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# Paleocene planktonic foraminiferal biogeography and the paleoceanography of the Atlantic Ocean

## ABSTRACT

The spatial and temporal distributions of organisms reflect the gradients and dynamics of that system we call climate. To describe such relationships for the Paleocene, quantitative analyses of planktonic foraminiferal distributions in the Atlantic have been combined with stable isotope studies of foraminifera from the same localities. Planktonic foraminiferal bioprovinces and bioprovincial indicators are described. The positioning of bioprovinces through time reflects meridional and zonal near surface estimated paleotemperature gradients. Vertical depth habitats and temperature preferences are estimated for many planktonic foraminiferal species. Permanent changes in some species distributions vertically in the water column can be correlated with permanent changes in their geographic ranges. Unusual poleward extensions of thermophilic foraminifera occurred during climatic maxima at 62 and 60 Ma in warm boundary currents that flowed as far south as the Falkland Plateau and as far north as western Greenland and the North Sea. The coolest water faunas of the Atlantic are found throughout the Paleocene on the Agulhas Plateau. Not all paleobiogeographic data correlate with the paleotemperature record of climate. While diversity at a site corresponds with the surface temperature and the surface-to-bottom temperature gradient, oceanwide planktonic foraminiferal diversity and the increasing diversity of tropical index species correlate with the carbon isotope, not the oxygen isotope, record. We suggest that primary production and nutrient availability were a primary influence on the evolution and distributions of Paleocene planktonic foraminifera.

## INTRODUCTION

The purpose of this paper is to investigate the relationships of planktonic foraminifera to oceanic paleotemperatures and paleocirculation patterns as indicated in the oxygen and carbon isotope records of the Paleocene. The paper derives from two independent studies conducted during the last several years: Premoli Silva charted the changing biogeographies of Paleocene planktonic foraminifera, their evolution, and ecophenotypic variability through the Paleocene in the open ocean and on the shelves of the Atlantic (Haq et al. 1977). Oxygen isotope analyses have been made on Paleocene planktonic and benthic foraminifera from DSDP (Deep Sea Drilling Project) sites in the Atlantic Ocean (Boersma and Shackleton 1977a, 1977b; Boersma et al. 1979). Records at individual sites through the Paleocene have been supplemented by synoptic measurements and with multiple analyses of several species at these additional sites.

We herein summarize the stratigraphic ranges and biogeographic patterns of most planktonic foraminifera of the Paleocene. Parameters discussed include faunal composition, diversity and dominance within faunas, ecophenotypic variability of biogeographic index species, and the varying character of Paleocene bioprovinces of the Atlantic Ocean. Oxygen and carbon isotope measurements are used to provide information on the temperature ranges occupied by each species, the relative order in which species stratify through the water column, and the type of thermocline through which species were distributed in specific areas of the Atlantic. We compare synoptic measurements of near-surface estimated paleotemperature, meridional temperature gradients, and thermal gradients through the water column to the distribution patterns of planktonic foraminifera of the Paleocene.

## METHODS

We selected the Atlantic basin for study because of the abundant, widely distributed Deep Sea Drilling sites that penetrated Early Tertiary calcareous sediments. The Atlantic is a well-studied ocean basin, and the paleotectonic history of the surrounding continental areas, especially the record of marine transgressions, is well delineated.

The bulk of our material comes from DSDP sites cored on Legs 1–74 (text-fig. 1, table 1), supplemented with shelf-depth land section material from lower and higher latitudes, piston cores, and commercial bore holes. We collected material from the most widely cored biostratigraphic intervals into sets of near-contemporaneous samples that were distributed over a wide geographic and latitudinal range. Some sites were sampled at closer intervals to trace foraminiferal variations



TABLE 1

Sites used in faunal and isotope studies reported on in this paper. Locations are shown in text-figure 1; paleolatitudes and depths are given in table 2.

<i>Eugubinus</i> Zone	Zone P1a-c	Zone P1d	Zone P2	Zone P3a	Zone P3b	Zone P4	Zone P5
Sample localities—faunal studies							
356	356	95	86	356	152	144	95
384	384	type Danian	94	384	153	329	98
152	95	West Greenland	151	Scotia Shelf	119	Delaware	20C
95	Pont Labau	20C	Senegal	Pont Labau	144	144	329
398		Senegal	398	398	Trinidad		398
type Danian		398			20C		
		356			398		
		North Sea					
Sample localities—isotope studies							
356	95	356	151	356	356	21a	384
357	357	384	V26-65	384	384	144	152
384	384		86		357	329	20C
152	356		356		20C	Agulhas Plateau	21
Agulhas Plateau			384		Agulhas Plateau	86	329
			95		152	527	527
					525	528	528
							525

las and Savin (1978) demonstrated size-related oxygen isotopic lightening of juvenile planktonic foraminifera.

In the present study only adults were used. Actual measurements of the species of one genus, *Chiloguembelina*, and subsequent oxygen and carbon isotopic analysis of the taxon in the same samples showed no consistent relationship between smaller size and lighter values in the size range 63–149  $\mu\text{m}$ . Other species have not yet been tested, except *Guembelitra cretacea* Cushman, which is carbon isotopically light in the proto-Brazil Current region of the Atlantic, but not in the equatorial Pacific (Boersma and Shackleton 1981).

#### Carbon isotopic corroboration

In a normally stratified ocean, carbon isotope values nearer the surface should be heaviest and decrease downward owing to the gradual oxidation and release of lighter carbon (Broecker 1974). By this reasoning, shallowest-dwelling foraminifera should record the heaviest carbon but lightest oxygen isotope values if they are precipitating their carbonate in equilibrium with sea water. Paleocene planktonic foraminifera that have been analyzed to date (Boersma et al. 1979) demonstrate a consistent correlation between heavy carbon and light oxygen and a decrease in carbon values as oxygen values increase among the species measured in a sample.

#### Benthic foraminiferal corroboration

To corroborate retention of original isotopic values, several benthic foraminifera are routinely measured in many samples. For the Early Tertiary, the relative values of several species of *Cibicides*, *Stilostomella*, *Bulimina*, *Oridorsalis*, and *Globocassidulina* to each

other and to the oxygen isotopically dependable genus *Uvigerina* (Shackleton 1974; Boersma and Shackleton 1977a, 1977b) are known. If the relative values of several species are inconsistent in a sample, recrystallization is often the problem, and we know that we have not measured original isotopic values.

#### TAXONOMY

Planktonic foraminiferal specific and generic concepts follow those of Fleisher (1974), Berggren (1977) and Premoli Silva (1977). For biogeographic analysis, foraminiferal taxa were organized into 12 groups according to:

#### 1. phylogenetic relationships in well-known lineages

TABLE 2

Present and past locations and depths of DSDP sites used in this study. Data sources are listed in caption of text-figure 1. Reconstructed paleodepths and paleolatitudes from Sclater et al. 1977; McCoy and Zimmerman 1977; and Haq et al. 1977.

Site	Depth (meters)	Latitude	Longitude	Paleodepth (meters)	Paleo- latitude
95	1633	24°00'N	86°85'W	1800	25°N
94	1793	24°64'N	88°16'W	2400	25°N
86	1462	22°48'N	90°75'W	1700	24°N
152	3899	15°72'N	74°47'W	3000?	12°N
151	2029	15°02'N	73°58'W	?	12°N
144	2957	9°23'N	54°52'W	2400	7°N
356	3203	28°22'S	41°28'W	3000?	30°S
21	2113	28°10'S	30°85'W	2113	30°S?
20C	4506	28°47'S	26°73'W	2900	28°S
329	1519	50°31'S	46°73'W	2000	55°S
357	2109	30°25'S	35°59'W	1800	35°S
384	3909	40°65'N	51°39'W	—	45°N
525	2467	29°04'S	2°59'E	—	30°S
527	4428	28°02'S	1°45'E	—	30°S
528	3800	28°31'S	2°19'E	—	30°S
117	1038	57°20'N	15°23'W	—	57°N
119	4447	45°01'N	58°49'W	—	44°N

(see Berggren 1977) that are primarily composed of taxa with similar wall structures;

- 2, morphologic similarity of generalized taxa—for example the globigerine forms that display large morphologic variability and poorly understood evolutionary trends; and
- 3, biogeographic uniqueness.

Each of the 12 groups is identified by generic name or by its most significant character, and is numbered starting roughly from older to younger. Species in each group are listed and their stratigraphic ranges plotted in text-figure 2.

#### Group 1—biserial heterohelics

This group includes all species belonging to the genera *Woodringina*, *Chiloguembelina* and *Zeauvigerina*. The unifying character is the biserial chamber arrangement; the wall is smooth to slightly hispid. Woodringinids with a twisted axis were among the first forms to appear at the beginning of the Tertiary.

#### Group 2—*Guembelitra*

This group includes species of the triserially coiled genus *Guembelitra* and its supposed descendant *Globoconusa* (Olsson 1960; Premoli Silva 1977). The walls are thin, smooth to finely spinose, and finely perforated.

#### Group 3—*Planorotalites*

This group consists of all the finely perforated globorotaliform species that are broadly isomorphic with the Neogene genus *Globorotalia*, s.s. Species of this group are:

*Planorotalites eugubinus* (Luterbacher and Premoli Silva)

*Planorotalites* aff. *eugubinus*

*Planorotalites compressus* (Plummer)

*Planorotalites ehrenbergi* (Bolli)

*Planorotalites planoconicus* (Subbotina)

*Planorotalites pseudomenardii* (Bolli)

*Planorotalites chapmani* (Parr).

The species most typical of this group is *Planorotalites pseudomenardii*, which represents the final evolutionary stage of the lineage that developed from *P. eugubinus* via *P. compressus* to *P. ehrenbergi* (Premoli Silva 1977). A second lineage, diverging in the late Early Paleocene, includes *P. chapmani* and the final form, *P. australiformis*, which ranged into the Early Eocene (McGowran 1968). The name *P. planoconicus* describes a separate plexus, which includes all the small planorotalitids that appeared in the Late Paleocene and ranged up into the Middle Eocene.

Under the name *Planorotalites* aff. *eugubinus* we identify a separate form with a flat spire and smooth walls, close morphologically to *Hedbergella holmdensis* Olsson but much smaller.

#### Group 4—*Subbotina*

The genus *Subbotina*, which was established by Brotzen and Pozaryska (1961) with *Globigerina triloculinoides* Plummer as the type-species is characterized by a honeycomb wall structure. The group includes:

*Subbotina eobulloides* (Morozova)

*Subbotina minutula* (Luterbacher and Premoli Silva)

*Subbotina triloculinoides* (Plummer)

*Subbotina eoacena* (Terquem) = *Subbotina patagonica* (Todd and Kniker)

*Subbotina triangularis* (White).

#### Group 5—"Subbotina" *pseudobulloides*

The "*S.*" *pseudobulloides* group has previously been considered to have the honeycomb wall structure similar to that described in *S. triloculinoides* (Hofker 1960). Most authors currently agree that the species *pseudobulloides* belongs to the genus *Subbotina*. Because of its globorotaloid chamber arrangement, however, we treat it and related forms as a separate group and therefore place the generic name in quotation marks. Members of this group are:

"*Subbotina*" *fringa* (Subbotina)

"*Subbotina*" *pseudobulloides* (Plummer)

"*Subbotina*" *quadrata* (White)

"*Subbotina*" *variata* (Subbotina).

#### Group 6—typical large morozovellids

This group includes most of the pseudo-keeled (= the muricocarinae of Blow 1979) globorotaliids described from the Late Paleocene to the early Middle Eocene. The ancestral unkeeled species of the Early Paleocene are tentatively left in the genus, but we use quotation marks to indicate the question of their generic attribution.

Two distinct lineages, identified by the number of chambers in the last whorl, diverged within the first million years of the Paleocene. The multi-chambered lineage derived from "*M.*" *edita* and includes:

"*Morozovella*" *edita* (Subbotina)

"*Morozovella*" *inconstans* (Subbotina)

"*Morozovella*" *trinidensis* (Bolli)

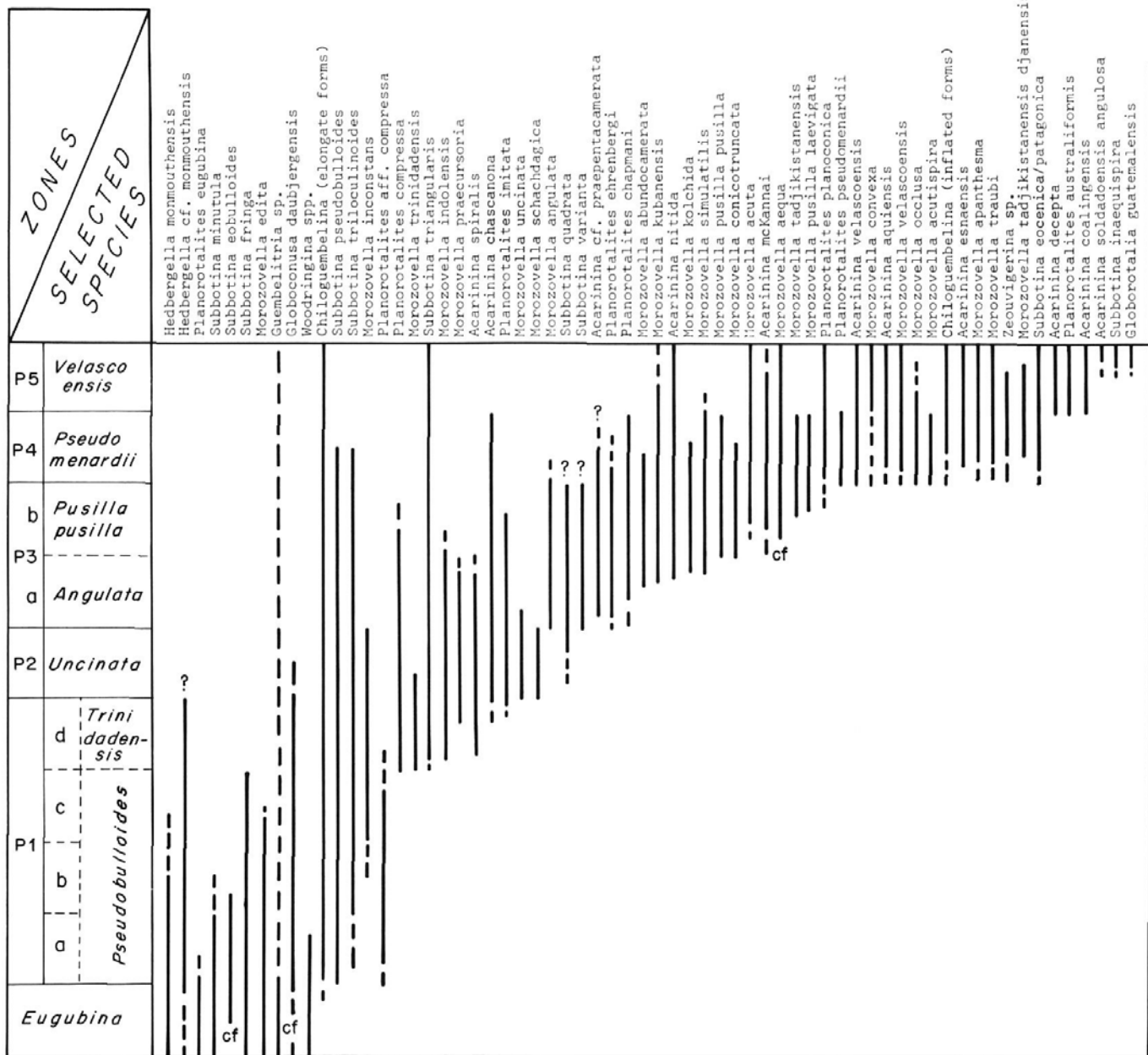
*Morozovella abundocamerata* (Bolli)

*Morozovella conicotruncata* (Subbotina)

*Morozovella pasionensis* (Bermudez)

*Morozovella velascoensis* (Cushman).





TEXT-FIGURE 2

Stratigraphic ranges of common Paleocene planktonic foraminifera in the Atlantic Ocean. Zonation is from Berggren (1972) and Hardenbol and Berggren (1978).

Members of the second lineage, with only four to five chambers in the final whorl, derived from "*M.*" *uncinata* and are:

- "*Morozovella*" *uncinata* (Bolli)
- Morozovella acuta* (Toulmin)
- Morozovella angulata* (White)
- Morozovella gracilis* (Bolli)
- Morozovella kolchidica* (Morozova)
- Morozovella marginodentata* (Subbotina)
- Morozovella subbotinae* (Morozova).

The affinities of *Morozovella acutispira* (Bolli and Cita) and *M. oclusa* (Loeblich and Tappan) are uncertain.

#### Group 7—weakly-keeled morozovellids

All the forms assigned to this group were previously attributed to the genus *Globorotalia* because they display a typical globorotaloid chamber arrangement. The unifying feature of the group is an acute periphery on which a weak "keel," actually a concentration of spines, developed at least on the first chambers of the final

whorl. The wall structure in all forms is similar to that of typical *Morozovella* (McGowran 1968). Species include:

*Morozovella aequa* (Cushman and Rona)  
*Morozovella apantesma* (Loeblich and Tappan)  
*Morozovella wilcoxensis* (Cushman and Ponton).

#### Group 8—small morozovellids

This group includes all small Paleocene-Eocene globorotaliids that never attained a size larger than 250  $\mu\text{m}$ , display a lenticular shape, and have an acute periphery marked by a weak keel consisting of a concentration of spines. The wall surface, at least in the first chambers of the last whorl, is covered by short pustules, although in general the walls are less coarse than those of typical large morozovellids. Species are:

*Morozovella indolensis* (Morozova)  
*Morozovella edgari* (Premoli Silva and Bolli)  
*Morozovella pusilla* (Bolli)  
*Morozovella albeardi* (Cushman and Bermudez)  
*Morozovella simulatilis* (Schwager).

#### Group 9—biconvex unkeeled morozovellids

This group includes small to medium-sized globorotaliids which, on the basis of their wall structure and general shape, resemble *Morozovella*, but display a biconvex profile with rounded to slightly compressed margin without a keel or concentrations of pustules. The species tentatively left in the genus *Morozovella* are:

*Morozovella convexa* (Subbotina)  
*Morozovella hispidocidaris* (Loeblich and Tappan)  
*Morozovella kubanensis* (Shuttkaya)  
*Morozovella nicoli* (Martin)  
*Morozovella planodorsalis* (Fleisher)  
*Morozovella tadjikistanensis* (Bykova)  
*Morozovella tadjikistanensis djanensis* (Shuttkaya)  
*Morozovella traubi* (Gohrbandt).

#### Group 10—typical acarininids

This group includes the ancestral forms of the lineages of *Acarinina* which proliferated during the Early to Middle Eocene. The species typifying this group is *Acarinina nitida*, the type-species of the genus. The chambers in this group are subspherical and pseudospinous. Species are:

*Acarinina coalingensis* (Cushman and Hanna)  
*Acarinina decepta* (Martin)  
*Acarinina nitida* (Martin)  
*Acarinina velascoensis* (Cushman)  
*Acarinina esnaensis* (LeRoy).

#### Group 11—smooth-walled acarininids

The species in this group were originally described under several different generic names, although they show closest affinity to *Acarinina*. Their wall is, however, much smoother than typical acarininids. Included species are:

*Acarinina spiralis* (Bolli)  
*Acarinina interposita* (Subbotina)  
*Acarinina irrorata* (Loeblich and Tappan)  
*Acarinina mckannai* (White)  
*Acarinina praepentacamerata* (Shuttkaya)  
*Acarinina soldadoensis* (Bronnimann)  
*Acarinina soldadoensis angulosa* (Bolli).

#### Group 12—globigerinid-like acarininids

This group, equivalent in part to the muricoglobigerinids of Blow (1979), includes three species originally described by Loeblich and Tappan (1957) as *Globigerina*. Common characters are the subspherical shape and a chamber arrangement similar to that of the true globigerinids. However, the hispid surface resembles the pseudospinose wall structure of typical *Acarinina*; therefore the generic name is placed in quotation marks. The three species, which may be ecophenotypes, are:

"*Acarinina*" *aquiensis* (Loeblich and Tappan)  
"*Acarinina*" *chascanona* (Loeblich and Tappan)  
"*Acarinina*" *tribulosa* (Loeblich and Tappan).

#### FORAMINIFERAL HABITATS AND BIOGEOGRAPHY

Haq et al. (1977) used principal components analysis of planktonic foraminiferal abundance through latitude to determine paleobiogeographic index species. These same species were used by Berggren (1978) to describe aspects of the synoptic paleobiogeographic and evolutionary history of the Atlantic Ocean during the Paleocene. In this paper we use similar index groups, and add several more, to detail the patterns of planktonic foraminiferal distributions through time.

#### Foraminiferal dissolution susceptibility

In order to produce accurate estimates of faunal composition, it was necessary to assure ourselves that original faunal composition was retained in our samples. Therefore, we had to establish the dissolution susceptibility of the planktonic foraminifera (Berger 1970). Paleocene planktonic foraminifera dissolved differentially as do their modern descendants. Based on their order of disappearance from dissolving and recrystallizing samples, we have constructed a solution susceptibility ranking for most of the taxonomic groups. The order of disappearance due to dissolution, pre-

sumably below the foraminiferal lysocline, from first to last is: 1, juveniles of most groups; 2, large morozovellids; 3, smooth-walled acarininids; 4, typical acarininids; 5, small morozovellids; 6, smooth-walled genera *Chiloguembelina*, *Woodringina*, and *Planorotalites*; 7, "*S.*" *pseudobulloides* group; 8, the subbotinids.

In the *P. eugubinus* Zone, when all species were extremely small, they appear to dissolve almost contemporaneously. *Guembelitra*, because of its erratic occurrence through time, cannot be fit into this ranking, but seems to have an intermediate susceptibility to dissolution.

In contrast, wall thickness may be the major feature controlling disappearance due to diagenetic recrystallization; in this situation smaller and thinner forms disappeared before more robust taxa. The order of disappearance due to recrystallization, from first to last, is: 1, juveniles of most groups; 2, smooth-walled groups and *Guembelitra*; 3, subbotinids and acarininids; 4, morozovellids.

#### Locus of first appearance

In order to ascertain whether provincial index species originated within the area where they later consistently occurred in maximum abundances, the locus of first appearance of several species not currently used as biostratigraphic zonal markers (Berggren 1972) was determined, and their subsequent stratigraphic occurrences noted. The stratigraphic ranges of selected Atlantic Paleocene planktonic foraminifera, shown in text-figure 2, were determined in samples described here (text-fig. 1) as well as through detailed study of literature on circum-Atlantic Paleocene faunas. Pacific faunas have also been surveyed, although not as exhaustively (Krasheninnikov and Hoskins 1973).

All Paleocene genera except *Acarinina* were present at the very beginning of the Paleocene immediately following the Cretaceous/Tertiary Boundary event. It is currently not possible to determine the locus of first appearance of any of these species at the initiation of the Paleocene, since the maximum possible time for the re-radiations was less than 125,000 yr (Smit 1981), and this is below our capacity to resolve even at deep-sea sites considered continuous across the boundary.

The first acarininid in the Atlantic appeared in late Zone P1 time at Site 95 (25°N paleolatitude) and Site 20C (29°S paleolatitude) but not in Trinidad or south of Florida until Zone P2. The first species, *Acarinina spiralis*, belonged to the smooth-walled group, which continued to predominate in subtropical to middle latitudes through the later Paleocene.

In the *Planorotalites compressus* lineage, acquisition of a narrowed periphery by *P. ehrenbergi* was observed first at Pont Labau, France (42°N paleolatitude) at the beginning of Zone P3a; this form then spread southwest to Site 398 before reaching the Caribbean (Site 151) in Zone P3b. This species is considered an indicator of higher middle latitudes and apparently first appeared there, at least in the Atlantic.

The *Subbotina eocaenica*-*S. patagonica* plexus was first found in sediments of Zone P3a age from the Scotia Shelf (43°N paleolatitude); it reached both lower and middle latitude sites by Zone P3b time. In this case, a high latitude index group apparently originated in high latitudes and later spread to other regions.

#### Planktonic foraminiferal diversity through the Paleocene

Planktonic foraminiferal diversity, expressed here simply as the total number of species in any one sample or at any one time, was derived by counting the total number of species in all three size fractions of each sample and adding them together. A breakdown of diversity values and species per genus for each zone of the Paleocene is given in table 3, and diversities at each site are shown in text-figure 3.

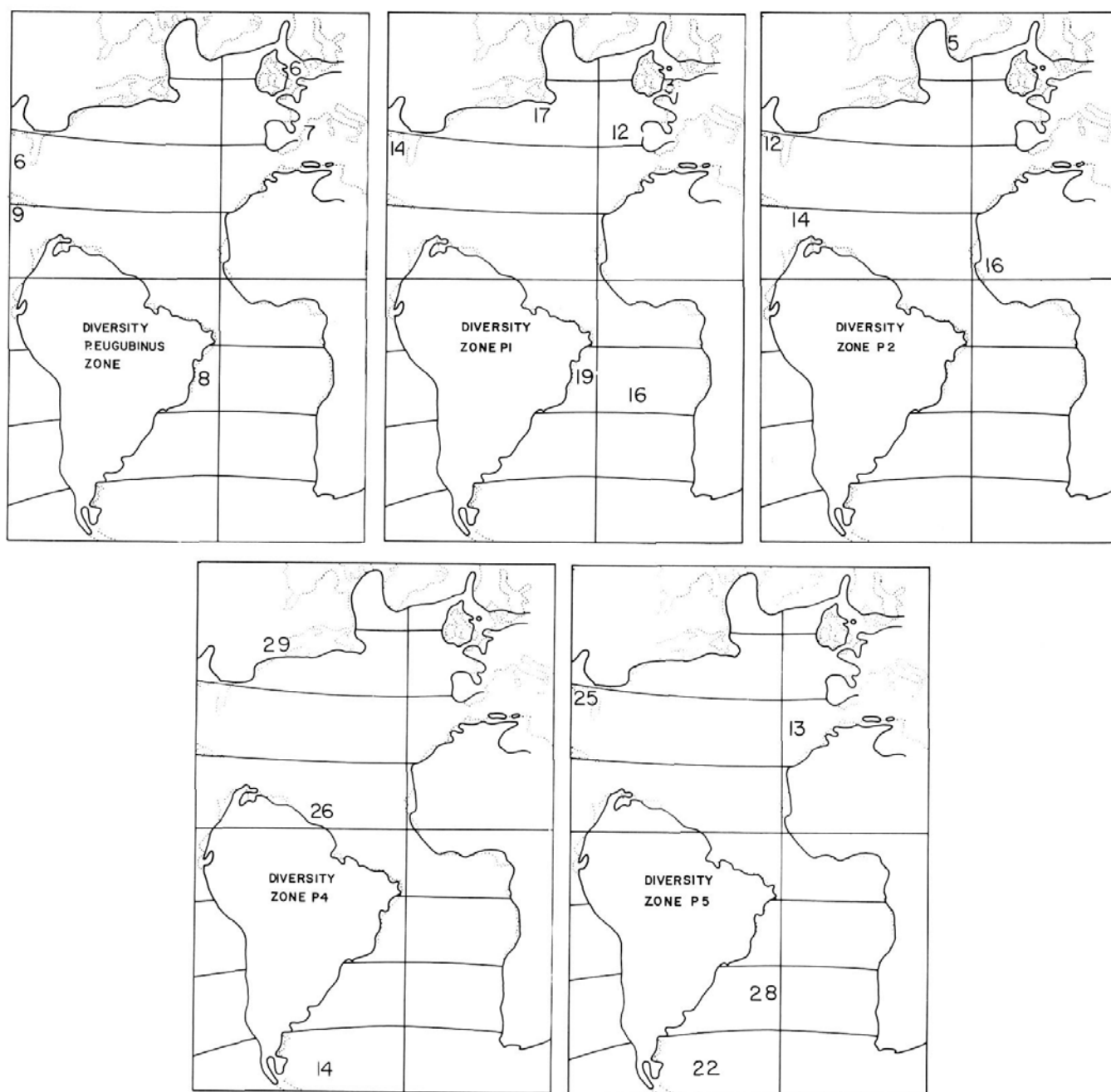
In the earliest *P. eugubinus* Zone at levels only 1–2 cm above the Cretaceous/Tertiary Boundary, there were already six species of planktonic foraminifera at higher and middle latitude sites. Site 356 on the Brazil margin and Site 95 in the central western Gulf of Mexico contained a few additional forms, resulting in diversity values of eight or nine species. By later in the *P. eugubinus* Zone, diversity values at middle latitudes reached 14.

In the early part of Zone P1, diversity was highest at Sites 356 and 384 in the North Atlantic; these large faunas contained 11 species, including several new forms of *Subbotina* (table 3). Subsequent proliferation of morozovellids caused diversity values to reach 18 by the end of Zone P1. Five or six species occupied

TABLE 3

Diversity of planktonic foraminifera through the Paleocene in the Atlantic Ocean. Table lists total diversity in each zone of the Paleocene as well as the total number of species of each genus listed.

Zone	Total Diversity	Morozovella	Subbotina	Acarinina	Planorotalites
<i>P. eugubinus</i>	11	1	3	—	2
P1d	18	8	2	1	2
P2	17	6	3	2	1
P3	32	14	5	6	3
P4	47	20	6	10	4
P5	64	16	6	16	3



TEXT-FIGURE 3

Diversity of planktonic foraminifera through the Paleocene in the Atlantic Ocean. Reconstructions for 65 Ma described in text-figure 1 caption. Vertical and horizontal lines are only reference lines, not accurate paleo-latitudes or longitudes.

higher latitude shelves, whereas values on lower latitude shelves were closer to nine. In text-figure 3 the very high values at middle latitude South Atlantic Site 20C are misleading; the fauna contained species suspected of belonging to Zone P2 and to have been emplaced by mixing.

Since no low latitude site could be counted, we may not have estimated the total species richness of Zone P2. Overall diversity was lower than in the preceding

Zone P1d; however, in middle latitude sites, it was higher than it had been in Zone P1d. Highest diversity was found in the Gulf of Mexico sites. Lower latitude shelves contained the same number of species as in Zone P1d.

In earliest Zone P3, diversity increased to 19 species; highest values were found in Trinidad and as at other times, diversity was greatest in the intermediate size fractions of most samples. By late Zone P3, time

species richness neared values of 32, owing to speciation of all genera but particularly of the morozovellids.

Diversity increased most markedly in Zone P4 due to increased numbers of both acarininids and morozovellids. Local diversity was highest at low latitude Site 144 and on the Delaware shelf. At Site 144 high values were due to the abundance of typical morozovellids and to a lesser extent, of acarininids; but in Delaware, high diversity resulted from differentiation of subbotinids and the presence of several rare acarininids and morozovellids.

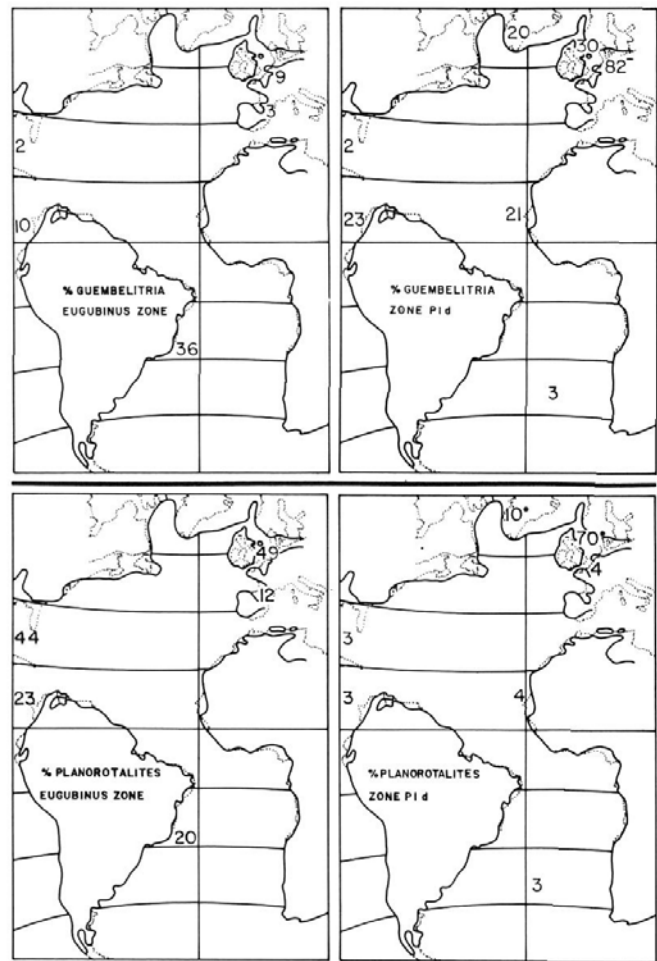
The highest diversity values for the Paleocene were tabulated for Zone P5 even though no truly tropical sample was examined. Highest diversities were found at Site 20C which, like Delaware in Zone P4, contained faunas with several subbotinids as well as diverse acarininids and morozovellids; some reworking may also have contributed to such high apparent diversity.

Through the Paleocene, the overall trend toward higher diversity is closely paralleled by the increasing numbers of morozovellids and acarininids. Subbotinids and planorotalitids did not diversify so extensively, but did increase at the same times as the other groups. Morozovellids expanded the most relative to all other groups in Zones P3b and P4, but along with most other genera expanded little between Zones P4 and P5. *Acarinina*, by contrast, expanded markedly in Zone P4 and again in Zone P5. It is the record of the acarininids, then, that parallels the trend of overall diversity through the Paleocene.

#### Provincial index species and the history of Atlantic bioprovinces

Abundance counts of planktonic foraminiferal species at higher and lower latitude open ocean sites and on shelves were used to determine provincial index species, any geographic endemics, species which characterized the shelf environment, and how species varied morphologically from one region to the next. Species were considered good bioprovincial indicators if they showed high abundance in a region, or were restricted to that region whether in high or low abundances. Provincial indicator species are listed in table 4; their relative abundances through time are shown in text-figures 4 to 7.

At the initiation of the Tertiary, the biserial and triserial heterohelicids and *Planorotalites eugubinus* ranged through all bioprovinces in nearly equal abundances; their distribution was essentially cosmopolitan (text-fig. 4). Heterohelicids were slightly more abundant at lower latitudes and *P. eugubinus* at middle and higher latitudes. During the course of the *P. eugubinus* Zone the rotaliform planktonics such as *Subbotina fringa* and



TEXT-FIGURE 4

Percent abundance of *Guembelitra cretacea* (top) and *Planorotalites* species (bottom) in counts from all size fractions combined, plotted for two zones of Early Paleocene on 65 Ma base maps.

*Morozovella edita* became more abundant at lower latitudes (text-figs. 5, 6). *Planorotalites* aff. *eugubinus* typified middle latitudes, but ranged down to the Agulhas Plateau.

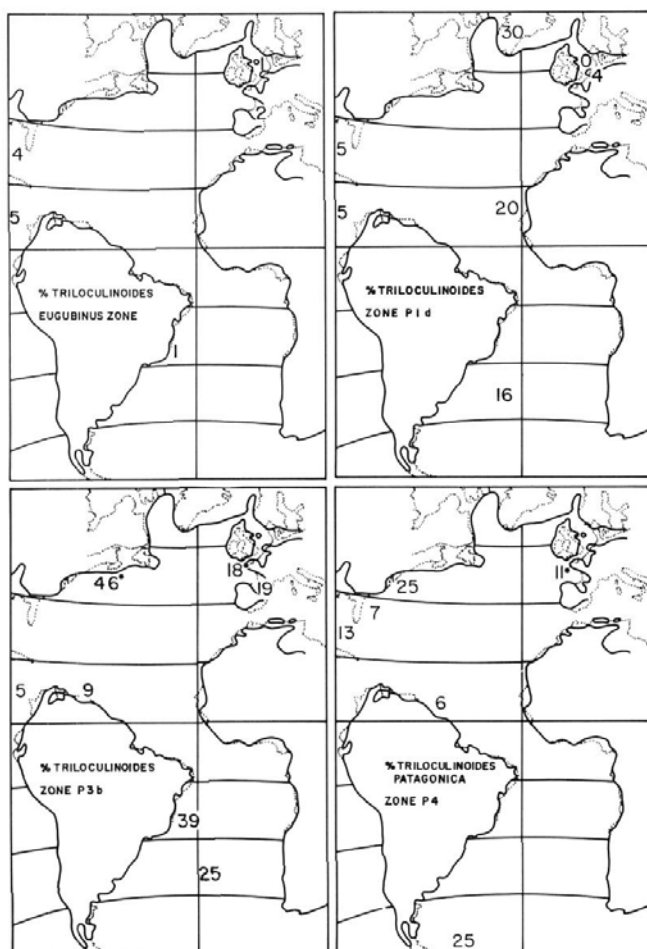
The predominance of elongated (rectilinear) taxa at lower latitudes decreased in Zone P1 time when *Chiloguembelina* changed its latitudinal distribution to become more typical in middle latitudes. Shelf faunas of higher latitudes were dominated by *Globoconusa daubjergensis* (Bronnimann), while *Planorotalites* spp. were still more common in mid-oceanic higher latitude sites. Samples from open ocean high latitude sites contained unusual faunas, owing to extensive dissolution at this time; shelf samples, however, appeared unaffected.

A further partitioning of groups into distinct provinces occurred throughout Zone P1. *Morozovella inconstans* increased in relative abundance at low latitudes. Later



TABLE 4  
Planktonic foraminiferal bioprovincial indicator species and the provinces (latitudes) they characterized in each zone of the Paleocene.

Zone	Low Latitudes	Mid-Latitudes	High Latitudes
<i>P. eugubinus</i> (early)	-----TRISERIAL AND BISERIAL HETEROHELICIDS-----		
<i>P. eugubinus</i> (late)	-----SUBBOTINIDS-----		
P1 early	<i>S. fringa</i> <i>M. edita</i> <i>P. eugubinus</i> <i>Morozovella</i> spp.	<i>Chiloguembelina</i>	<i>G. daubjergensis</i> <i>P. compressus</i>
P1 late	<i>Morozovella</i> spp. <i>M. trinidadensis</i>	<i>S. pseudobulloides</i> —	<i>P. compressus</i> <i>G. daubjergensis</i>
P2	<i>morozovellids</i>	<i>S. pseudobulloides</i> <i>S. triloculinoides</i>	—
P3a	<i>M. angulata</i> <i>morozovellids</i>	<i>S. pseudobulloides</i> <i>Chiloguembelina</i> <i>S. triloculinoides</i>	<i>S. triloculinoides</i> <i>Chiloguembelina</i>
P3b	<i>morozovellids</i>	<i>Subbotina</i> spp. <i>Planorotalites</i> spp.	—
P4	<i>M. velascoensis</i>	smooth <i>Acarinina</i> <i>S. patagonica</i>	subbotinids
P5	<i>morozovellids</i>	<i>morozovellids</i> subbotinids	smooth <i>Acarinina</i> subbotinids <i>Chiloguembelina</i>

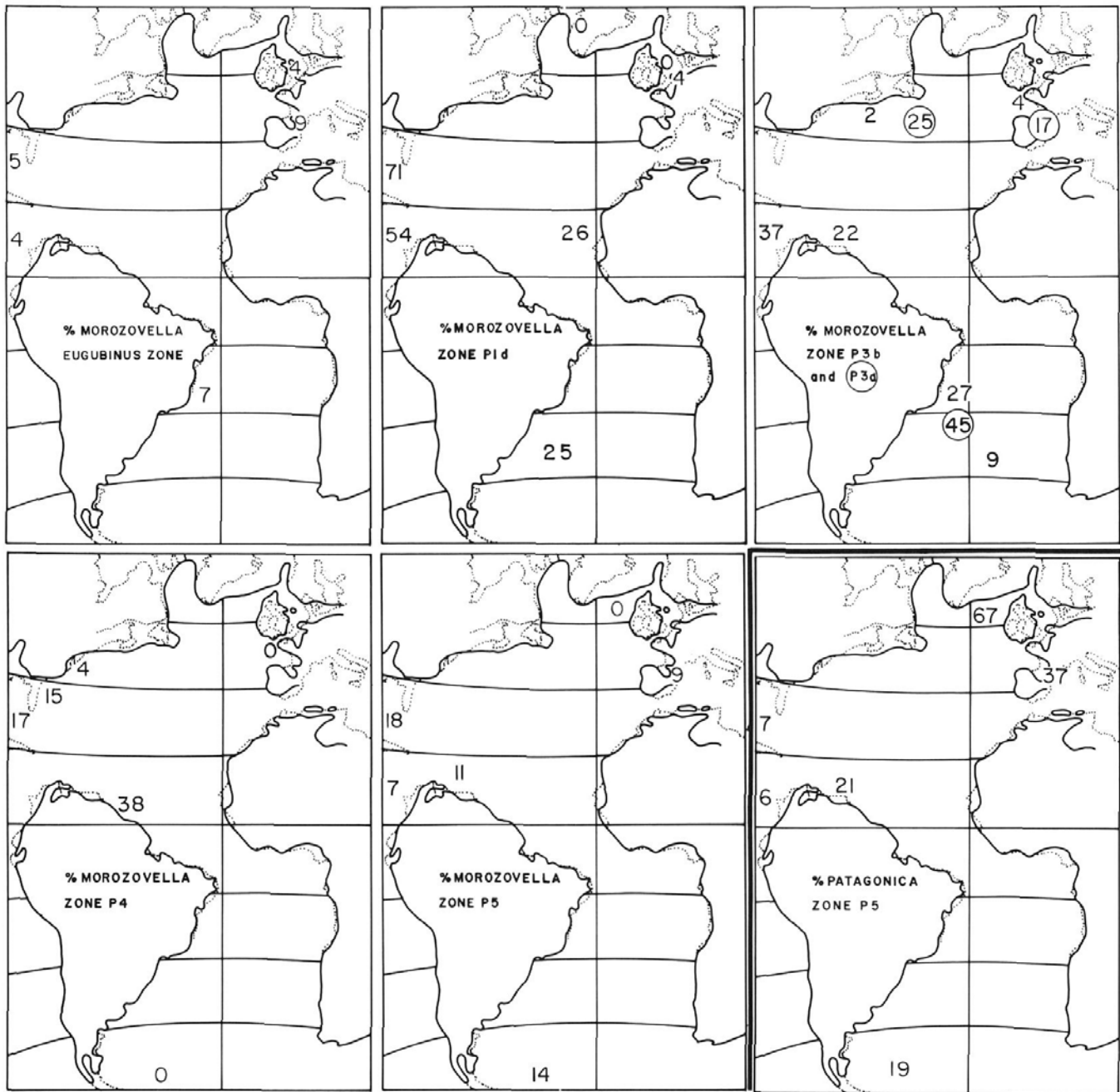


TEXT-FIGURE 5  
Percent abundance of *Subbotina triloculinoides* and its successor in Zone P4, *Subbotina patagonica*; plots from all size fractions combined for several zones of the Paleocene. Reconstructions for 65 Ma are from McCoy and Zimmerman (1977). Asterisk (\*) indicates values anomalously high, probably due to dissolution.

in Zone P1, lower and middle latitude sites were differentiated by the ratio of *M. trinidadensis* to "*Subbotina*" *pseudobulloides*, the former predominating at lower latitudes and in the Gulf of Mexico (text-figs. 6, 7). Higher latitude sites were characterized by *Globoconusa daubjergensis*, *Planorotalites compressus*, and *S. triloculinoides* (text-figs. 4, 5). In Zone P1d the only large morozovellid to appear in the North Sea and Denmark did so. *Planorotalites compressus* reached substantial abundances at high latitudes for the last time during this subzone. In the South Atlantic, abundances of "*S.*" *pseudobulloides* relative to the morozovellids were greater at eastern than at western sites, implying a greater warm-water influence in the western sector. Large morozovellids were particularly abundant in the Gulf of Mexico at this time.

During Zone P2 the morozovellids continued to dominate lower latitude faunas, while "*S.*" *pseudobulloides* and *S. triloculinoides* predominated at middle latitude sites. Higher latitude sites were barren of carbonates at this time.

In earliest Zone P3 time, morozovellids extended their latitudinal range as far north in the Atlantic as Labrador; they did not, however, extend across the North Atlantic as previously in Zone P1d (text-fig. 5). Abundances of morozovellids increased also at middle latitudes, while *Chiloguembelina* and low-spired subbotinids were predominant at higher latitudes. Later in Zone P3, these forms increased their import in middle latitudes. The "*S.*" *variata* morphotype of "*S.*" *pseudobulloides* was more typical in these latitudes, while the latter taxon was more common in the tropics. In Zone P3b most carbonates were dissolved at higher latitude sites so that the foraminifera could not be studied.



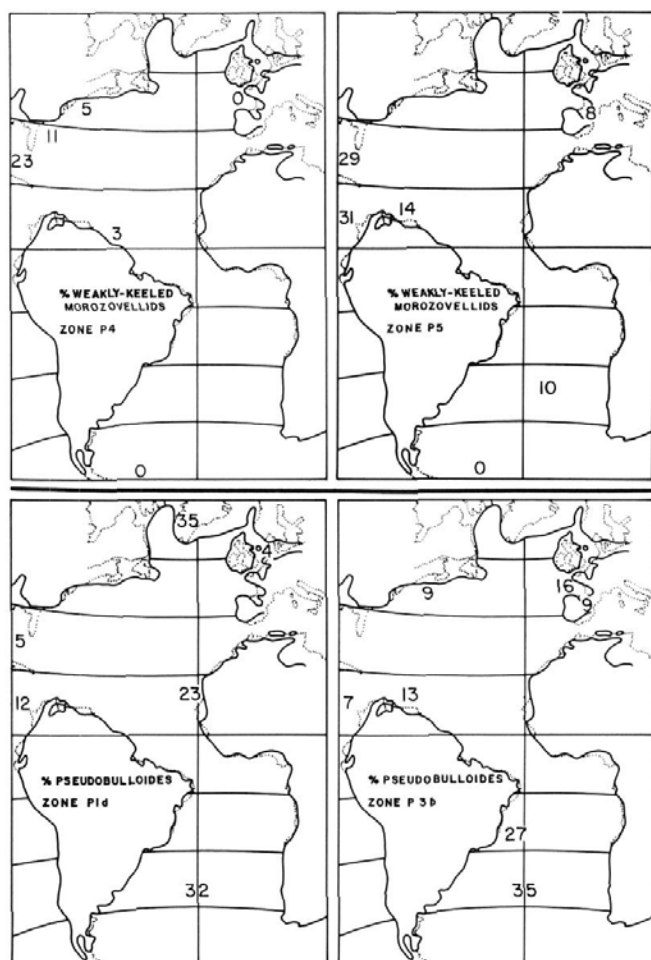
TEXT-FIGURE 6

Percent abundance of all true *Morozovella* in counts from all size fractions combined, and plotted for several zones of the Paleocene on 65 Ma base maps. Plots of *Subbotina patagonica* (bottom right) should be compared with the distributions of *S. triloculinoidea* in text-figure 5.

In Zone P4 time, the morozovellids continued to dominate lower latitudes; the large morozovellids dominated in the tropics, but weakly keeled taxa were more common in the Gulf of Mexico and in the area of the present Gulf Stream (text-figs. 6, 7). Following their radiation at this time, the acarininids became more important at middle latitudes where they occurred in nearly equal abundance with the *S. patagonica* plexus (text-fig. 5). Spiney acarininids were more characteristic of the lower latitudes; in general, the smooth-

walled group predominated in the higher end of the latitudinal range of the genus. At this time, in faunas from Delaware, the *S. patagonica* plexus, *S. patagonica*-*S. eoacena*, showed maximum morphotypic variability of both size and coiling arrangement. The subbotinids continued to dominate in high latitudes.

During Zone P5 the large morozovellids again extended their latitudinal range as far north as Nova Scotia (Gradstein and Srivastava 1980). At lower latitudes they



TEXT-FIGURE 7

Percent abundance of "*Subbotina*" *pseudobulloides* (bottom) and weakly keeled morozovellids (top) in counts from all size fractions combined, plotted on 65 Ma base maps of McCoy and Zimmerman (1977).

were replaced in import by the weakly keeled morozovellids (text-fig. 7). Due to the extinction of several subbotinids and the decreased import of most planorotalitids, middle latitude faunas lost their distinctive character and contained faunas mainly of morozovellids and acarininids, with subsidiary amounts of the low-spired subbotinids. Near the western South Atlantic Falkland Plateau (55°S paleolatitude), smooth-walled acarininids increased in import so that in this unusual area high latitudes were characterized by acarininids, subbotinids, and *Chiloguembelina* spp. as well as large numbers of the unique, biconvex morozovellid *Morozovella tadjikistanensis* and the *Planorotalites chapmani*-*P. australiformis* group. Similar faunas lacking the morozovellids and with fewer acarininids occurred on the eastern South Atlantic Agulhas Plateau (45°S paleolatitude) at this time.

#### ATLANTIC PALEOCENE PALEOTEMPERATURES AND PALEOOCEANOGRAPHY

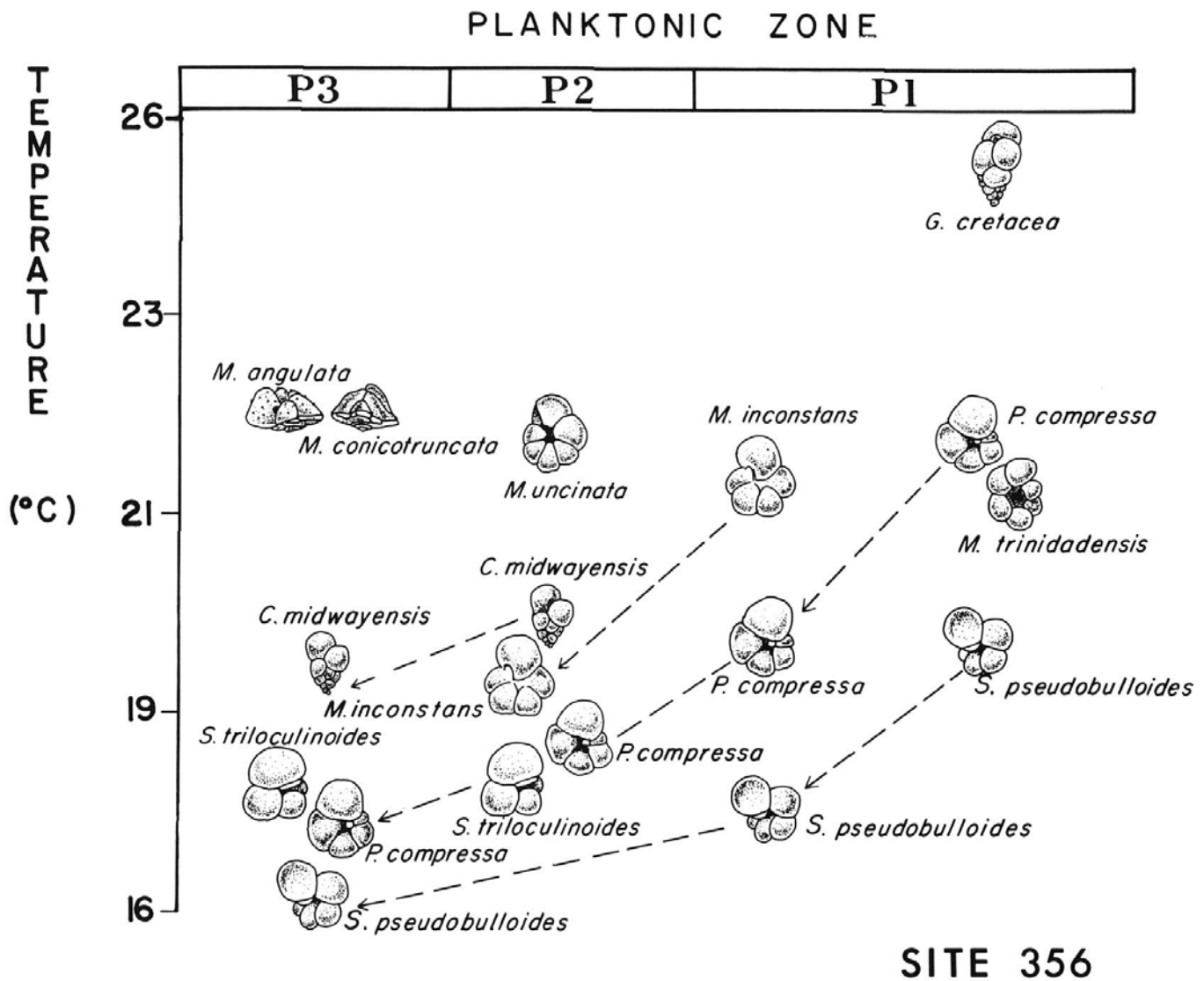
By measuring the oxygen and carbon isotopic composition of individual planktonic foraminiferal species and of many species in one sample at multiple sites we can attempt to:

- 1, determine which planktonic foraminiferal species lives at warmest temperatures, hence closest to the ocean surface; and the order in which other species stratify according to temperature through the water column;
- 2, estimate the temperature tolerances of a species at various times and locations by tabulating all the temperatures it registers from higher to lower latitudes;
- 3, provide a picture of the distribution of surface temperatures, hence of the circulation patterns of surface water masses by plotting the warmest temperature, nearest surface measurement for each sample on maps; and
- 4, combine the record of temperature change with evidence on circulation in order to demonstrate how climate has affected the ocean and ultimately the distribution patterns of planktonic foraminifera.

#### Vertical stratification according to paleotemperature

The stratification of selected Atlantic Paleocene planktonic foraminifera is derived from their comparative oxygen isotope values measured in each sample. Douglas and Savin (1973, 1978) and Boersma et al. (1979) have analyzed the depth stratification of Paleocene foraminifera. Douglas and Savin obtained conflicting results for keeled versus unkeeled species, but could use the foraminiferal stratification arrays to depict paleothermoclines. Boersma et al. (1979), in analyses of planktonic stratification at 10 Atlantic DSDP sites, determined a generalized stratification order for planktonics in each zone of the Paleocene. They also demonstrated the consistent carbon isotopic stratification of Paleocene planktonics, with heaviest carbon isotope values displayed by forms registering the lightest oxygen isotope values.

The stratification patterns of planktonic foraminifera in each zone of the Paleocene at Sites 356 and 384 are shown in text-figures 8 and 9. The warmest temperature, shallowest-dwelling species belong to the genera *Morozovella*, *Acarinina*, *Guembelitra*, and *Globocosa*. Large morozovellids, heavily calcified globorotaliids that are often umbilically conical, lived at higher temperatures than the bi-convex, smaller morozovellids. Typical acarininids also apparently lived close to the surface but registered slightly higher paleotemperatures than the small or biconvex morozovellids. The shallowest-dwelling acarininids were spin-ey, were often larger, and had a larger number of



TEXT-FIGURE 8

Temperature (relative depth) stratification of common planktonic foraminifera based on oxygen isotope analyses of individual species from the *P. eugubinus* Zone to Zone P3 of the Paleocene at Site 356 in the South Atlantic. Note the change in relative ordering of *P. compressus* (= *P. compressa*) from Zone P1d to Zone P2. [For *S. pseudobulloides*, read "*S.*" *pseudobulloides*.]

chambers. Those with acute peripheries lived at warmer temperatures than those with rounded edges or than the globigerinid-form group.

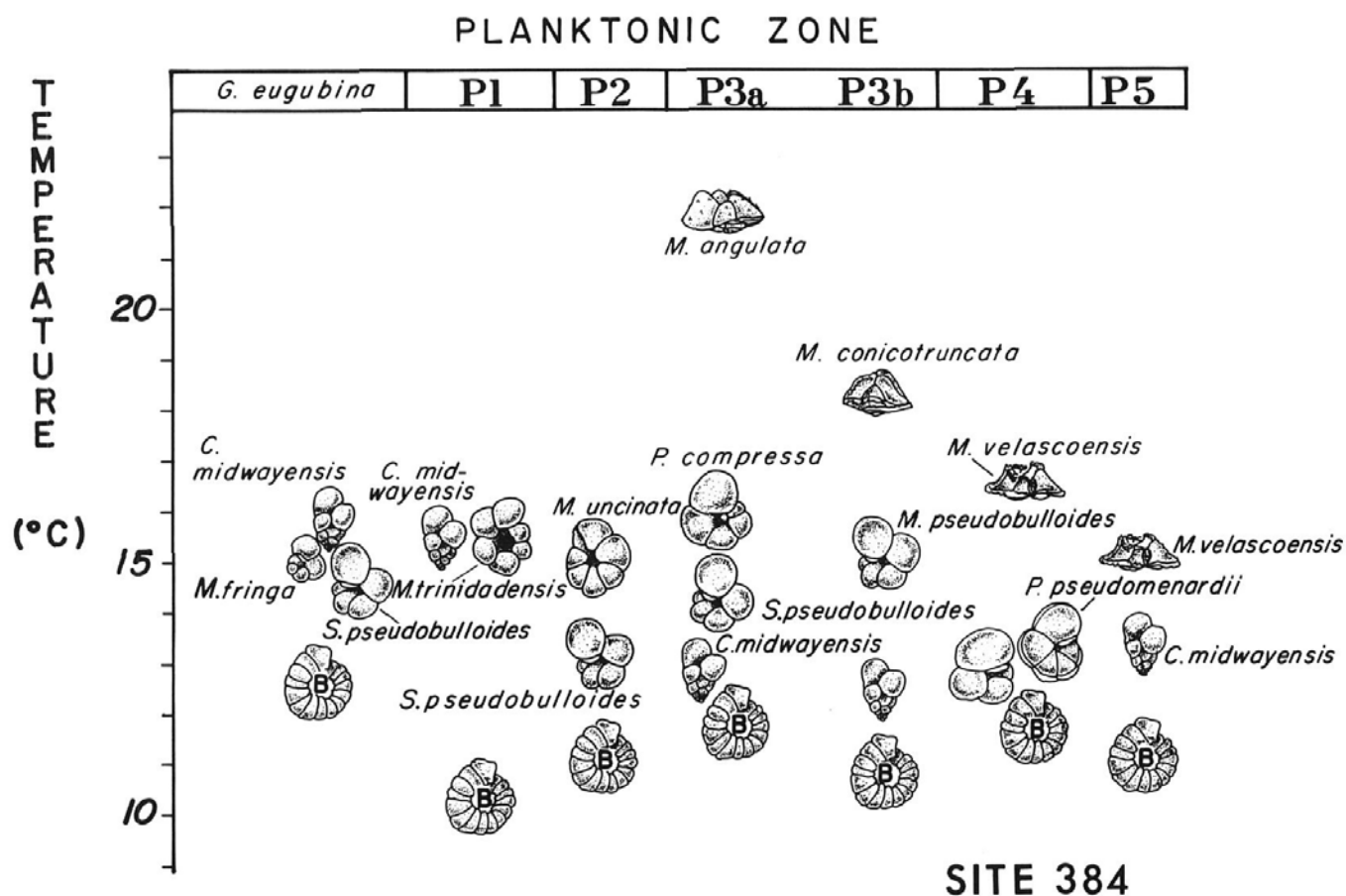
Typical of intermediate relative temperatures (depths) were the smooth-walled genera *Chiloguembelina* and *Planorotalites*. The species consistently recording the coolest temperature values and therefore assumed to occupy the deepest levels among Paleocene planktonics were the subbotinids; *Subbotina triloculinoides* and other true subbotinids generally stratified lower than the "*S.*" *pseudobulloides* group.

#### Paleotemperature tolerance ranges of individual species

Paleotemperature tolerance range is a measure of an ecologic amplitude of a species for this environmental

parameter. We have tabulated the oxygen isotope values for 20 species everywhere they were measured, from higher to lower latitudes in warmer and cooler times, converted those values to estimated temperatures, and summarized the ranges occupied by each species according to the latitudinal position of the sample in table 5. That genera registering the warmer temperatures (lightest oxygen isotope value) do so in low latitude sites and then give cooler temperature values in higher latitude sites suggests that the estimated values do approximate the temperatures occupied by each species.

Warmest temperatures were generally recorded by the large morozovellids, *Guembelitia* and *Globoconusa*. These forms registered temperatures between 25 and



TEXT-FIGURE 9

Temperature (relative depth) stratification of common planktonic foraminifera, based on oxygen isotope analyses of individual species through the Paleocene at middle latitude Site 384 in the western North Atlantic. Although temperatures registered by all species are generally lower than at Site 356 (text-fig. 8), the same order of stratification is retained. Note the change in the relative depth habitat of *Chiloguembelina midwayensis* after Zone P1. [For *compressa*, read *compressus*. For *S. pseudobulloides*, read "*S.*" *pseudobulloides*.]

19°C in lower latitudes, but ranged from 21 to 14°C in middle latitudes. *Globoconusa daubjergensis* was measured at high southern latitudes where it indicated near surface temperature values of about 13°C.

The intermediate temperature genera, *Subbotina*, *Chiloguembelina* and *Planorotalites*, registered decreased temperatures at increasing latitudes; and temperatures near 11 to 12°C at high latitudes in the South Atlantic. The coolest temperatures of the Paleocene were registered by *Planorotalites chapmani* on the Agulhas Plateau. The lack of other, well-preserved, higher latitude material precluded further interpretation of the lower temperature ranges of most species.

*Guembelitra* demonstrated the widest temperature range of any genus, even without data from higher latitudes. Very broad temperature ranges were also demonstrated by "*Subbotina*" *pseudobulloides*, *Morozovella velascoensis*, and *Chiloguembelina* spp. Narrow temperature ranges (for species measured at three

or more sites) were produced by *Planorotalites* aff. *eugubinus*, *P. eugubinus*, and *S. triloculinoides*. Since *S. triloculinoides*, a higher latitude indicator, has not been measured at higher latitudes, we know only that its temperature range is very limited in lower and middle latitudes.

#### Variation in stratification patterns

Variation in stratification patterns has been noted; there are times and/or places where the relative ordering of two species changes. For example, from Zone P1 to P2 (text-fig. 8), the relative ordering of *Planorotalites compressus* changed; it dropped from its place near the top of the stratification order to levels below the newly radiating morozovellids. The younger, derivative species of *Planorotalites* retained this lower relative position.

A similar change in the habitat of *Chiloguembelina* spp. can be seen at Site 384 (text-fig. 9). During the *P. eugubinus* Zone and Zone P1, the *Chiloguembelina*



TABLE 5

Estimated paleotemperatures recorded by 18 species of planktonic foraminifera during the Paleocene at lower through higher latitudes.

Species	Number of Analyses	Low Latitudes	Mid-Latitudes	High Latitudes
<i>G. cretacea</i>	10	25°–18°C	19°–18°C	—
<i>G. daubjergensis</i>	5	20°C	16°–14°C	13°C
<i>M. inconstans</i>	5	21°–19°C	17°–15°C	—
<i>M. trinidadensis</i>	4	21°C	14°C	—
<i>M. uncinata</i>	10	22°–16°C	18°–15°C	—
<i>M. angulata</i>	5	24°–20°C	21°–17°C	—
<i>M. conicotruncata</i>	9	23°–21°C	19°–15°C	—
<i>M. velascoensis</i>	11	23°–20°C	19°–14°C	—
<i>A. coalingensis</i>	5	21°C	16°–15°C	—
<i>A. mckannai</i>	3	—	17°–16°C	14°C
<i>C. midwayensis</i>	35	20°–18°C	16°–12°C	12°–11°C
<i>S. pseudobulloides</i>	34	21°–16°C	16°–11°C	—
<i>S. triloculinoides</i>	15	19°–13°C	16°–12°C	—
<i>P. compressus</i>	17	21°–13°C	16°–13°C	—
<i>P. ehrenbergi</i>	2	—	14°–12°C	—
<i>P. pseudomenardii</i>	6	18°–15°C	15°–12°C	11°C
<i>P. eugubinus</i>	5	18°C	—	—
<i>H. monmouthensis</i>	3	—	17°–13°C	13°C

*midwayensis* plexus lived at equivalent levels with the morozovellids. After Zone P1c (there is no material from Zone P1d at this site), *Chiloguembelina* spp. moved below the morozovellids and some subbotinids; the group retained this lower position through the remainder of the Paleocene.

The other notable change in stratification ordering involved a reversal in the relative positioning of *S. triloculinoides* below "*S.*" *pseudobulloides*. At Site 356 (text-fig. 8), *S. triloculinoides* can be found above "*S.*" *pseudobulloides* in cooler intervals. In this instance *S. triloculinoides* is also more abundant in the samples and many individuals possess bullae. The difference in both morphotypic expression and abundance suggests that the order reversal is not merely an artifact of overlapping isotope values, but reflects a shallowing of the habitat of *S. triloculinoides* at this site. Berger et al. (1978) described a similar development of abnormal final chambers and a change in depth habitat of *Globigerina bulloides* during the last glacial.

#### Carbon isotope measurements of individual species

Carbon isotopes were measured on each species in the same samples as the oxygen isotopes. Carbon isotope values registered by the warmest-dwelling species varied through pre-Zone P4 time from a low of 0.5‰ to a high near 3.5‰. With one exception, species that registered the most negative oxygen isotopes also registered the highest carbon isotope values. These include most species of *Acarinina* and *Morozovella*. In the Early Paleocene, intermediate carbon isotope values were recorded by the subbotinids; species of *Chiloguembelina* and *Planorotalites* recorded the lowest carbon isotope values among the cool-water preferring species. Anomalously low carbon isotope values were registered by *Guembelitra cretacea*

which, in the Atlantic, always registered the lightest oxygen and carbon isotope value in any sample.

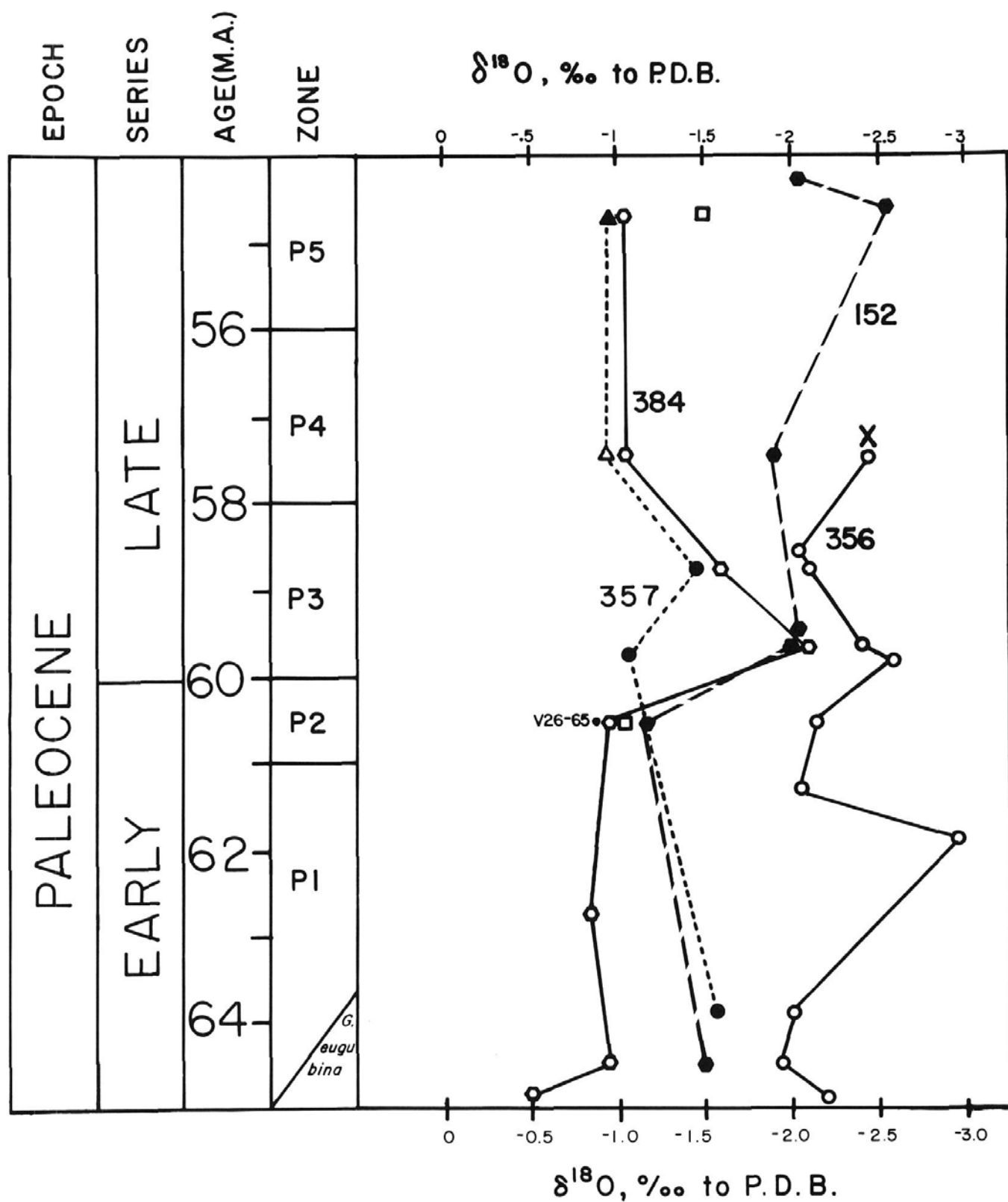
The carbon isotope ranges of species differ significantly. In pre-Zone P4 time, most species have an average range of 1.3‰. The widest carbon isotope range throughout the Paleocene or at any one time during the epoch is demonstrated by species of *Chiloguembelina*. Younger species of *Acarinina*, *Morozovella*, and *Planorotalites* have carbon isotope ranges approximately half as large as the older, precursor species.

#### Paleocene oxygen and carbon isotope records of climate

Paleocene oxygen and carbon isotope records have been measured in detail at Sites 384, 356 (Boersma et al. 1979), 151/152 and 357 (text-figs. 10, 11). Synoptic measurements made throughout the Atlantic, Caribbean, and Gulf of Mexico are shown in text-figure 12 and table 6. For the following discussion, the isotopic values have been converted to equivalent paleotemperatures (Epstein et al. 1953).

At the surface at Site 356 (text-fig. 10), estimated paleotemperatures in the earliest Paleocene *P. eugubinus* Zone were warm, near 24°C. By the end of the *P. eugubinus* Zone, temperatures decreased to near 21°C. These cooler temperatures prevailed through Zone P1a–c, but rose to a high of 25°C in Zone P1d. In Zone P2, temperatures returned to near 22°C, then rose again to near 24°C in Zone P3a. The remainder of Zone P3 was slightly cooler, with values near 21°C. In the Late Paleocene, Zone P4 temperatures at this site averaged 23 to 24°C just before recrystallization became too intense for further measurements upsection.

The pattern of near surface temperature fluctuations at other sites is similar to that at Site 356. At Caribbean



TEXT-FIGURE 10

Oxygen isotope records through the Paleocene at four sites in the Atlantic Ocean. Site 152 is in the Caribbean, Sites 356 and 357 are middle latitude South Atlantic sites, and Site 384 is situated at higher middle latitudes in the western North Atlantic (see text-fig. 1). Records are based on unispecific analyses of planktonic foraminifera; species registering the most isotopically negative values are used to construct the curve (table 6). These are *Guembelitra cretacea* in the earliest Paleocene and several *Morozovella* species in younger samples. Data come from Boersma et al. 1979 and Boersma and Shackleton in press.

TABLE 6

Oxygen isotope values of Paleocene planktonic and benthic foraminifera at Atlantic sites. Included are the oxygen isotopically most negative planktonic foraminiferal species and a benthic value. Data come from Boersma et al. 1979; Boersma and Shackleton in press and unpublished data from N. J. Shackleton.

Location	Species	$\delta^{18}\text{O}$
<i>P. eugubinus</i> Zone		
356, 29-3-33	<i>G. cretacea</i>	-2.49
	benthics	0.13
29-3-24	<i>C. morsei</i>	-1.98
384, 13-3-27	<i>G. cretacea</i>	-0.58
	benthics	-0.12
13-2-143	<i>C. morsei</i>	-0.97
	benthics	-0.24
152, 10-1-131	<i>G. cretacea</i>	-1.52
	benthics	0.52
V22-127, 160	<i>G. daubjergensis</i>	-0.17
	<i>Gavelinella beccariformis</i>	0.11
Zone P1		
356, 29-2-80	<i>G. cretacea</i>	-2.09
	<i>Nuttallides truempyi</i>	0.06
26-6-80	<i>G. cretacea</i>	-2.90
	benthics	-1.06
26-2-62	<i>M. inconstans</i>	-2.14
	benthics	-0.14
384, 12-1-81	<i>M. inconstans</i>	-0.72
	benthics	-0.32
357 30cc	<i>Tubitextularia</i>	-1.65
	<i>N. truempyi</i>	-0.19
Zone P2		
V26-65, 235	<i>M. praecursoria</i>	-0.88
	benthics	0.38
384, 11-4-10	<i>M. uncinata</i>	-0.98
	benthics	0.70
356, 25cc	<i>M. uncinata</i>	-2.34
	benthics	-0.19
86, 9-2-124	<i>M. uncinata</i>	-1.05
	<i>N. truempyi</i>	-0.26
151, 10-2-106	<i>M. uncinata</i>	-1.32
	benthics	0.48
Zone P3a		
152, 9-1-93	<i>N. truempyi</i>	-0.04
	<i>M. angulata</i>	-2.01
356, 25-4-30	<i>M. angulata</i>	-2.79
	<i>N. truempyi</i>	-0.02
384, 11-3-30	<i>M. angulata</i>	-2.22
	benthics	0.12
Zone P3b		
384, 11-2-6	<i>M. conicotruncata</i>	-1.78
	<i>N. truempyi</i>	0.09
356, 20-3-20	<i>M. conicotruncata</i>	-2.24
	benthics	0.22
357, 29-1-120	<i>M. conicotruncata</i>	-1.42
	<i>G. beccariformis</i>	0.03
V16-55, 182	<i>Acarinina nitida</i>	-0.20
	<i>G. beccariformis</i>	0.85
152, 8-1-93	<i>M. conicotruncata</i>	-2.01
	<i>Gavelinella danica</i>	-0.41
527, 30-2-59	<i>M. conicotruncata</i>	-0.90
Zone P4		
384, 8-2-54	<i>M. conicotruncata</i>	-1.17
	benthics	0.33
V22-126, 300	<i>A. mckannai</i>	-0.50
	<i>N. truempyi</i>	0.64
329, 33-4-54	<i>Acarinina</i> sp.	-1.14
	<i>G. danica</i>	-0.10
152, 6-2-178	<i>M. velascoensis</i>	-1.85
144A, 3-3-44	<i>M. velascoensis</i>	-2.48
	<i>N. truempyi</i>	0.05
21A, 3-6-130	<i>M. conicotruncata</i>	-0.92
	<i>N. truempyi</i>	-0.06

TABLE 6 Continued

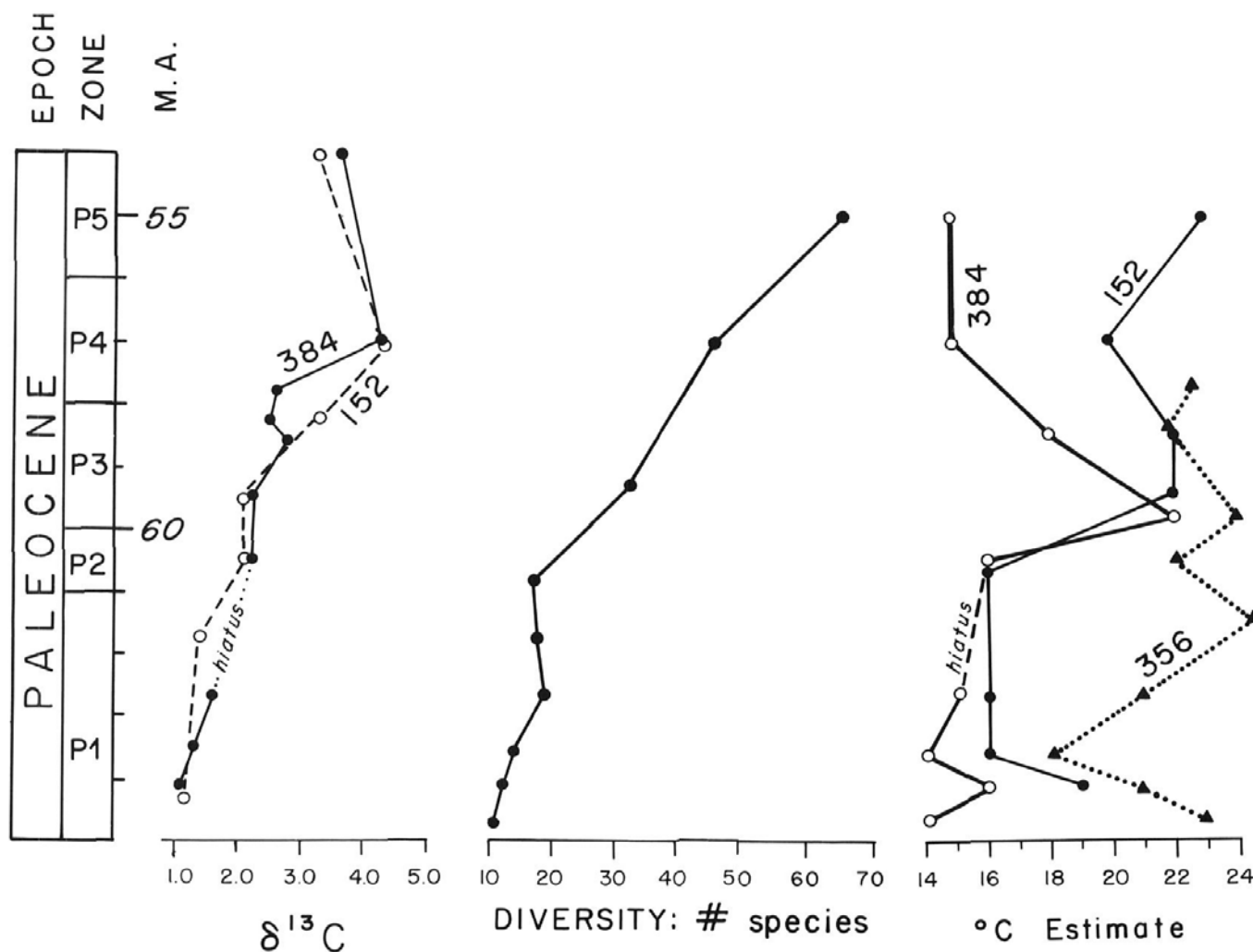
Location	Species	$\delta^{18}\text{O}$
525, 37-1-40	<i>M. cf. marginodentata</i>	-0.87
	<i>N. truempyi</i>	0.26
Zone P5		
384, 6-2-105	<i>M. velascoensis</i>	-1.18
	benthics	0.02
152, 3-4-118	<i>Acarinina</i> sp.	-2.63
20C, 6-3-55	<i>A. coalingsensis</i>	-0.92
	<i>N. truempyi</i>	0.36
94, 33-2-79	<i>M. subbotinae</i>	-1.55
	benthics	-0.17
329, 33-1-44	<i>Acarinina</i> sp.	-1.68
	<i>G. beccariformis</i>	0.11
525, 31-6-60	<i>M. marginodentata</i>	-0.76
	<i>N. truempyi</i>	-0.03
527, 24-3-10	<i>M. velascoensis</i>	-1.06
	<i>Cibicides</i> sp.	0.23
528, 22-2-6	<i>M. velascoensis</i>	-1.05
	<i>N. truempyi</i>	-0.01

Sites 152 and nearby 151 (12°N paleolatitude) temperatures were generally lower than or equal to those at Site 356. In the cooler intervals of Zones P1 and P2, temperatures at Site 152 were near 16°C, but closer to 21°C in the warmer, earliest part of Zone P3. There was a noteworthy rise to maximum values of 23 to 24°C at the very end of Zone P5.

At higher middle latitudes in the North Atlantic, lower temperatures prevailed (text-fig. 10). During the cooler episodes in Zone P1, temperatures ranged from 14 to 16°C. At Site 384 the temperature high early in Zone P3 reached near 21°C, in contrast to temperatures of 17°C at the end of the Paleocene. These younger samples, however, are less well preserved and such low temperatures may be the result of alteration of original isotopic composition.

The temperature record from the middle to high latitude South Atlantic is less complete due to multiple hiatuses and coring gaps at Sites 357, 329, 525, 527–529, and on the Agulhas Plateau. In the Early Paleocene, temperatures at Sites 357 and 21 on the Rio Grande Rise were cooler than at nearby Site 356. This temperature differential was more pronounced at times of temperature lows and during the high at the beginning of Zone P3. In the Late Paleocene, temperatures on the Rio Grande Rise and Falkland Plateau were roughly equivalent, near 17 to 18°C. Even cooler values were consistently registered at this time on the Agulhas Plateau where near surface values neared only 13 to 14°C.

*Carbon isotope record:* Carbon isotope values of planktonic foraminifera increased steadily through the course of the Paleocene (text-fig. 11). A major excursion occurred in Zone P4 (Boersma et al. 1979) when



TEXT-FIGURE 11

Comparison of oxygen and carbon isotope records and overall planktonic foraminiferal diversity in the Atlantic through the Paleocene. The temperature record is derived from oxygen isotope values in text-figure 10. The carbon isotope records for Sites 384 and 152 are representative of other Atlantic sites where the high Late Paleocene  $^{13}\text{C}$  values do not drop off until the Paleocene/Eocene Boundary. Diversity is simply the total number of species identified in each zonal interval.

values at the surface and among the deeper, cooler-dwelling planktonics all increased by nearly 1‰, resulting in a surface-to-bottom carbon isotope gradient near 3‰. This is twice the gradient of the highly productive Late Pleistocene (Broecker 1974). The values at the surface dropped only slightly by the very end of the Paleocene.

#### Meridional paleotemperature gradients

Near surface meridional temperature gradients, estimated from the equator to near 50° North and South latitude, can be read from text-figure 12 and are compared to today's gradient of nearly 25° through 50° of latitude. For low latitude values from the *P. eugubinus* Zone through Zone P3b we used measurements from Site 356, which consistently produced the warmest temperature values in the Atlantic. Since this site did

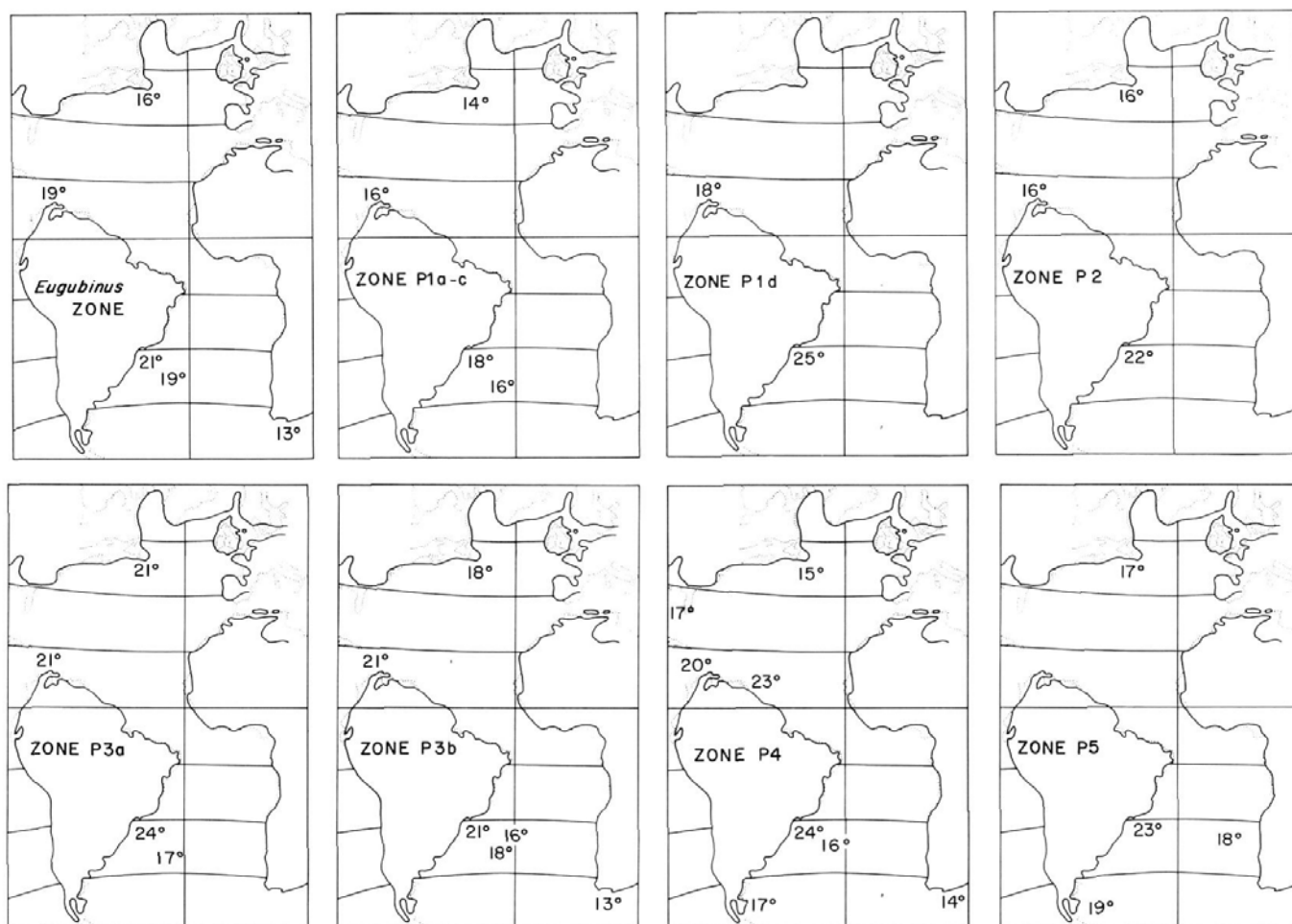
not lie at the equator, we have not necessarily used the maximum possible temperature value to construct the gradient. For Zone P4, an equatorial value from Site 144 could be used to construct the gradient which may be more accurate.

Notable aspects of these gradients are:

- 1, the very low north-south gradient relative to that of today;
- 2, the higher gradients in the South than in the North Atlantic;
- 3, the strong gradient to cooler temperatures from west to east in the South Atlantic middle latitudes (Shackleton and Boersma 1981).

#### Surface-to-bottom paleotemperature gradients

Vertical temperature gradients among the planktonic foraminifera and from the photic zone to the ocean



TEXT-FIGURE 12

Distribution of estimated near surface temperature values (in °C) in the Atlantic during the Paleocene (Boersma et al. 1979; Boersma and Shackleton in press). Estimates were derived from the most oxygen isotopically negative taxon in each sample (see table 6).

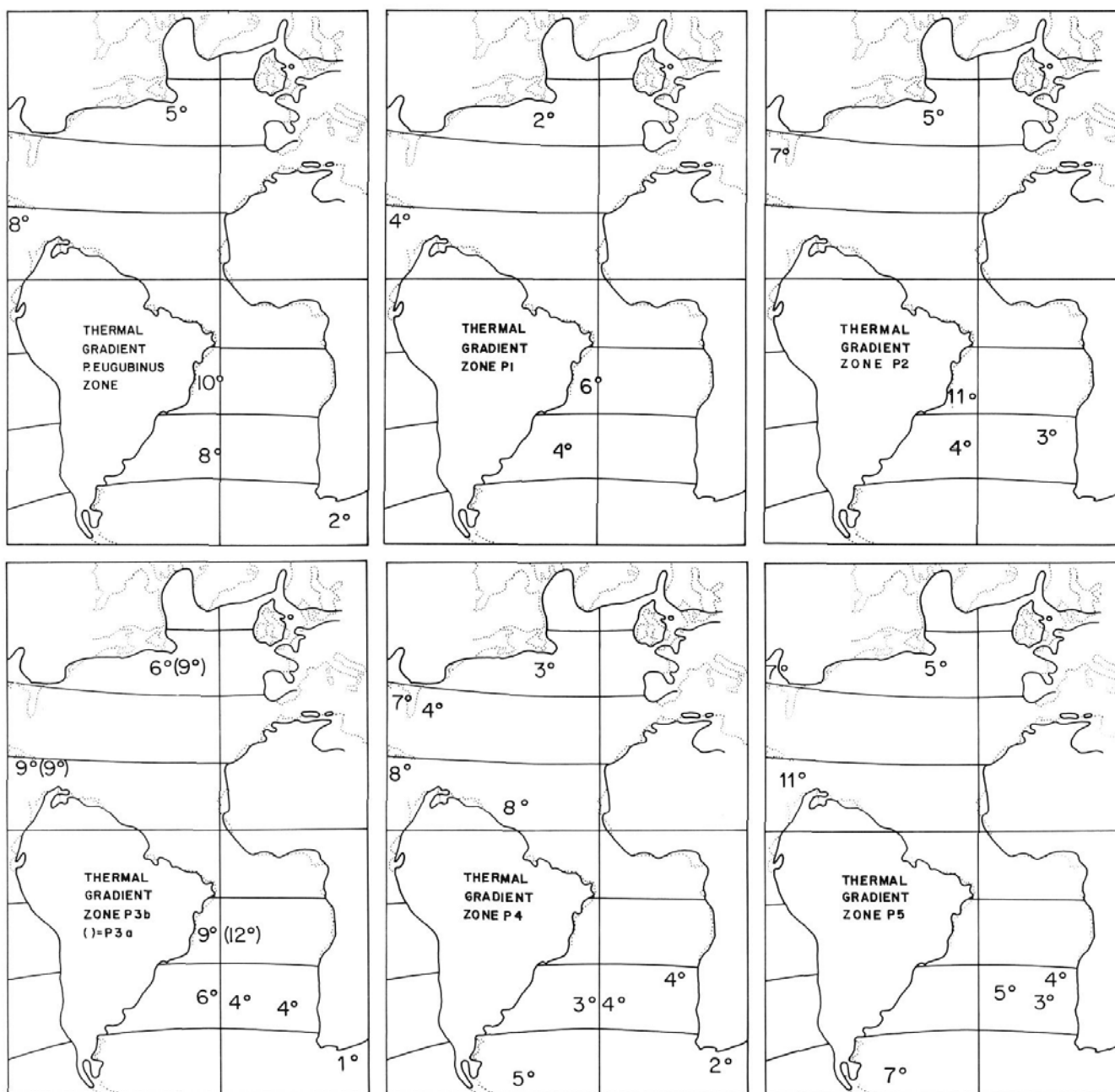
bottom are an indication of local thermoclines (Douglas and Savin 1978). The vertical gradations in temperature, and theoretically in water densities, should have a strong influence on the vertical distribution of the included plankton. During the Paleocene, paleotemperature gradients through the water column were largely a reflection of variations in near surface temperatures, since bottom temperatures both through depth and latitude were remarkably uniform and high relative to today's (Boersma and Shackleton 1977a, 1977b). We have estimated that Paleocene bottom temperatures, from paleodepths of 1000 to 3500 m, varied through latitude by only 1 to 2°C and through time by only 2 to 3°C. Surface-to-bottom estimated paleotemperature gradients have been plotted in text-figure 13.

During the *P. eugubinus* Zone, the largest surface-to-bottom temperature differential, near 10°C, was found at Site 356 on the Brazil margin. The smallest gradient, near 3°C, occurred on the Agulhas Plateau at sites of

paleodepths nearly equivalent to Site 356. Thermal gradients at North Atlantic Site 384 and in the Caribbean were roughly equal, although Caribbean Site 152 had a nearly 1000-m greater estimated paleodepth. These gradients illustrate clearly how it is that the change in surface temperatures from place to place is responsible for variations in the vertical temperature gradients.

In Zone P1 time the gradient at Site 356 continued near 10°C. Caribbean waters had slightly cooler surface and bottom temperatures, resulting in a lower gradient, near 6°C. Gradients at all middle latitude sites were lower than in the *P. eugubinus* Zone and more closely approximated values typical of the Agulhas Plateau. Such gradients at middle latitudes imply the expansion of the larger bulk of cool ocean water and the reduction of the warm-water skin of the ocean to lower latitudes until Zone P1d when a marked increase in near surface temperatures caused a temporary widening of gradients at the few sites where sediments





TEXT-FIGURE 13

Near surface-to-bottom estimated paleotemperature gradients (in °C) in the Atlantic Ocean during the Paleocene. Near surface values are derived from the oxygen isotopically most negative species in each sample. Bottom values come from unispecific or mixed benthic foraminiferal measurements made in the same samples. The gradient is the difference in estimated temperature between the surface values and the bottom values.

of this age could be analyzed. We have no middle or higher latitude measurements for this time period.

A second widening of thermal gradients occurred in Zone P2 due to a cooling of bottom water temperatures, but little change in near surface values. Eastern South Atlantic sites at middle latitudes consistently registered cooler near surface temperatures and therefore lower, 3 to 4°C, temperature gradients from

this time to the end of the Paleocene than sites to the west.

In earliest Zone P3a, accompanying a slight rise in bottom temperatures there was a large increase in near surface values, resulting in a steeper thermal gradient at all sites; this increase was particularly noticeable in the Caribbean and the western boundary of the North Atlantic. The widened gradients continued throughout

Zone P3, although they were the result of cooler temperatures both at the surface and at depth in the later part of this zone.

Thermal gradients of Zone P4 time were similar to those of Zone P3b, were lowest in North Atlantic sites, and increased toward the equator. At equatorial Site 144 there was an 11°C-differential between surface and bottom. While lower gradients characterized the Rio Grande Rise, this was the time of the widest gradients on the Agulhas Plateau.

By Zone P5 time, middle latitude thermal gradients ranged from 5 to 7°C; there are no measurements for this time in the equatorial zone.

#### SUMMARY

In brief, the vertical and meridional thermal gradients are largely the result of 4 to 5°C fluctuations in near surface temperatures overlying a more uniform and constant bulk of 12°C bottom and intermediate waters throughout the Atlantic. Marked increases or decreases in temperatures are most clearly reflected in changes in the surface temperature values and vertical temperature gradients in western boundary areas of both the North and South Atlantic. During the temperature maxima, lack of cooled near surface waters emanating from either polar region allowed penetration of warmed boundary currents with their widened thermal gradients and steeper thermoclines as far as 55°N and S latitude. During the temperature minimum of Zone P2 the cool-water sphere of the ocean expanded, restricting the warm surface "skin" of the ocean to areas equatorward of approximately 25°N and S latitude.

#### SYNTHESIS

Combining faunal and isotopic results has allowed us to designate three major biogeographic provinces in the Paleocene Atlantic in terms of:

- 1, geographic extent;
- 2, aspects of provincial ecology related to paleotemperatures, surface water circulation, and biologic production; and
- 3, foraminiferal biotopes, in particular, index species, characteristic bioprovincial diversities and ecophenotypes and their variations through time (text-fig. 14).

#### Warm-water province

This largely low latitude Atlantic bioprovince (text-fig. 13) extended from 0 to 28°N, 0 to 29°SW and 0 to 25°SE. Paleotemperatures ranged from 25 to 16°C, although values above 21°C were registered only during the temperature maxima in Zones P1d, P3a, and at the

end of Zone P5. Such high temperatures were measured farther to the south in the proto-Brazil Current system, than to the north in the proto-Gulf Stream (text-fig. 12). Meridional paleotemperature gradients through this province were higher in the South than in the North Atlantic. The highest vertical paleotemperature gradients (text-fig. 13), near 11 to 12°C, were recorded in this province; like near surface temperatures they were usually higher in the southwestern boundary current than in the Caribbean, Gulf of Mexico or proto-Gulf Stream region.

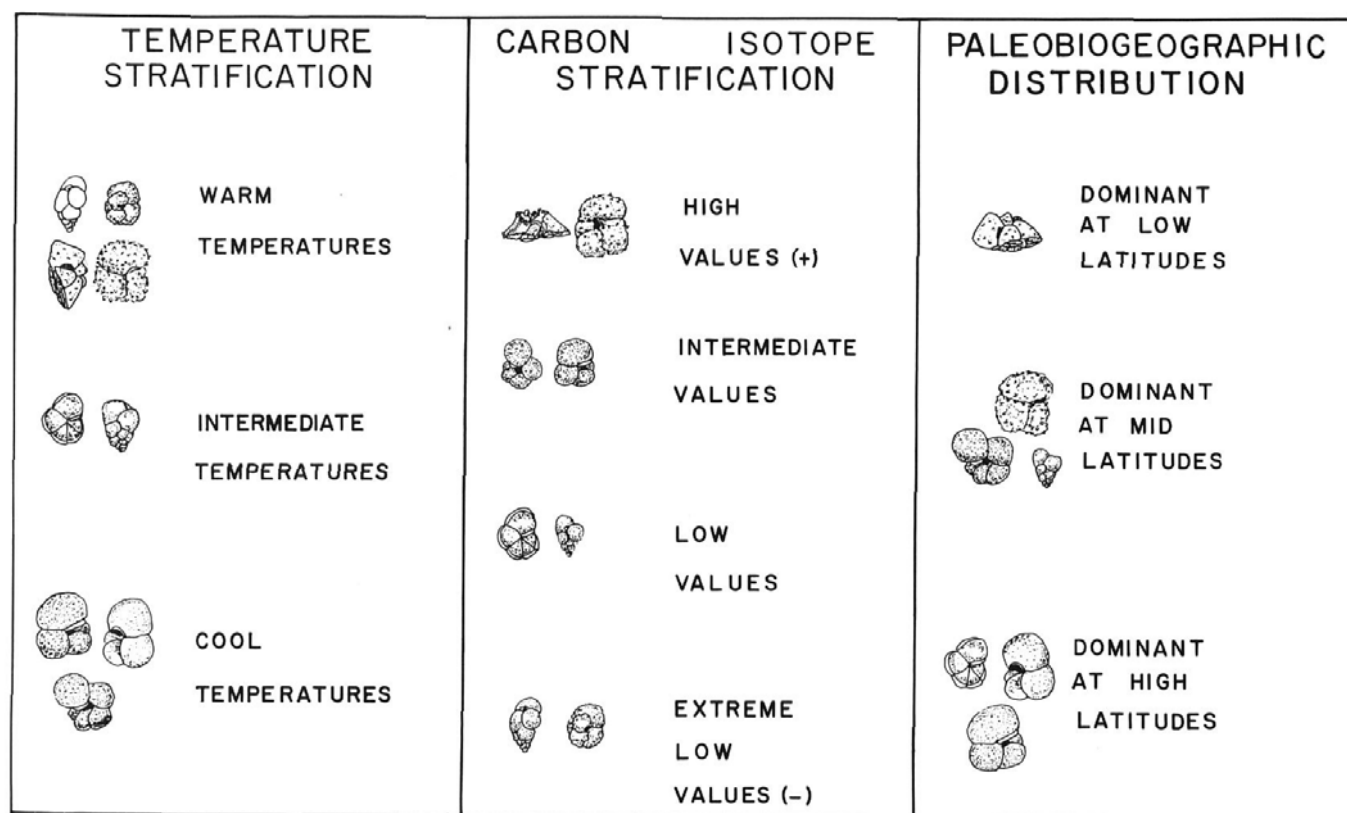
Carbon isotope values in this province are generally average for the Atlantic except at Sites 144 and 94, where some of the Late Paleocene maximum Atlantic values occurred, and at Site 356 where, in the earliest Paleocene, extremely light values were registered by the heterohelids (Boersma et al. 1979).

Faunas of the warm-water province (table 4, text-fig. 14) were consistently characterized by maximum abundances of *Morozovella* spp., particularly of the large morozovellids, and high percentages of "S." *pseudobulloides*. Faunal contents varied from extreme dominance of morozovellids during the Zone P1d temperature maximum to nearly equal percentages of these two groups at other times, including the temperature maximum in Zone P3a (text-fig. 15). After the extinction of "S." *pseudobulloides* in Zone P4 the province was characterized by varying abundances of the several groups of morozovellids and the typical acariniids which are the most solution susceptible genera of all the adult planktonic foraminifera.

A major change in the faunal character of the province occurred in the early Paleocene; prior to Zone P1d substantial amounts of *Chiloguembelina* and *Planorotalites* spp. occurred in lower latitudes, but were not seen there again in abundance after Zone P1. The isotopic evidence (text-fig. 8) indicates that both groups changed their habitat to cooler waters, perhaps at increased depths, in this bioprovince at the same time that they decreased markedly in abundance, subsequently to proliferate at higher latitudes (text-fig. 15).

From the stratigraphic range data (text-fig. 2), it appears that the index species of this bioprovince evolved here prior to their appearances in other bioprovinces; similarly, higher and temperate latitude bioprovincial index species occurred in this province later than elsewhere.

High diversities for the Paleocene are consistently found in this bioprovince, the average number of species ranging from 8 at the initiation of the Paleocene to 28 near its end (text-fig. 3). Species dominance varied from high to low, but the dominance of *M. trinidadensis* was unusually pronounced in the Gulf



TEXT-FIGURE 14

Comparison of temperature and carbon isotope stratification and paleobiogeographic indications of the nine most common and useful planktonic foraminiferal groups during the Paleocene. Warm temperature taxa are *Guembelitra cretacea*, *Globoconusa daubjergensis*, and all species of *Morozovella* and *Acarinina*. The most carbon isotopically positive forms are species of *Morozovella* and *Acarinina*. Low latitude index species belong to the genus *Morozovella*. Species registering intermediate temperatures belong to the genera *Planorotalites* and *Chiloguembelina*. Both these genera characteristically produce low carbon isotope values. *Planorotalites* is dominant first at middle, later at higher latitudes; *Chiloguembelina* was dominant first at lower, then at middle latitudes. Species registering coolest temperatures belong to the genus *Subbotina*. These forms register intermediate carbon isotope values and are characteristic of higher latitudes.

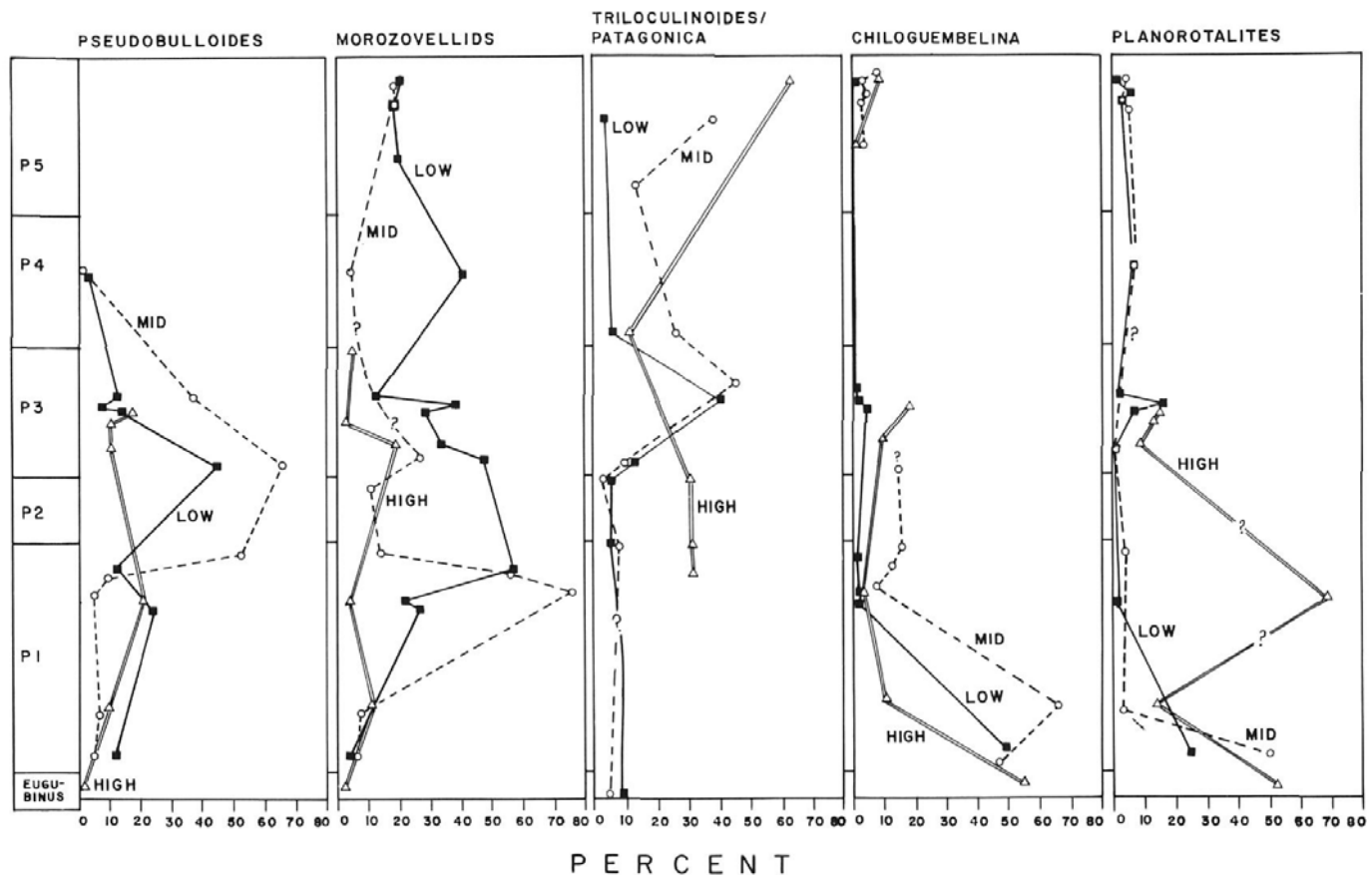
of Mexico during the early Paleocene temperature maximum. The high diversity correlates well with the steep thermoclines in this province (text-fig. 13) suggesting increased niche availability due, in part at least, to the large vertical temperature gradients.

*Spurious temperature drop in Zone P3b:* Comparison of the faunal fluctuations (text-fig. 15) in the warm water province and the curves of paleotemperatures through Zone P3b (text-fig. 10) produced conflicting results. Species abundance changes included significant decreases in morozovellids and "*S.*" *pseudobulmoides* as well as an increase in *S. triloculinoides*; this faunal "signal" suggested a cooling at this time (Haq et al. 1977). The temperature record, however, shows only a slight decrease in near surface temperatures, but not at all latitudes.

To resolve the apparent contradiction we looked at other indicators of climate. Examination of the diver-

sity data (table 3) revealed a large diversification of morozovellids at this time, including new species displaying for the first time distinct keels and umbilical ornamentation. The evidence of dissolution increased dramatically in many of the samples, and higher latitude faunas were depauperate due to dissolution. The abundance of radiolarians increased at Site 384 and first appeared in the Caribbean at this time (Edgar, Saunders et al. 1973). At some sites there was a large increase in surface carbon isotope values that reached their actual maximum later in Zone P4.

We suggest that the faunal "signal" in Zone P3b is not one of a temperature drop associated with climatic cooling but the result of increased dissolution that has enriched the subbotinids at the expense of other species. And we also believe that the dissolution is related to the increased production in many areas, which is indicated by both increased radiolarian abundance and the values of carbon isotopes at the surface.



TEXT-FIGURE 15

Percent abundance of the five major planktonic foraminiferal groups at low, middle, and higher latitudes in the Atlantic through the Paleocene. Abundance counts of planktonic foraminifera are combined from all size fractions. The low latitude curve (solid line with squares) combines data from lower latitude Sites 144, 152, 151, 356 and Trinidad. Middle latitude sites (dotted curve with circles) used in this diagram are 384, 21, 20C, 95, 86, J4, Pont Labau and Delaware. Higher latitude data (double line curve with triangles) come from Sites 329, 117A, 119, the Scotia Shelf, North Sea, Denmark and West Greenland (see text-fig. 1).

#### Temperate province

The temperate province occupied the middle latitudes of both the North and South Atlantic and extended into higher latitudes in western boundary areas, but was truncated in eastern boundary areas (text-fig. 13). The North Atlantic sector extended from 25 to 45°N; in the South Atlantic the boundaries were at approximately 25 and 40°SE, and 30 and 55°SW.

Paleotemperatures registered in these areas ranged from 21 to 14°C, but averaged closer to 17 to 19°C through most of the Paleocene (text-fig. 12). Due to a strong temperature differential between the southern boundary currents, there was a large thermal gradient of approximately 10°C across the South Atlantic at 30°S latitude. The warm temperatures in the proto-Brazil Current derived from the equatorial region; the eastern boundary current was apparently fed by waters deriving from the Antarctic, unlike today when the Ben-

guela System derives from the subtropical Indian Ocean and transports relatively warm, highly productive waters to the Agulhas region. In the Paleocene the coolest temperatures and no siliceous fossils were characteristic of this area as well as the eastern boundary current as far north as the Walvis Ridge.

Typical vertical thermal gradients in this region (text-fig. 13) ranged from 2 to 9°C; these were considerably less than those in the warm-water province except during the temperature maximum in Zone P3a when the thermal gradient in the North Atlantic western boundary areas increased to equal that typical of the Caribbean or other similar areas of the warm-water province.

In this province, maximum carbon isotope values at the surface, and consequently maximum carbon isotope gradients from the surface to the bottom, were often registered by the planktonic foraminifera. In Zone

P3a, the highest gradients and values for the Atlantic were found in the South Atlantic sector of this province.

Bioprovincial indicators (table 4, text-fig. 14) include the subbotinids, primarily "*S.*" *pseudobulloides*, the chiloguembelinids and *Planorotalites* spp. prior to Zone P4; after this time the smooth-walled acariniids and *S. patagonica* plexus typified this bioprovince. The index groups of this intermediate province demonstrate intermediate solution susceptibility.

In the South Atlantic there is a demonstrable gradient in the ratio of the temperate bioprovincial indices to *Morozovella* spp. and other typically warm-water species, which are more abundant at the western end of the gradient. This gradient parallels the consistent east to west increase in near surface paleotemperatures and vertical temperature gradients in the middle latitude South Atlantic. The higher temperatures and vertical gradients during Zone P3a and P5 accompanied higher numbers of morozovellids and acariniids in the region generally.

*Foraminiferal diversity and the paleonutricline:* Diversity of planktonic foraminifera varied from 12 species in the Early Paleocene to 29 in later zones (text-fig. 3) when some of the maximum diversity values for the entire Paleocene were found in this province, both in the North and South Atlantic sectors. Comparison with the paleotemperature gradients and the theoretical thermocline in this province suggests no relationship between the somewhat lower gradients and the maximum diversity values. However, the maximum carbon isotope values typical of this province correlate directly with the high diversities and suggest that, in at least some areas, niche differentiation and foraminiferal diversity are related to the differences in nutrient or oxygen-related characteristics of the water column, but not to paleotemperatures directly.

Comparison of global planktonic foraminiferal diversity through the Paleocene and the carbon and oxygen isotope records in the Atlantic (text-fig. 11) demonstrates the parallelism between the record of carbon isotopes through the Paleocene and the gradual increase in planktonic foraminiferal diversity. The values in these two records increase despite and diachronously with the major fluctuations in the oxygen isotope records of paleotemperature. This parallelism, suggesting that planktonic foraminifera diversified as near surface-water productivity increased (Broecker 1974) through the Late Paleocene (Boersma et al. 1979), further corroborates the idea that nutrient supply and production can create niche space and stimulate adaptive diversification of planktonic foraminifera.

*Distribution of heterohelicids and the paleonutricline:* Until Zone P1, *Chiloguembelina* spp. and related forms

such as *Tubitextularia* or *Woodringina* were a larger component of lower latitude faunas (text-fig. 15); in Zone P1, however, they increased in abundance at middle latitudes and continued to characterize this region and the temperate bioprovince of the Atlantic Ocean through the Paleocene. At Site 384 (text-fig. 9) and Site 357 (table 6), there is evidence that the change in bioprovince was accompanied by a change in their depth habitats; that *Chiloguembelina* and *Tubitextularia* dropped from levels above most other species of planktonic foraminifera to levels below the morozovellids and other nearest surface forms, but above the subbotinids. *Chiloguembelina* retained this relative position through the remainder of the Paleocene.

Boersma et al. (1979), using the record of carbon isotope gradients through the Early Paleocene, hypothesized that the biserial and possibly the triserial heterohelicids lived at levels of lowered oxygen content in the water column, presumably at the level of maximum decomposition of organic matter. Our data suggest that in the *P. eugubinus* Zone this level would have lain close to the ocean surface but dropped during Zone P1 to levels deeper in the water column (as indicated by the cooler temperatures registered by the foraminifera). If true, this suggests that in the *P. eugubinus* Zone, the main levels of both production and organic decomposition lay close to the ocean surface, but that the zone of lowered oxygen descended to levels of lower temperatures and possibly depths during the Early Paleocene as organic production increased through the ocean and the carbon isotope gradient widened.

These changes in the character and depth of the nutricline may explain the unusual distributions and depth habitat changes of planktonic foraminifera in the earliest Paleocene. In the early *P. eugubinus* Zone the six extant planktonic foraminiferal species had essentially cosmopolitan distributions despite the distinct latitudinal paleotemperature gradients (text-fig. 12). More characteristic of this time period was a world-wide, uniformly low surface-to-bottom carbon isotope gradient (Boersma et al. 1979) and the hypothesized position of the levels of production and oxidation near the ocean surface. Assuming that the carbon isotope gradient is a reflection of the dissolved inorganic carbon reservoir (Broecker 1974), then uniformly low carbon utilization and low fertility are indicated. Low nutrient supply may explain the small size of most earliest Paleocene plankton (Percival and Fischer 1977). Their cosmopolitan distributions may reflect the invasion of all available niches along the temperature spectrum by early, generalized species in adaptation to a low food supply (Valentine 1971).

As organic production increased in Zone P1, foraminifera differentiated into bioprovinces. The main zone



of organic oxidation descended to levels of cooler temperatures where the zone of oxygen depletion was either more extensive or otherwise suited to the proliferation of chiloguembelinids in the temperate rather than the warm-water province of the Atlantic.

#### Cool-water province

We have much less data from either foraminiferal or isotopic studies of this province, which can be located only generally at latitudes higher than 40°SE, 55°SW, and 45°N in the Atlantic (text-fig. 13). To date, the only temperature measurements were made on the Agulhas Plateau where the minimum temperatures of the Atlantic, near 13°C, were registered (text-fig. 12). The thermal gradient in this area was 5°C or less, and only this large during the temperature high in Zone P4.

Typical index groups for this bioprovince include the subbotinids and planorotalitids, in particular the *Planorotalites chapmani*-*P. australiformis* plexus (table 4, text-fig. 14). The acarininids, which rarely occur in this province, were smooth-walled and small. In general the dominance of subbotinids is high; however, the faunas are often small due to dissolution, which could artificially increase the proportion of subbotinids. In these faunas the majority of species are found in the 63–149  $\mu$ m fraction.

The stratigraphic range data (text-fig. 2) demonstrate that the species *Subbotina patagonica* evolved in this region before its appearance in other, lower latitude areas. Morozovellids are rarely found in this province; in the North Atlantic they occur only during the temperature maxima in Zones P1d and P3a, but not afterwards. As in other bioprovinces there was a change in bioprovincial indices during the course of Zone P1; prior to this change the province contained representative amounts of subbotinids, planorotalitids, and chiloguembelinids (text-fig. 15). After Zone P1 the chiloguembelinids and planorotalitids decreased in import.

Like the paleotemperature gradients, the diversity of planktonic foraminifera is low in this province; faunas characteristically contain from three to six species (text-fig. 3).

#### CONCLUSION

Our combined analyses of planktonic foraminiferal distributions and oxygen and carbon isotopes have demonstrated the close relationships between the ecology of Paleocene bioprovinces and their foraminiferal biotopes. Ecologic factors directly correlating with paleotemperature have a strong influence on foraminiferal distributions, particularly in the warm-water province. Ocean circulation patterns may, however, disrupt provincial boundaries during climatic paleotemperature maxima or minima. Faunal characteristics of the ear-

liest Paleocene *Planorotalites eugubinus* Zone in general and of the temperate bioprovince throughout the Paleocene are limited by temperature-related factors, but better explained by the gradients in nutrients, and the carbon isotopic record of organic production and oxidation. Similarly, the evolutionary radiation of planktonic foraminifera directly paralleled the record of production and fertility in the Atlantic through the Paleocene Epoch.

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