the South Pacific and the Scotia Sea and it tended to be more frequent in his northern Subantarctic samples.

SUMMARY

Nine species of planktonic Foraminifera have been encountered in the Antarctic and Subantarctic waters. The only species that occurs abundantly in Antarctic waters is Globigerina pachyderma. Six species occur commonly in Subantarctic waters; these are Globigerina bulloides, Globorotalia inflata, Globorotalia truncatulinoides, Globorotalia scitula, Globigerinita glutinata and Globorotalia cavernula. Globigerina quinqueloba and Globigerinita uvula are more frequent in the Antarctic region, but are also ubiquitous in Subantarctic waters. All species show widely overlapping distributions, but their centers of maximum concentrations are generally located either in Antarctic or Subantarctic waters.

Two species have distinct seasonal occurrences. Globorotalia truncatulinoides is most abundant between early May and late October, while Globorotalia inflata proliferates between early August and early January.

In winter (June through September) the upper 100 m of water around Antarctica is comparatively barren of plankton (including Foraminifera) and the bulk of the planktonic populations inhabit the deeper waters between 250 m and 1000 m.

In comparing the fossil assemblages in surface sediments studied by Blair (1965) with living populations from the same regions, we have noted that the equivalent frequencies of Globigerina pachyderma (20%), G. bulloides (20%), Globorotalia truncatulinoides (5%), and G. inflata (10%) are all located north of the mean position of the Antarctic Convergence in the bottom sediments, whereas these frequencies for living populations are now south of the Antarctic Convergence. The southward retreat of Antarctic G. pachyderma and the advance of the three Subantarctic species indicate the extent of a warming trend since the deposition of the most recent sediments and their skeletal remains.

These findings agree with Hays' (1965) observations that the boundary between Antarctic and Subantarctic Radiolaria in bottom sediments is located 3° to 10° north of the mean position of the Antarctic Convergence. He noted also that north of the Convergence the radiolarian species in the thin top layer of cores are indicative of a recent warming period during the past few thousand years.

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Austral seasons are indicated

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