

STABLE ISOTOPE PALEOECOLOGY OF MIDDLE EOCENE PLANKTONIC FORAMINIFERA AND MULTI-SPECIES ISOTOPE STRATIGRAPHY, DSDP SITE 523, SOUTH ATLANTIC

P. N. PEARSON,¹ N. J. SHACKLETON² AND M. A. HALL²

ABSTRACT

Multi-specimen isotopic analyses have been conducted on twenty species of planktonic foraminifera from the middle Eocene of DSDP Site 523, South Atlantic. Continuous stratigraphic series have been obtained for the better represented species over a sequence which spans about two million years. The fauna to be subdivided into three principal habitats using carbon and oxygen isotope data. The first group are the mixed layer dwellers, including a number of species from the genera *Acarina*, *Morozovella*, *Muricoglobigerina* and *Globigerinatheka*. This assemblage was apparently depth stratified within the mixed layer and a marked seasonal turnover is suggested by the oxygen isotope paleotemperatures. The second group is the thermocline community, which includes various species of *Subbotina*, *Hantkenina* and *Clavigerinella*. A single species, *Subbotina* aff. *inaequispira*, occupied a distinct sub-thermocline habitat. The mixed layer dwelling *Acarina* spp. tend to show a marked change in their carbon isotopic ratios with respect to size fraction in the 125 to 530 μm range. Such a pattern, which may indicate a symbiotic association, is not shown by the deeper dwelling *Subbotina* spp. Integrated isotope stratigraphy of several species from different habitats provides a tool for examining long-term palaeoceanographic changes, such as vertical water mass distinctions, the degree of seasonality and the thermal structure of the water column.

INTRODUCTION

Studies of modern planktonic foraminifera have shown that they have complex life histories, occupying a diverse set of niches within the pelagic ecosystem, and are variously specialized in the exploitation of trophic resources and in their preference of habitat (see Hemleben and others, 1989 for review). One of the objectives of planktonic foraminiferal paleobiology is to understand fossil faunas in such a context. The isotopic ratios of both carbon and oxygen as incorporated into the test calcite provide independent and complementary lines of evidence for the living environments and life histories of extinct species. Furthermore, if a whole fauna can be well understood in terms of its paleoecology, so isotopic analysis may provide a tool for investigation into past oceanographic conditions.

Various authors have discussed the advantages and problems of isotopic techniques of foraminiferal shells for palaeoceanographic analysis (e.g. Savin 1977; Berger and Vincent 1986; Miller and others, 1987). Since the studies of

Emiliani (1954, 1955) it has been appreciated that the oxygen isotopic ratios ($\delta^{18}\text{O}$) of test calcite may give information on the temperature of calcification. The equilibrium isotopic fractionation between calcite and seawater is temperature dependent (Urey, 1947; O'neil and others, 1969) such that calcite secreted in warm seawater is isotopically lighter with respect to oxygen than that secreted in colder water. Emiliani (1954) argued that, because temperature generally decreases with water depth in the oceans, it is possible to subdivide a fauna into its various species and derive an isotopic estimate of their depth order in life. Such an approach has proved successful for modern species with known depth stratification (Shackleton and Vincent, 1978; Fairbanks and others, 1982) and has been applied extensively to extinct forms (e.g. Berger and others, 1978; Douglas and Savin, 1978). However, it should be stressed that the oxygen isotope paleotemperature is only an indirect proxy for the depth of calcification (see discussion below).

The ratio of the stable isotopes of carbon ($\delta^{13}\text{C}$) may also provide evidence for the life environments of extinct species, particularly depth. Temperature has only a minor influence on the carbon isotopic ratio (Emrich and others, 1970), but other factors are important. The principal consideration is the isotopic ratio of total dissolved inorganic carbon (ΣCO_2) in seawater local to the foraminifer, from which it precipitates its shell. Local differences in the $\delta^{13}\text{C}$ of ΣCO_2 result from the fact that the light isotope is preferentially removed during organic photosynthesis, leaving the remaining seawater 'heavy'. Photosynthesis occurs in the surface waters which consequently become enriched with respect to ^{13}C . Sinking of organic particles through the water column culminates in their oxidation at depth, whereupon the light isotope is returned to the water. A gradient of $\delta^{13}\text{C}$ in ΣCO_2 through the water column is therefore established (Kroopnick, 1974). Hence the characteristic carbon isotope value of a species should provide evidence independent of the oxygen isotopic estimate of its depth habitat relative to other species from the same sample.

Certain problems must be confronted when interpreting isotopic measurements of fossil faunas. Firstly, it is difficult to know whether an extinct species secreted its calcite in isotopic equilibrium with seawater. Only for living organisms may this assumption be investigated. Encouragingly, it has been found that modern planktonic foraminifera mostly secrete carbonate close to equilibrium with respect to oxygen, although departures in the order of $<1\%$ have been reported (Vergnaud-Grazzini, 1976; Kahn, 1979). For carbon, however, the problem can be more pronounced. Exceptional departures from equilibrium as large as -6.0% have been reported (Erez and Honjo, 1981). It seems certain that the degree of vital effect differs between species, perhaps having a relationship with the presence or absence of photosynthesising symbionts and light intensity, which

¹ Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, England

² Godwin Laboratory for Quaternary Research, Free School Lane, Cambridge CB2 3RS, England

themselves may be depth related (Spero and Williams, 1988, 1989; Spero, 1992).

A second consideration involves post-depositional alteration of the isotopic ratio. Very often, as is the case for the samples analysed in this study, preservation may appear good under the optical microscope but investigation with the scanning electron microscope reveals evidence of diagenetic alteration (see Plates 1–3). Much of the degradation of surface ultrastructure in these samples is due to dissolution (see, for example, Pl. 3.4–3.5), which itself is unlikely to have a great effect on isotopic ratios. More of a concern is that the internal structure of freshly broken specimens does not usually have the pristine granular appearance characteristic of a recent test, implying that some ‘recrystallisation’ has occurred (Pl. 2.9; Pl. 3.17). The details of the processes involved remain obscure. However, the consistency of the results obtained here from various samples in different states of preservation suggests that individual tests have remained largely closed systems and recrystallisation of calcite has occurred without significant gross macroscopic transport of atoms in solution (see also Barrera and Huber, 1990). For the samples analysed here significant sparry calcite overgrowths are rare and in those cases which have been observed are unlikely to be volumetrically important. The dissolved nature of the middle Eocene section at Site 523 is paradoxically advantageous. Early dissolution on the sea floor probably removed any aragonite (e.g. pteropods) and much of the very fine material which might have otherwise been gradually redistributed through the sediment (Matthews and others, 1980).

METHODS

DSDP Site 523 was drilled by hydraulic piston corer in the Angola Basin, which lies to the east of the Mid-Atlantic Ridge and North of the Walvis Ridge (28°33.131'S, 2°15.078'W). The preservation of planktonic foraminifera in this site is variable due mainly to periods of carbonate dissolution (Poore, 1984). The least affected interval was between cores 42 and 51 at the bottom of the hole and is the focus of the present study. This section spans Chron C-20-R and C-20-N of the Middle Eocene, equivalent to low latitude planktonic foraminiferal Zones P11 and part of P12. Sampling was at 20 cm intervals. The sedimentation rate, uncorrected for compaction, through the lower part of the core was about 7m/m.y. (Hsu, LaBreque and others, 1984). The interval between samples is therefore approximately 30,000 years. Since each sample extends over about 2 cm of core, it represents a time averaged population of at least 3,000 years with bioturbation causing further time averaging.

Isotopic analyses were conducted at the Godwin Laboratory, University of Cambridge. The original sediment samples were broken up in water and the foraminifera extracted by sieving on a 63 µm sieve. In the >250 µm size fraction, about 25 individuals of the same species were picked for a single sample, although occasionally fewer than this in cases of rarity. In smaller size fractions samples usually consisted of more than 50 specimens. Samples were analysed in a VGIsogas SIRA-9 mass spectrometer.

THE FAUNA

The Middle Eocene fauna recovered at Site 523 is typical for mid-latitude open ocean environments of the time. Acarininids and subbotinids are dominant through most of the interval. More typically low-latitude forms such as the morozovellids and hantkeninids are present, but are only occasionally suitably abundant for isotopic analysis.

The most abundant acarininids belong to the *Acarinina bullbrooki*—*A. matthewsae* plexus (Pl. 1.1–6, 10). The taxonomy of these forms is complex and objective criteria for the separation of taxa difficult to establish. Intermediates are common and occasionally more loosely coiled five-chambered forms are found. For this group, the classifications of Stainforth and others (1975) and Blow (1979) have been followed. Also abundant, and easily distinguished, are forms belonging to the *A. pseudotopilensis* group for which a good evolutionary lineage can be established. The earlier representatives tend to be large, inflated and rounded (*A. triplex*; Pl. 1.7–9, 11–12) and are very common in cores 48 to 50. These show a perfect gradation to a typical *A. pseudotopilensis* morphology (Pl. 1.13–15) which becomes the predominant morphotype. There follows gradual transition to a more angular shape, particularly of the last formed chamber around which muricae become concentrated in a circum-cameral configuration. These trends, combined with a loosening of the coiling mode, eventually result in the form *Truncorotaloides topilensis* (Pl. 1.16–18). Unlike the other acarininids, the coiling ratio is strongly biased, and in fact oscillates between dextral to sinistral dominance. *Acarinina primitiva* is also present in this material (Pl. 1.19), although less abundant.

Three distinct taxa belonging to the genus *Muricoglobigerina* are present: *M. esneheensis* (Pl. 1.20), *M. angulosa*. and *M. senni* (Pl. 1.22–25). Certain very heavily calcified individuals of *M. senni* are enveloped by a crust of euhedral calcite crystals formed late in the ontogeny, presumably at gametogenesis (Pl. 1.24–25). Variability in the expression of this feature between samples may account for the greater spread of isotopic values measured for this species (see below).

Three separate groups are included in the genus *Morozovella*. The *M. crassata* group shows great variability in the chamber shape as seen in side view, from a slender biconvex shape (*M. crassata*; Pl. 2.4–6) to an anguloconical morphology convergent on *Acarinina*, but possessing a muricocarina (*M. densa*; Pl. 2.7). *M. aragonensis*, a large anguloconical form (Pl. 2.1–3, 8–9) is present in some samples. The extinction of this species is used to define the end of Zone P11 in the low latitudes (Berggren and Miller, 1988), but its last occurrence in this site is considerably earlier, at a horizon well within Chron C-20-R. Also included provisionally in the genus ‘*Morozovella*,’ following McGowran (1968) and Premoli Silva and Boersma (1988) is the species *broedermanni* (Pl. 1.21), although it lacks a muricocarina. ‘*M.*’ *broedermanni* varies considerably in abundance through the section.

The genus *Subbotina* is taxonomically difficult due to a high degree of morphological plasticity. Two lineages (*S. frontosa* and *S. aff. inaequispira*) are, however, easily distinguished. *S. frontosa* (Pl. 2.19–21) is distinguished from

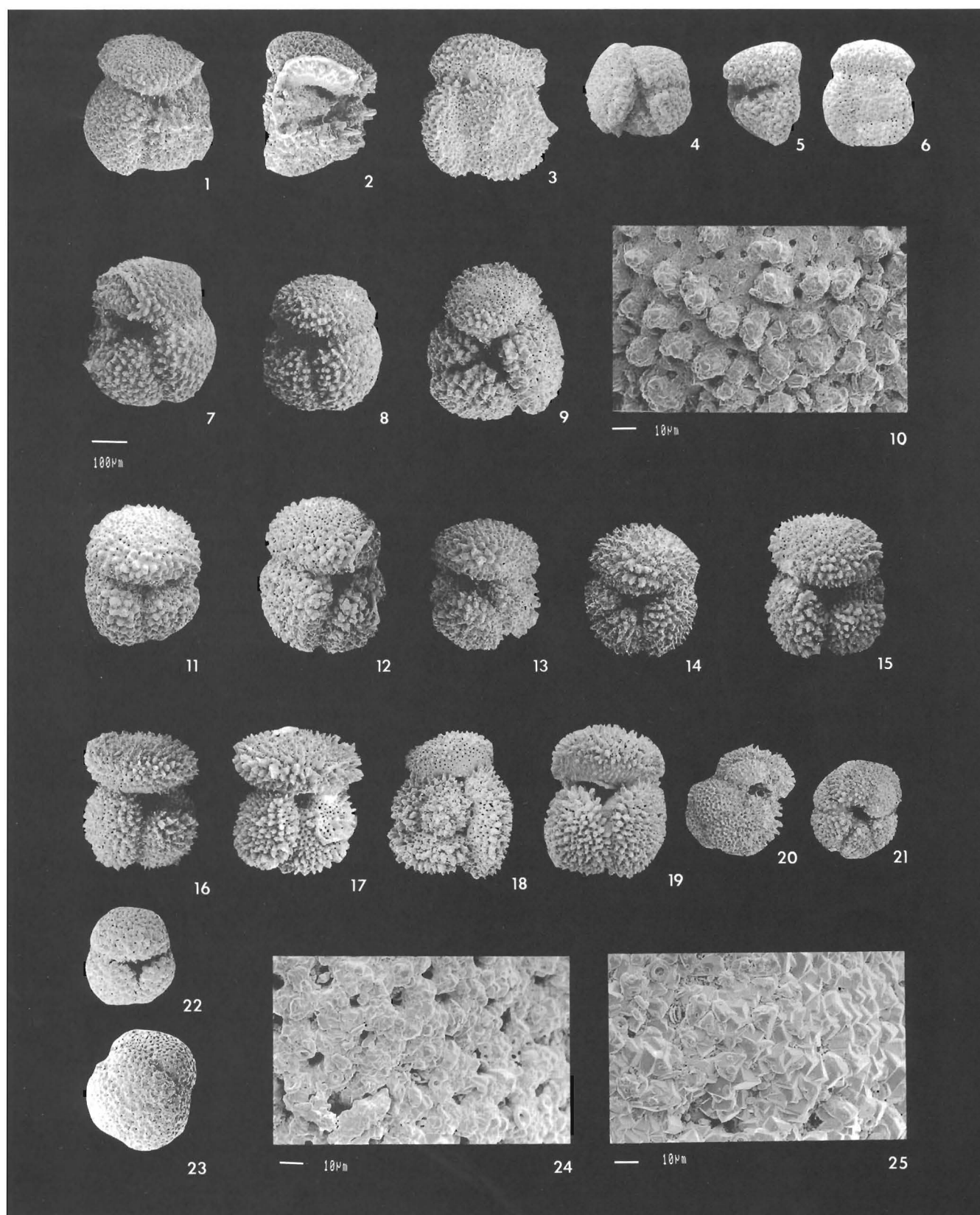


PLATE 1

Mixed layer dwelling planktonic foraminifera. 1-3: *Acarinina bullbrookii*; 4-6, 10: *Acarinina matthewsae*; 7-9, 11-12: *Acarinina triplex*; 13-15: *Acarinina pseudotopilensis*; 16-18: *Truncorotaloides topilensis*; 19: *Acarinina primitiva*; 20: *Muricoglobigerina esnehensis*; 21: '*Morozovella*' *broedermanni*; 22-25: *Muricoglobigerina senni*.

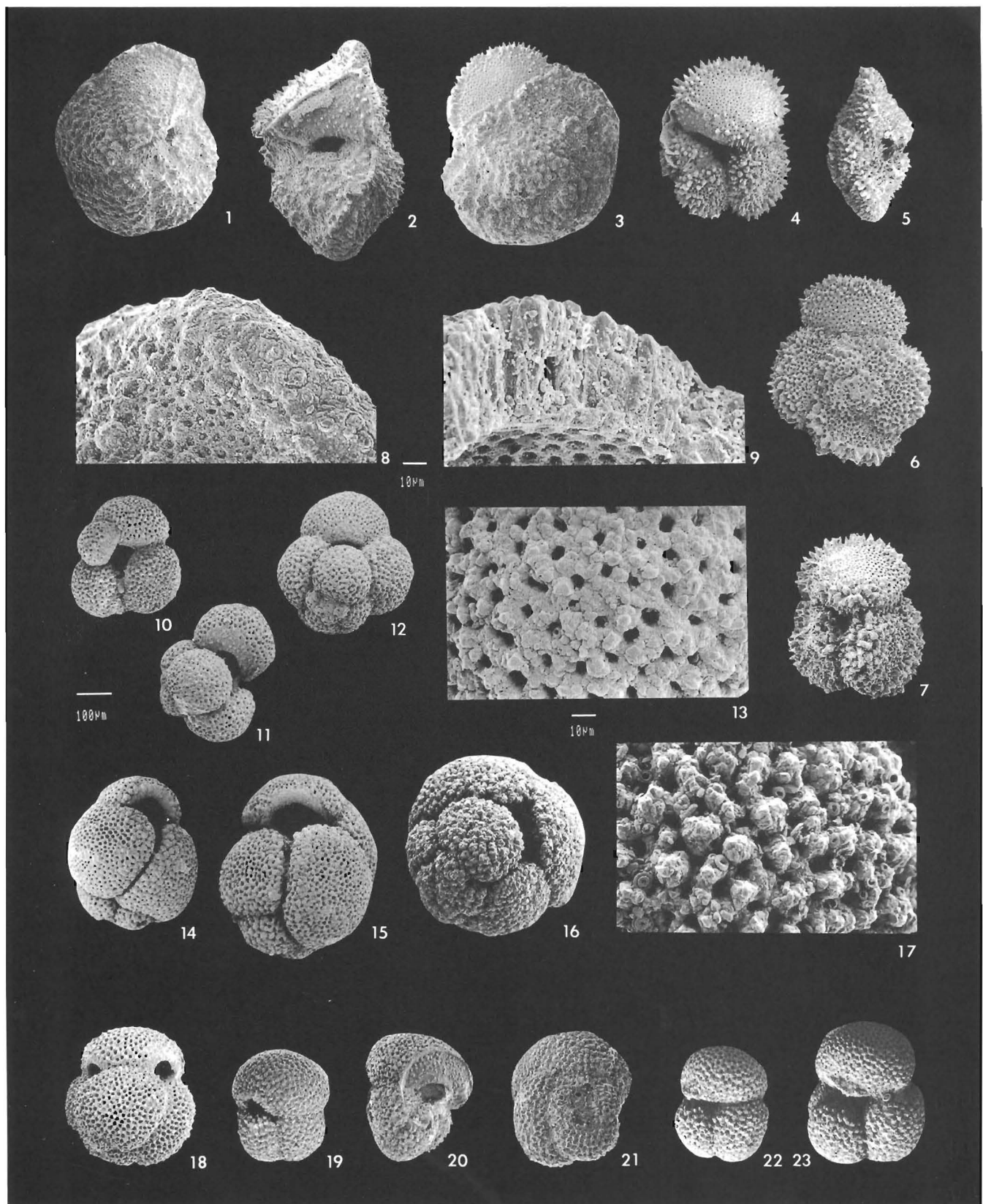


PLATE 2.

Mixed layer and thermocline dwelling planktonic foraminifera. 1-3, 8-9: *Morozovella aragonensis*; 4-6: *Morozovella crassata*; 7: *Morozovella densa*; 10-13: *Guembelioides higginsii*; 14-15: Specimens intermediate between *Guembelioides* and *Globigerinathea*; 16-17: *Globigerinathea subconglobata*; 18: *Globigerinathea index*; 19-21: *Subbotina frontosa*; 22-23: *Subbotina linaperta*.

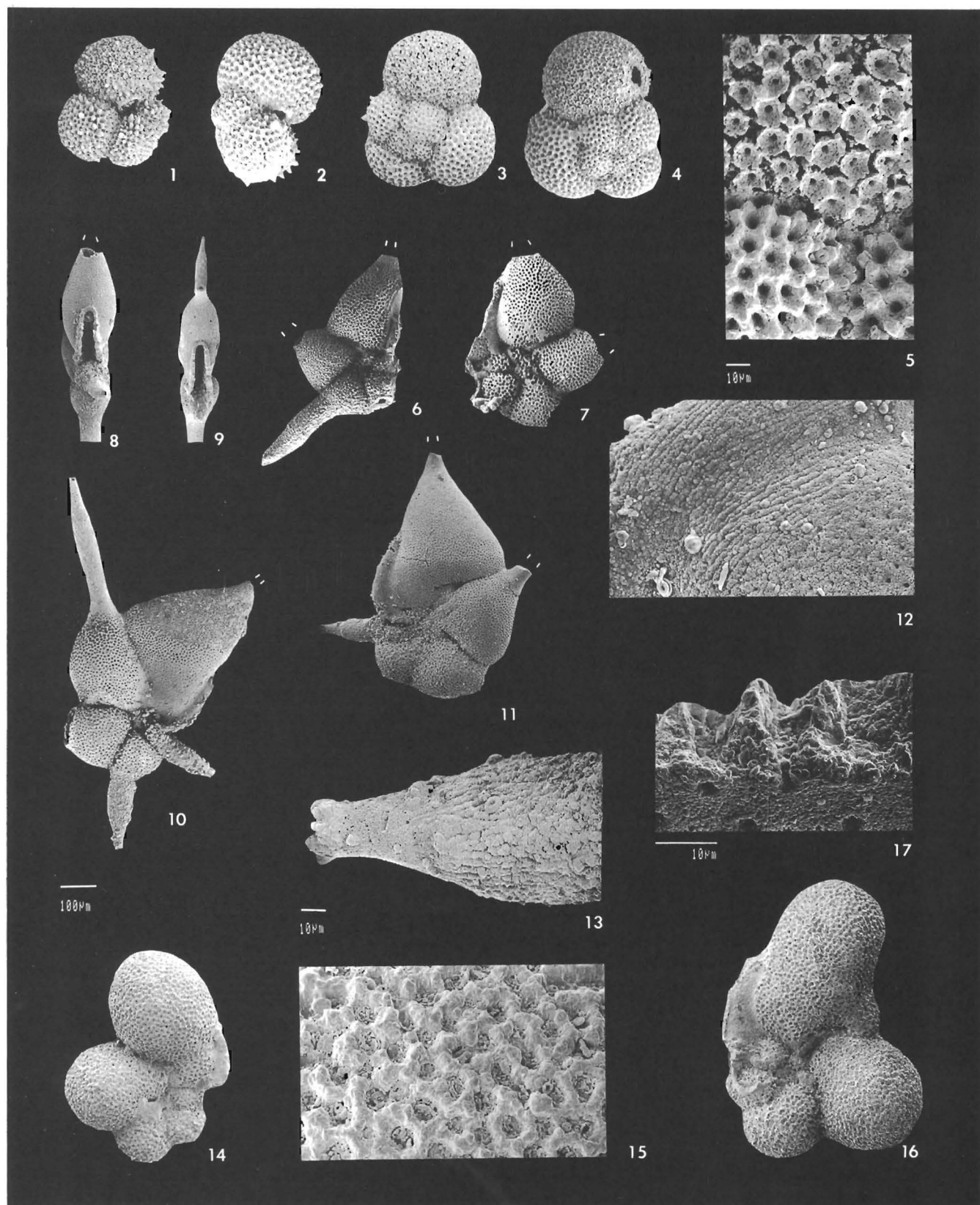


PLATE 3

Sub-thermocline and thermocline dwelling planktonic foraminifera. 1-5: *Subbotina* aff. *inaequispira*; 6-7: *Hantkenina liebusi*/H. *mexicana*; 8-10: *Hantkenina liebusi*; 11-13: *Hantkenina dumblei*; 14-17: *Clavigerinella eocanica*.

other species by its large, often radially compressed final chamber, arched aperture and dextral coiling preference. *S. aff. inaequispira* (Pl. 3.1–5) has a distinctive cancellate wall texture with deep pore-pits and a coiling mode in which the height of the spire increases with ontogeny. Mound-like projections sometimes occur at the intersection of the inter-pore ridges (see particularly Pl. 3.1–2) which often dissolve first leaving a distinctive texture in which isolated rosettes of calcite are centered on the mural pores (Pl. 3.5). This form seems to be related to *Subbotina*'s (1953) taxon *inaequispira*, but the coiling mode also suggests a possible relationship with *Globorotaloides*. Other more generalised forms have been included under the names *S. linaperta* (Pl. 2.22–23) and *S. eocaena* following Toumarkine and Luterbacher (1985) and other authors.

The high-spined species *Guembelitrionides higginsii* (Pl. 2.10–13) is common in some samples. Specimens lacking supplementary apertures but otherwise identical are included here. Some problematic specimens (Pl. 2.14–15) seem to show transition towards the genus *Globigerinatheka* (Pl. 2.16–18). Within that genus the taxon *G. index* is the most commonly occurring form.

The tubulospinate *Hantkenina* group is patchily abundant. Earlier individuals tend to be more stellate (*H. liebusi*, showing transition towards *H. mexicana*; Pl. 3.6–7), whereas later individuals gradually develop a more rounded periphery (*H. liebusi*; Pl. 3.8–10 and *H. dumblei*; Pl. 3.11–12). The surface microstructure of these forms is interesting in that they not only possess apertural flanges of constant width (Pl. 3.8–9) and the finger-like terminations to the tubulospines (the coronet structure described by Ramsay, 1962; Pl. 3.13) which are typical of the subgenus *H. (Aragonella)*, but also surface striations, particularly on the apertural flange (Pl. 3.12) and spiralling up the tubulospines (Pl. 3.10, 13) which Blow (1979) suggested was found only in *H. (Hantkenina)*. In terms of microstructure, gross morphology and stratigraphic occurrence these forms seem to be intermediate between the two subgenera.

Clavigerinella eocanica (Pl. 3.14–17) is abundant in one sample only. The finely 'cancellate' wall texture (Pl. 3.15; contrast with Pl. 3.12) suggests a relationship with *Subbotina* or a related form rather than smooth walled forms such as *Hantkenina* (see also Hillbrandt, 1976; Blow, 1979). Other groups present, but not included in the isotopic study are the pseudohastigerinids (commonly showing a bipartite apertural system), planorotalitids and the heterohellicids.

PREVIOUS WORK ON PALEOGENE DEPTH HABITATS

Douglas and Savin (1978) studied interspecific differences in the isotopic ratios of Paleocene species as part of an investigation of foraminiferal depth habitat from the Cretaceous to Recent. In a Paleocene sample from DSDP Site 45 on the Shatsky Rise these authors recorded a lower oxygen isotope palaeotemperature for a single mixed *Subbotina* sample than for various species of *Acarinina* and *Morozovella*. However, their general conclusion was that the uniformitarian argument for inferring depth habitats was upheld by the isotopic evidence, stating 'species with globi-

gerine morphology have consistently occupied shallower depths than have species with globorotaliid morphology' (Douglas and Savin, 1978, p. 175).

Boersma and others (1979) made over 200 further measurements on Paleocene planktonic foraminifera, most notably from DSDP Site 384 in the Western North Atlantic and Site 356 in the mid-latitude South Atlantic. They demonstrated a consistent pattern: the globular genus *Subbotina* gives cooler palaeotemperatures than the anguliconical forms, indicating a deeper habitat. These authors therefore brought attention to the striking difference between *Subbotina* and its modern homeomorph (*Globigerina*) which is a shallow dweller. Poore and Matthews (1984) obtained an oxygen isotopic ordering for Late Eocene and Oligocene faunas which revealed a similar pattern—that the subbotinids and the globular *Catapsydrax* group gave cooler palaeotemperatures than other forms from the same samples. Shackleton and others (1985) presented about 250 carefully size controlled analyses from the Paleocene of Pacific DSDP Site 577. Once again they recorded a deeper water signature for the subbotinids with respect to both carbon and oxygen isotopes. A zone-by-zone appraisal of the Eocene was given by Boersma and others (1987), demonstrating that this pattern is continuous throughout the Paleogene. Shallower water values for both carbon and oxygen isotopes are registered consistently by *Acarinina*, *Morozovella* and *Globigerinatheka* spp., whereas deeper water ratios are observed in the globular genera *Subbotina* and *Catapsydrax* and others such as *Turborotalia*, *Pseudohastigerina*, *Hantkenina* and the heterohellicids. Other work has supported this general picture (e.g. Stott and others, 1990; Corfield and Cartledge, 1991).

Previous isotopic investigations at Site 523 were conducted by Oberhänsli and others (1984). They reported a seemingly reversed oxygen isotopic depth ranking in the Middle Eocene for the genera *Subbotina* and *Acarinina*. However, this anomaly can largely be explained because one species they included in *Subbotina* (i.e. '*Subbotina senni*') is probably unrelated to the genus (here it is included in *Muricoglobigerina*). *Muricoglobigerina senni* does indeed have a light oxygen isotopic ratios, but various species of true *Subbotina* tested were found to be heavy (see below).

DEPTH AND SEASONALITY

Carbon and oxygen isotopic ratios for all samples analysed in this study are given in the Appendices. It is emphasised that each analysis was conducted on a crushed sample of about 25 specimens (or more for the smaller size fractions). The advantage of large samples is that isotopic differences between species are more clearly measured rather than variability between individuals, which for example, might live over a range of depth habitats or at different times of the year. Such individual variability, which would act as 'noise' in a stratigraphic or ecological study, is mostly averaged out in a relatively large sample.

As discussed above, both the carbon and oxygen isotopic ratios of foraminiferal test calcite are related to the depth of calcification. In general, calcite precipitated in deep waters is expected to be characterised by heavy $\delta^{18}\text{O}$ and light $\delta^{13}\text{C}$

relative to the surface waters. Thus different species may be ranked according to their isotopic ratios of both carbon and oxygen, which give independent estimates of their relative depth. It should be remembered, however, that species-specific disequilibrium fractionation or diagenetic effects might tend to give a spurious order.

Tables 1 and 2 show the fauna ordered by carbon and oxygen isotopic analyses in the >250 μm size fraction. In these tables, and in most of the ensuing discussion, analyses are treated regardless of stratigraphic position. In fact, some stratigraphic variation does exist in the isotopic ratios (see Fig. 4) and would tend to add to the scatter of points.

The inverse correlation of the oxygen and carbon isotopic ordering is only approximate. Why is this so? If both isotopic variables are depth related, then the water column at any one time should be characterised by a single curve on a plot of $\delta^{18}\text{O}$ versus $\delta^{13}\text{C}$. The exact shape of this line is unknown, and will depend on a variety of oceanographic considerations such as the strength and depth of the thermocline, levels of primary productivity and light penetration, and possibly the presence of marked subsurface discontinuities related to different vertical water masses (Shackleton and Vincent, 1978). Failure of multi-species data, such as those presented here, to plot on a single curve may be due to several reasons in addition to the problems of diagenesis and disequilibrium fractionation. Seasonality is probably the most important factor.

Present-day surface water temperatures change markedly in an annual cycle, resulting in seasonal variations in the $\delta^{18}\text{O}$ of foraminiferal calcite (e.g. Erez and Honjo, 1981; Williams and others, 1981). Williams and others (1981) and have shown that this seasonality is preserved in the sedimentary record because different species reach peak abundance at different times of year. However, no seasonal change in the $\delta^{13}\text{C}$ of foraminiferal calcite was found in the study of Williams and others (1981). Comparable results were given by Deuser and others (1981), Deuser (1987) and Deuser and Ross (1989) from the Sargasso Sea, where seasonal temperature variations are reflected in surface water

TABLE 2. Species ordered by oxygen isotopic ratios.

HABITAT	SPECIES	$\delta^{18}\text{O}$	n
Mixed layer dwellers	<i>Muricoglobigerina angulosa</i>	-0.45	29
	<i>Muricoglobigerina senni</i>	-0.34	81
	<i>Globigerinatheka subconglobata</i>	-0.34	3
	<i>Morozovella crassata</i>	-0.30	2
	<i>Globigerinatheka index</i>	-0.28	35
	<i>Morozovella aragonensis</i>	-0.19	4
	<i>Acarinina matthewsae</i>	-0.19	100
	<i>Muricoglobigerina esnehenensis</i>	-0.16	7
	<i>Acarinina bullbrooki</i>	-0.13	25
	' <i>Morozovella</i> ' <i>broedermanni</i>	-0.13	9
	<i>Acarinina triplex</i>	-0.10	18
	<i>Acarinina pseudotopilensis</i>	+0.04	51
Thermocline dwellers	<i>Guembelitrionides higginsii</i>	+0.17	28
	<i>Hantkenina</i> spp.	+0.36	13
	<i>Subbotina frontosa</i>	+0.36	61
	<i>Clavigerinella eocanica</i>	+0.39	1
	<i>Subbotina eocaena</i>	+0.40	12
Sub thermocline	<i>Subbotina linaperta</i>	+0.46	61
	<i>Subbotina</i> aff. <i>inaequispira</i>	+0.83	46

foraminiferal calcite by changes in the $\delta^{18}\text{O}$ of about 1.0‰, but the amplitude of seasonal variations in $\delta^{13}\text{C}$ is relatively minor.

The extent of seasonal variations in carbon and oxygen isotopes would be expected to differ from one environment to another. Spero and Williams (1989) have modelled how the isotopic composition of individual tests of modern *Orbulina universa* would be expected to vary year-round in a variety of different oceanic settings. Provided that such environments are accompanied by a seasonal turnover of fauna then such information can also be retrieved from multi-specimen analyses of different species over a long, stable time interval, as is the case for this study.

The entire isotopic data set is plotted on a carbon vs oxygen graph in Figure 1. The wide J-shape of this plot closely resembles the expected pattern suggested by Spero and Williams (1989) for an open-ocean site with a year-round stable thermocline. These authors illustrated a similar pattern from box-core data of Recent and Late glacial *O. universa* from Ontong-Java, western equatorial Pacific (data of Killingley and others, 1981, and Schiffelbein and Hills, 1984). An adapted version of the model of Spero and Williams (1989) is employed as the basis for ecological interpretation in this study (Fig. 2). The advantage of studying an open ocean site is its relative simplicity (Oberhansli et al., 1984), compared to other environments which may be complicated by upwelling or other factors (Spero and Williams 1989; Sautter and Thunell, 1991).

The fields in which different species plot within the 'J' are shown in Fig. 3. Employing the model proposed in Fig. 2, it is possible to suggest divisions of the fauna first by depth habitat and then by seasonal abundance. Three major divisions emerge: the mixed layer dwellers which have the heaviest carbon ratios and show variability with respect to oxygen (*Acarinina* spp., *Muricoglobigerina* spp., *Morozovella* spp., *Globigerinatheka* spp., *Guembelitrionides higginsii*); the thermocline dwellers with closely similar, intermediate carbon and oxygen ratios (most *Subbotina* spp., *Hantkenina* spp. and *Clavigerinella*); and a single subthermocline dweller, *Subbotina* aff. *inaequispira*, with the

TABLE 1. Species ordered by carbon isotopic ratios, in descending order.

HABITAT	SPECIES	$\delta^{13}\text{C}$	n
Mixed layer dwellers	<i>Morozovella crassata</i>	+3.39	2
	<i>Muricoglobigerina angulosa</i>	+3.35	29
	<i>Globigerinatheka index</i>	+3.29	35
	' <i>Morozovella</i> ' <i>broedermanni</i>	+3.22	9
	<i>Acarinina pseudotopilensis</i>	+3.18	51
	<i>Morozovella aragonensis</i>	+2.99	4
	<i>Acarinina triplex</i>	+2.95	18
	<i>Globigerinatheka subconglobata</i>	+2.95	3
	<i>Acarinina bullbrooki</i>	+2.70	25
	<i>Acarinina matthewsae</i>	+2.64	100
	<i>Muricoglobigerina esnehenensis</i>	+2.55	7
	<i>Guembelitrionides higginsii</i>	+2.28	28
Thermocline dwellers	<i>Muricoglobigerina senni</i>	+2.22	81
	<i>Subbotina linaperta</i>	+1.89	61
	<i>Hantkenina</i> spp.	+1.85	13
	<i>Subbotina frontosa</i>	+1.84	61
	<i>Clavigerinella eocanica</i>	+1.79	1
	<i>Subbotina eocaena</i>	+1.75	12
Sub-thermocline	<i>Subbotina</i> aff. <i>inaequispira</i>	+1.68	46

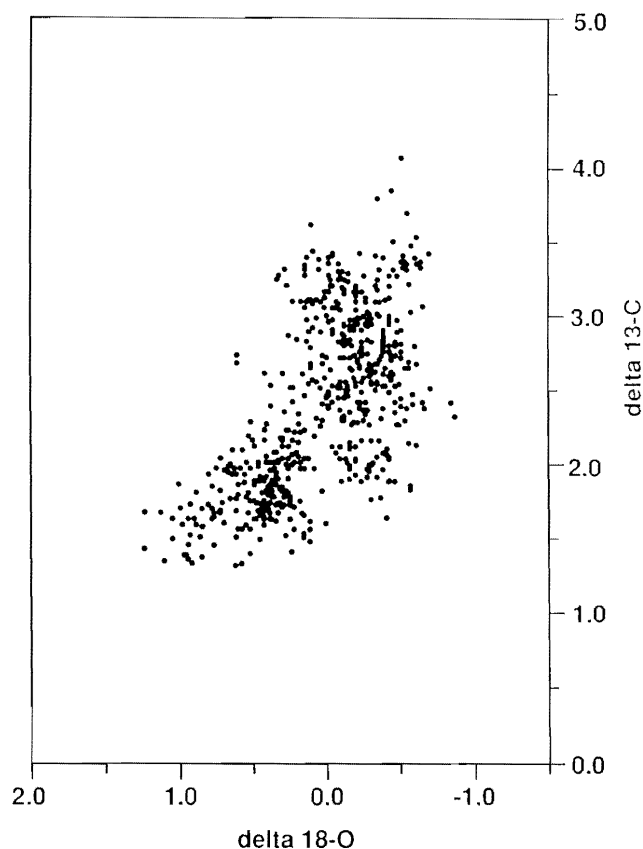


FIGURE 1. Carbon vs. oxygen isotopic ratios for all samples analysed in this study.

lightest carbon and heaviest oxygen ratios. This last species has a distinctive stratigraphic record (see below), including a dramatic carbon excursion not experienced by the other species, strongly suggesting that it calcified in a distinct water mass not inhabited by the other species.

DEPTH ORDERING

The relative depth habitats of those species which lived in the mixed layer are difficult to assess with confidence because of the assumptions involved. Oxygen isotopic ratios above the thermocline would be expected to be determined more by seasonal temperature variations than by depth (see below). Estimating an order on the basis of carbon isotopic ranking assumes no seasonal changes in light intensity or the carbon isotopic gradient of dissolved CO_2 . It also assumes that each of these morphotypes registered the same carbon isotopic vital response. However, in spite of these problems, workers on present-day communities have concluded that the depth order for carbon isotopes of large shells is approximately correct (Kahn 1979; Erez and Honjo, 1981).

The suggested depth order for the mixed layer dwellers therefore follows the carbon isotope ordering of Table 1. It is likely that the muricate species were stratified within the mixed layer, similar to modern *Globigerinoides* spp. *Muricoglobigerina angulosa* and *Morozovella crassata* give the heaviest $\delta^{13}\text{C}$ values, along with *Globigerinatheka* spp. and the *Acarinina pseudotopilensis* lineage, indicative of the

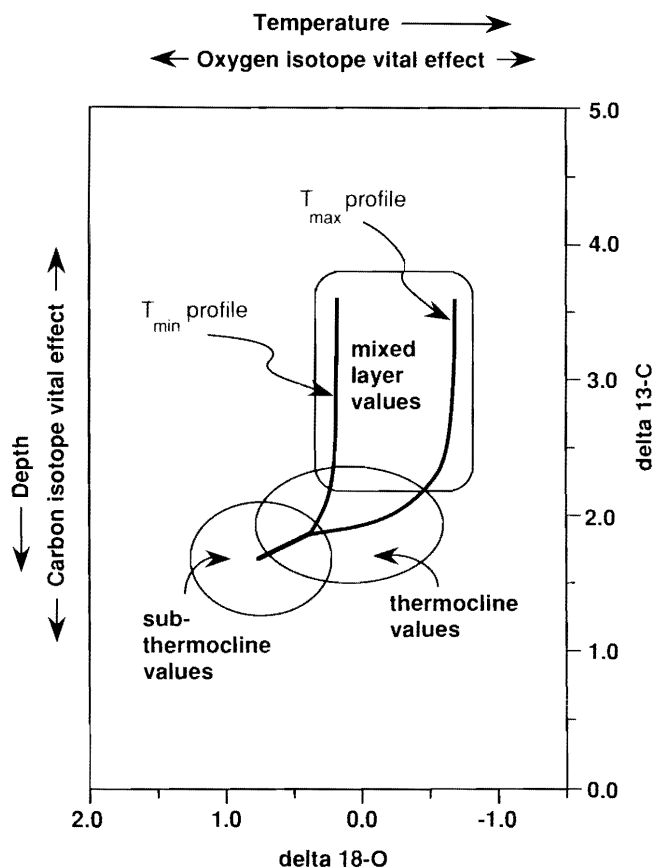


FIGURE 2. Model for the interpretation of the paleoecology of planktonic foraminifera from an open ocean site with year-round stable thermocline (modified from Spero and Williams 1989). See text for discussion.

shallowest water. *Acarinina matthewsae* and *A. bullbrooki* clearly give consistently lighter $\delta^{13}\text{C}$ values suggesting a slightly deeper habitat. Also occupying the mixed layer are *Morozovella aragonensis*, '*Morozovella*' *broedermanni*, *Muricoglobigerina senni* and *Muricoglobigerina esneensis* lineages. The *Muricoglobigerina senni* group seems to give anomalously light $\delta^{13}\text{C}$ values approaching typical subbotinid levels, although the oxygen isotope palaeotemperatures for this morphotype are among the highest. One possibility is that this species reached maturity just above the thermocline, exploiting a seasonal deep chlorophyll maximum.

Deep dwelling species of planktonic foraminifera typically sink while juveniles to their typical adult depth where most calcification occurs (Hemleben et al., 1989; Lohmann and Schweitzer, 1990; Lohmann, 1992). If the absence of symbiotic associations for the deeper dwelling community is assumed and seasonal temperature variations in this environment were negligible, both carbon and oxygen isotopes may be used to estimate relative depth at maturity (Tables 1 and 2). In fact, there is little systematic isotopic variation within the thermocline community. Clearly distinct from these, however, was *Subbotina* aff. *inaequispira* which, it is suggested, calcified in a distinct sub-thermocline water mass. (The apparent overlap of isotopic ratios between this species and the thermocline assemblage seen in Fig. 3 is mostly a function of stratigraphic variation, see Fig. 4).

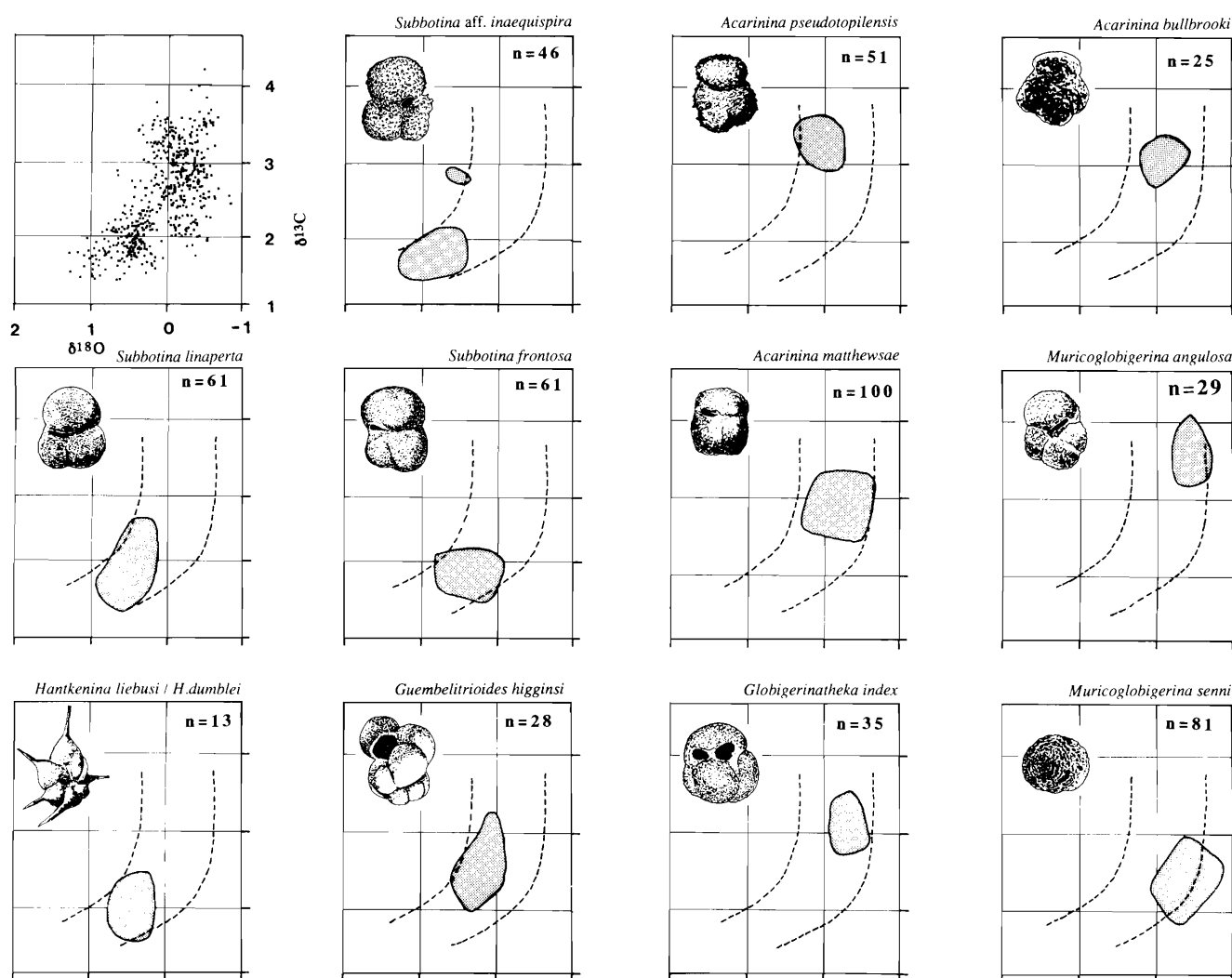


FIGURE 3. Carbon vs. oxygen plots for the most common species in this study. Inset: the complete data-set as Fig. 1. The fields given by each species are shaded and the number of analyses given. Three anomalous values for *Subbotina* aff. *inaequispira*, which record a transient carbon isotope excursion are outlined separately.

ORDERING BY SEASONAL ABUNDANCE

Modern planktonic foraminifera species have been known, since the study of Bé (1960), to peak in abundance at different times of the year. Most current knowledge is based on observations off Bermuda and in the Sargasso Sea (Tolderlund and Bé, 1971; Williams and others, 1981; Erez and Honjo, 1981; Hemleben and others, 1985; Deuser, 1987; Deuser and Ross, 1989). It seems from these studies that a particular assemblage of species is characteristic of the summer (*Globigerinoides ruber*, *G. quinquiloba* and *Neoglobobulimina pachyderma*) and another assemblage characterises the winter (*Globorotalia truncatulinoides*, *G. inflata*, *G. hirsuta* and *Globigerinella siphonifera*). Other species are present all year round. A seasonal succession also occurs at higher latitudes (Reynolds and Thunell, 1985; Sautter and Thunell, 1989).

Seasonal turnover of the Eocene fauna at Site 523 is indicated by the oxygen isotope palaeotemperature data for those taxa which are thought to have inhabited the mixed layer (Table 2). Maximum temperatures are given by the

Muricoglobigerina angulosa group and *M. senni*. Minimum temperatures are given by the *Acarinina pseudotopilensis* group, *Morozovella broedermanni* and *Guembeltrioides higginsii*. Other morphotypes give intermediate values. No obvious relationship between morphological features and seasonal preference is obvious in either modern or Eocene planktonic foraminiferal communities.

STRATIGRAPHY

Carbon and oxygen isotopic records through the section of nine of the better represented species are shown in Figure 4. Both long- and short-term trends in the data exist. As discussed in detail above, the morphotypes can be divided into three groups: (1) mixed layer dwellers (*Acarinina* spp. and *Muricoglobigerina senni* etc.), (2) thermocline dwellers (most of the subbotinids plus *Hantkenina* and *Clavigerinella*), and (3) a single sub-thermocline intermediate water dweller (*Subbotina* aff. *inaequispira*). Thus, the stratigraphic record of these forms may be used to assess how these three different environments varied in relation to one another.

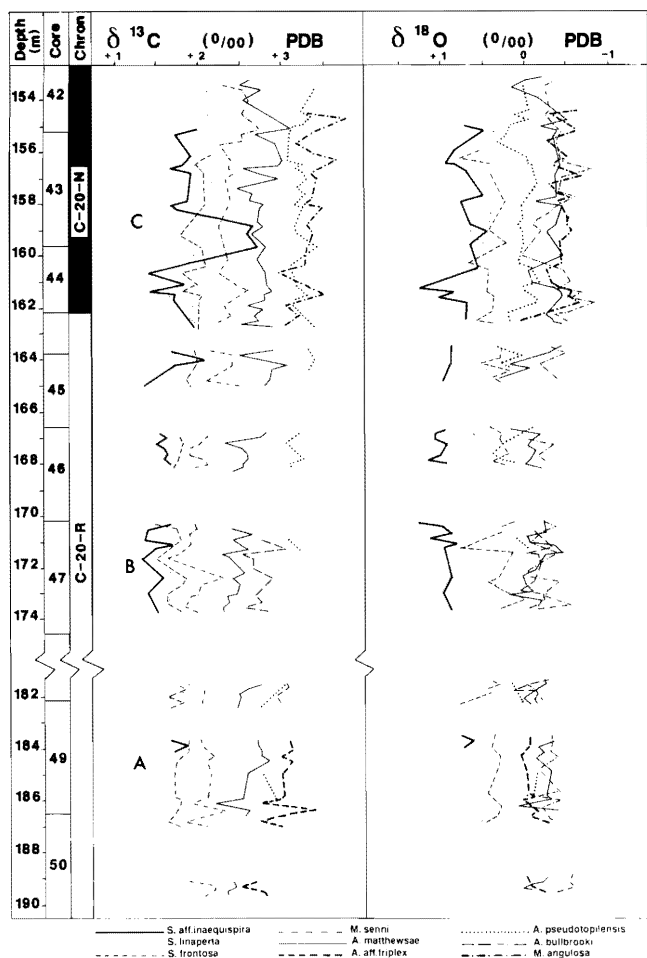


FIGURE 4. Carbon and oxygen stable isotope stratigraphy for various well-represented species from the section. Analyses were conducted on specimens of typical adult size in the $>250\ \mu\text{m}$ fraction. Gaps in the sequence result from poor preservation due to dissolution. The major gap between 174 and 182 m.b.s.f. was not recovered. Short-term carbon isotope excursions are indicated A–C (see text for discussion).

It is clear from the oxygen isotope record that either the thermal or productivity structure of the water column changed through time. The values given by the thermocline dwellers are fairly constant throughout the interval. The distinction of these forms from a typical mixed layer value decreased gradually from an initial $\Delta\delta^{13}\text{C}$ of nearly 1‰, until the interval of Cores 45 and 46 where it was no more than 0.3‰, and then the difference increased again up section. However, the distinction of the thermocline community from the sub-thermocline dweller shows the opposite trend: being negligible in Core 49, rising to 0.6‰ in cores 45 and 46, then decreasing again. One interpretation of this pattern is that the overall temperature gradient through the water column remained constant during the interval, but the thermocline shallowed gradually and then deepened.

The carbon isotope record shows a gradual enrichment in ^{13}C from Core 47 up, and is shown by all species. The most obvious feature is the dramatic short-lived excursion of about +1.0‰ between 158 and 161 m in the record of the deepest dweller, *S. aff. inaequispira* (marked C in Fig. 4; see also Oberhansli and others, 1984). It is not seen in the records of the other species, suggesting that it represents a

transient change in the provenance of intermediate water. At this time the oxygen isotopic difference between this species and the other subbotinids disappears. The excursion spans three samples and therefore lasts in the order of 100,000 years. The reasons for the excursion are still obscure and its potential as a stratigraphic correlation tool remains to be investigated.

ONTOGENETIC EFFECTS

If isotopic ratios are found to change significantly with size fraction, two separate classes of explanation may account for the pattern: (1) changes in depth habitat during ontogeny and (2) changes in the degree of isotopic disequilibrium (the vital effect) with age.

The analyses presented so far have all been conducted on multi-specimen samples of typical adult size greater than $250\ \mu\text{m}$ diameter. It should be remembered that different individuals of the same species may in fact live over a considerable depth range (Killingley and others, 1981) and that the analysis for each individual represents the cumulative record of calcification through life. Species may change their depth habitat daily (Holmes, 1982) or systematically through their life cycle. Emiliani (1971) analysed the oxygen isotopic composition of several modern species in different size fractions and interpreted the results as evidence of gradual sinking in some species of *Globorotalia*, whereas other species registered little or no significant change in their oxygen isotopic ratios with size. Berger and others (1978) showed that for most species the change in $\delta^{18}\text{O}$ was small, in the order of 0.5‰, generally becoming isotopically heavier with size. A further consideration is that for many species, both spinose and non-spinose, calcification is accelerated in the final stages of the life cycle at depth, associated with gametogenesis (Bé and Hemleben, 1970; Hemleben and others, 1985; Lohmann and Schweitzer, 1990). Such late stage calcification may involve the addition of new chambers or bullae, or the deposition of a calcite crust over the entire test. Consequently, sedimented shells tend to give heavier $\delta^{18}\text{O}$ than their counterparts from plankton tows (Duplessey and others, 1981; Bouvier-Soumagnac and Duplessey, 1985).

If ontogenetic depth changes are to be documented, it must be assumed that isotopic equilibrium is maintained throughout growth, or at least that any disequilibrium effect is constant. However, Kahn (1979) records a deviation from oxygen isotopic equilibrium of -0.57‰ for smaller tests of modern *Globigerinella aequilateralis* (= *G. siphonifera*), whereas larger tests are very close to equilibrium. Such an effect would mimic gradual sinking. This result contrasts with the study of Williams and others (1981) in which small tests of the same species from the Sargasso Sea were found to be in approximate equilibrium, whereas larger tests were slightly isotopically lighter.

Carbon isotopes seem more affected by vital effects. Berger and others (1978) reported that $\delta^{13}\text{C}$ of several modern species increased with size by as much as +2‰. At face value, such a result would indicate a shallowing during life and conflict with the oxygen isotopic evidence. However, these authors concluded that the deviation was a measure of metabolic vigour, and consequently of growth rate.

Other studies which have confirmed the general pattern of $\delta^{13}\text{C}$ increase with ontogeny are those of Erez and Honjo (1981), Kahn and Williams (1981), Bouvier-Soumagnac and Duplessey (1985) and Zimmermann and others (1987). It seems from the amassed data of these authors that ontogenetic $\delta^{13}\text{C}$ change is most pronounced in symbiont-bearing species such as *Globigerinoides ruber*, *G. sacculifer* and *Orbulina universa*, although examples do exist for species classified as symbiotic, facultatively symbiotic and symbiont barren by Hemleben and others (1989).

Carbon and oxygen stable isotope data of different species through the size range 125–530 μm are presented in Figure 5 and Appendix 2. Size fractions smaller than 125 μm were not analysed due to poor preservation resulting from strong dissolution of fine particles. These analyses have been conducted on several samples throughout the section. No significant change in $\delta^{18}\text{O}$ for any of the morphotypes is seen through the range examined. However, a clear pattern emerges from the carbon isotopes. All the muricate species analysed record large changes in $\delta^{13}\text{C}$ of around +2.0‰, whereas the subbotinids show no such deviation. This result accords with the study of Shackleton and others (1985) on the Palaeocene, who, in addition, found that several different morozovellid taxa also showed major $\delta^{13}\text{C}$ changes with size. Shackleton and others (1985) interpreted the result mainly in terms of changing depth

habitat with ontogeny. Here it is suggested that it is more likely a vital effect, as was argued by Berger and others (1978) for Recent species.

An intriguing possibility is that a large ontogenetic variation in the carbon isotopic ratios is a fingerprint of a host-symbiont metabolism. This might apply to ancient and modern planktonic foraminifera. If this is so, it would indicate that the muricate genera *Acarinina*, *Morozovella* and *Muricoglobigerina* lived in association with symbionts, but that the globular subbotinids did not.

DISCUSSION: THE PROBLEM OF HOMEOMORPHY

The deep water habitat for *Subbotina*, as first discussed by Boersma and others (1979), has been corroborated in this study. All subbotinids which were tested, excepting one, were found to have isotopic ratios indicative of a thermocline habitat. The exception was *S. aff. inaequispira*, which the isotopic evidence suggests lived even deeper in a distinct water mass below the thermocline. Thus it appears that by the middle Eocene the globular subbotinids had diversified into the deeper water environments while the keeled and angular forms (*Morozovella*, *Acarinina*) inhabited the mixed layer. The clash between the isotopic evidence and the uniformitarian argument for determining depth habitat by analogy with modern homeomorphs is evident.

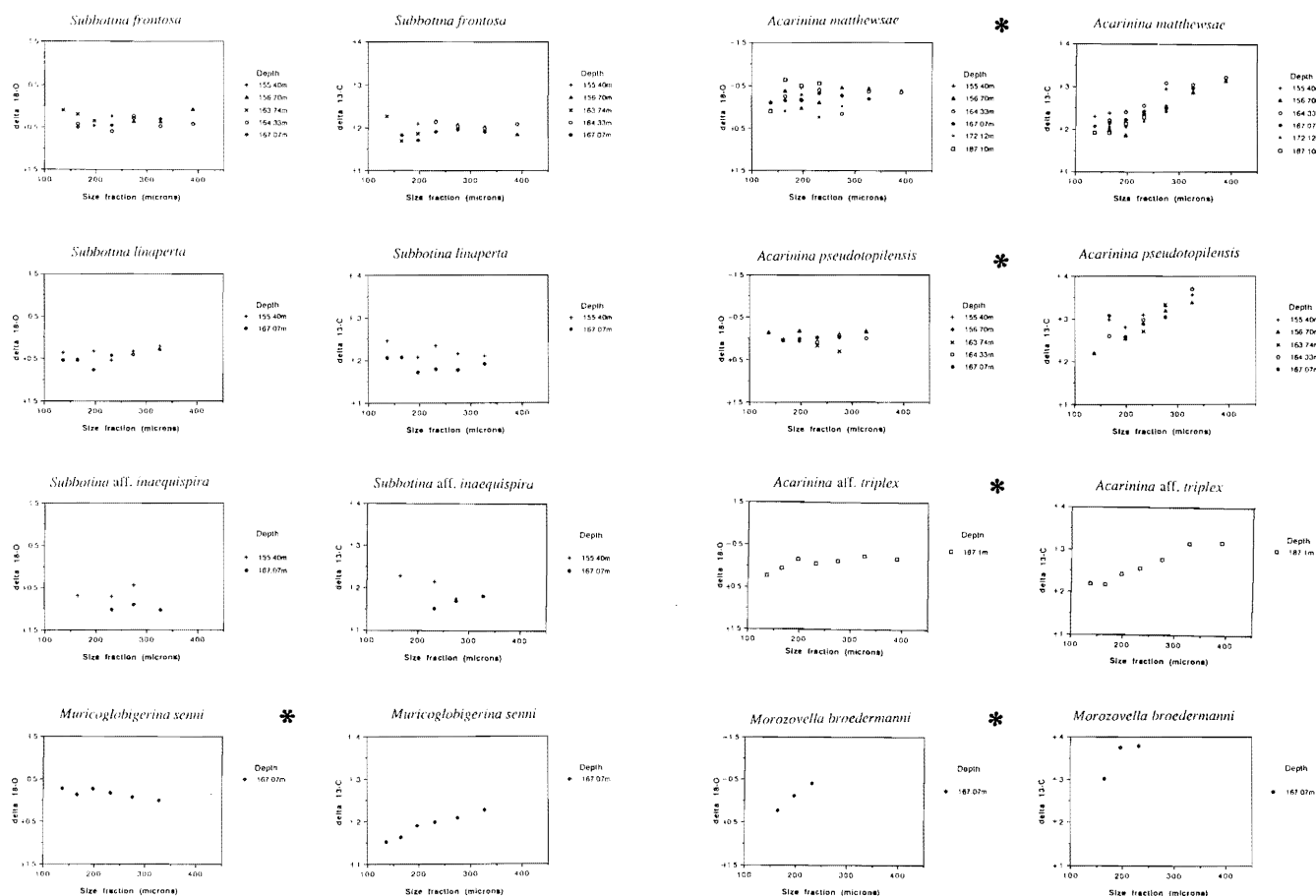


FIGURE 5. Carbon and oxygen isotopic ratios for different size fractions of selected species. Samples were selected from seven of the best preserved samples distributed through the sequence. Species which are interpreted as mixed-layer dwellers (Fig. 3) are marked with asterisks. These show a trend of increasing $\delta^{13}\text{C}$ with size fraction.

It is important, however, that the degree of homeomorphy should not be overstated. While certain morphologies 'match' well between Palaeogene and Recent faunas, other comparisons are less obvious. Furthermore, the isotopic evidence for some 'homeomorphs' does indeed suggest similar depth habitats. Investigations by Poore and Matthews (1984), Keigwin and Corliss (1986), Boersma and Premoli Silva (1989) and others have shown that the biserial heterohelics give isotopic ratios indicative of a thermocline environment throughout their range from the Cretaceous to Recent. The Eocene planispiral clavate form *Clavigerinella eocanica* is a deep dweller (this study) like modern *Hastigerina digitata*. Eocene *Globigerinatheka* compares favourably in terms of its 'isotopic niche' with the modern spherical form *Orbulina*, although it is doubtful if these can indeed be regarded as good homeomorphs. Lastly *Guembeliitrioides higginsi* is here shown to be a mixed layer dweller like modern *Globigerinoides*, which it closely resembles.

The root of the problem is with the compressed and keeled forms and the globular subbotinids which are analogous to the modern globigeriniform species not only in terms of their general shape, but also in their spinose wall texture. The radially directed spines in *Globigerina* support a frothy external cytoplasm, providing an ideal environment for photosynthesising symbionts. However, it was inferred from the carbon isotope data that all of the subbotinid species studied had a relatively simple carbon metabolism, suggesting that they had not evolved a symbiotic association (see above). This is possible: it should be remembered that *Globigerina bulloides*, a typical modern globular spinose species, is symbiont barren.

Perhaps the real uniformitarian argument should be that those species which have evolved an association with symbionts have become adapted to the shallow water oligotrophic environments, whereas those without symbionts are less likely to be successful in this zone. In the Paleogene it seems that *Acarinina* and *Morozovella* could have possessed symbionts on account of their large ontogenetic change in $\delta^{13}\text{C}$. Unlike modern *Globorotalia*, these forms have a rough (muricate) wall texture which may have regulated external cytoplasm flow. They also have isotopic ratios indicative of a shallow mixed layer environment. Thus it may be that the evolution of symbiosis is the major driving force of Globigerinacean evolutionary ecology, as has been argued for the evolution of benthic foraminifera and hermatypic corals (Lee and others, 1979; Goreau, 1977).

If this is the case, then the problem of heterochronous morphological convergence still remains an enigma. However, it is important to consider the historical constraints that phylogeny may place on adaptation, and also aspects of the microenvironment of the foraminiferal test.

Throughout the Cenozoic it seems that there has always been a large, very variable plexus of globigeriniform morphotypes from which more specialised, better defined lineages have evolved. The globigeriniform plexus undoubtedly has a very complicated evolutionary history spanning the principal genera *Eoglobigerina*, *Subbotina*, *Catapsydrax* and *Globigerina*. The details of this history are poorly understood due to extreme taxonomic difficulties associated with the general lack of characters in these forms. Never-

theless, isotopic evidence indicates that after the extinction of virtually all the specialised Paleogene lineages which previously dominated the mixed layer, the globigeriniform group opportunistically invaded the whole range of depth habitats (Poore and Matthews, 1984; Keigwin and Corliss, 1986; Corfield and Cartledge, 1991). It is probable that some shallow dwelling species evolved symbiotic associations at this time, and it may be that such a species was the ancestor of modern *Globigerina*. When more specialised globorotaliid forms evolved once again in the Miocene, they probably lacked symbionts and were able to compete more successfully in the deeper water thermocline and sub-thermocline habitats.

If the above scenario is true, then it follows that the morphogenetic pathways in the evolution of the globorotaliid test have little to do with the macroenvironment of the animal, or indeed the presence or lack of symbionts. Perhaps, then, the repeated trend towards compression of the test is related to optimising internal functions and processes such as protection of the nucleus, the regulation of internal cytoplasm flow, the compartmentalisation of vital functions, or the maintenance of chemical balances between the inorganic and organic components of the organism. Such strategies might be adopted regardless of external conditions.

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APPENDIX 1. Continued.

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APPENDIX 1

ISOTOPE DATA FOR FIGS. 1 AND 3.

Species	Depth (m.b.s.f.)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Acarinina bullbrooki</i>	167.27	-0.19	2.70
<i>Acarinina bullbrooki</i>	170.80	-0.12	3.24
<i>Acarinina bullbrooki</i>	171.01	-0.20	2.76
<i>Acarinina bullbrooki</i>	171.38	-0.33	3.03
<i>Acarinina bullbrooki</i>	171.58	-0.02	2.53
<i>Acarinina bullbrooki</i>	171.70	-0.15	2.64
<i>Acarinina bullbrooki</i>	172.10	-0.20	2.67
<i>Acarinina bullbrooki</i>	172.51	0.07	2.90
<i>Acarinina bullbrooki</i>	172.72	-0.09	2.81
<i>Acarinina bullbrooki</i>	173.08	0.05	2.68
<i>Acarinina bullbrooki</i>	173.20	-0.19	2.71
<i>Acarinina bullbrooki</i>	173.44	-0.21	2.75
<i>Acarinina bullbrooki</i>	173.60	-0.11	2.56
<i>Acarinina bullbrooki</i>	173.80	-0.09	2.86
<i>Acarinina bullbrooki</i>	181.64	-0.26	3.04
<i>Acarinina bullbrooki</i>	181.80	-0.02	3.06
<i>Acarinina bullbrooki</i>	182.00	0.15	2.90
<i>Acarinina bullbrooki</i>	182.10	-0.13	2.91
<i>Acarinina bullbrooki</i>	182.32	-0.09	2.96
<i>Acarinina bullbrooki</i>	182.52	-0.13	2.73
<i>Acarinina bullbrooki</i>	184.20	-0.41	3.01
<i>Acarinina bullbrooki</i>	189.58	-0.17	2.54
<i>Acarinina matthewsae</i>	139.60	-0.32	2.55
<i>Acarinina matthewsae</i>	140.00	0.15	2.55
<i>Acarinina matthewsae</i>	140.90	-0.13	2.66
<i>Acarinina matthewsae</i>	141.70	0.13	2.69

Species	Depth (m.b.s.f.)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Acarinina matthewsae</i>	141.90	0.07	2.52
<i>Acarinina matthewsae</i>	142.10	0.09	2.56
<i>Acarinina matthewsae</i>	145.10	0.33	2.61
<i>Acarinina matthewsae</i>	152.20	-0.22	2.56
<i>Acarinina matthewsae</i>	152.60	0.04	2.59
<i>Acarinina matthewsae</i>	153.30	-0.27	2.65
<i>Acarinina matthewsae</i>	153.50	-0.01	2.53
<i>Acarinina matthewsae</i>	153.70	0.13	2.79
<i>Acarinina matthewsae</i>	154.10	-0.18	2.56
<i>Acarinina matthewsae</i>	155.00	-0.55	3.04
<i>Acarinina matthewsae</i>	155.20	-0.24	3.14
<i>Acarinina matthewsae</i>	155.40	-0.42	2.71
<i>Acarinina matthewsae</i>	155.64	-0.38	3.12
<i>Acarinina matthewsae</i>	155.80	-0.28	2.96
<i>Acarinina matthewsae</i>	156.43	-0.27	3.03
<i>Acarinina matthewsae</i>	156.63	-0.46	2.98
<i>Acarinina matthewsae</i>	156.70	-0.47	2.55
<i>Acarinina matthewsae</i>	156.92	-0.45	2.74
<i>Acarinina matthewsae</i>	157.11	-0.40	2.99
<i>Acarinina matthewsae</i>	157.47	-0.41	2.49
<i>Acarinina matthewsae</i>	157.70	-0.38	2.66
<i>Acarinina matthewsae</i>	157.93	-0.42	2.63
<i>Acarinina matthewsae</i>	158.13	-0.15	2.81
<i>Acarinina matthewsae</i>	158.24	-0.49	2.77
<i>Acarinina matthewsae</i>	158.81	-0.42	2.74
<i>Acarinina matthewsae</i>	158.98	-0.40	2.81
<i>Acarinina matthewsae</i>	159.22	-0.29	2.67
<i>Acarinina matthewsae</i>	159.74	-0.36	2.83
<i>Acarinina matthewsae</i>	160.50	-0.49	2.73
<i>Acarinina matthewsae</i>	160.71	-0.08	2.82
<i>Acarinina matthewsae</i>	161.22	-0.13	2.85
<i>Acarinina matthewsae</i>	161.44	-0.37	2.89
<i>Acarinina matthewsae</i>	161.59	-0.45	2.81
<i>Acarinina matthewsae</i>	161.80	-0.48	2.82
<i>Acarinina matthewsae</i>	162.02	-0.43	2.61
<i>Acarinina matthewsae</i>	162.20	-0.37	2.79
<i>Acarinina matthewsae</i>	162.39	-0.27	2.68
<i>Acarinina matthewsae</i>	162.40	-0.31	2.69
<i>Acarinina matthewsae</i>	162.63	-0.35	2.74
<i>Acarinina matthewsae</i>	162.70	-0.38	2.53
<i>Acarinina matthewsae</i>	162.83	-0.49	2.92
<i>Acarinina matthewsae</i>	163.74	-0.46	2.90
<i>Acarinina matthewsae</i>	163.92	-0.31	2.51
<i>Acarinina matthewsae</i>	164.12	-0.12	2.84
<i>Acarinina matthewsae</i>	164.33	0.16	3.10
<i>Acarinina matthewsae</i>	164.49	-0.08	2.89
<i>Acarinina matthewsae</i>	164.68	0.12	3.09
<i>Acarinina matthewsae</i>	164.88	0.29	2.88
<i>Acarinina matthewsae</i>	165.08	-0.46	2.82
<i>Acarinina matthewsae</i>	166.87	0.16	2.83
<i>Acarinina matthewsae</i>	167.07	-0.22	2.74
<i>Acarinina matthewsae</i>	167.27	-0.10	2.33
<i>Acarinina matthewsae</i>	167.47	-0.07	2.52
<i>Acarinina matthewsae</i>	167.67	-0.16	2.59
<i>Acarinina matthewsae</i>	167.88	0.19	2.61
<i>Acarinina matthewsae</i>	168.08	-0.05	2.54
<i>Acarinina matthewsae</i>	168.20	-0.02	2.54
<i>Acarinina matthewsae</i>	168.38	-0.24	2.42
<i>Acarinina matthewsae</i>	169.70	-0.12	2.47
<i>Acarinina matthewsae</i>	170.40	-0.24	2.34
<i>Acarinina matthewsae</i>	170.60	-0.37	2.39
<i>Acarinina matthewsae</i>	170.80	-0.26	2.64
<i>Acarinina matthewsae</i>	171.01	-0.01	2.42
<i>Acarinina matthewsae</i>	171.22	-0.05	2.52
<i>Acarinina matthewsae</i>	171.38	-0.36	2.61
<i>Acarinina matthewsae</i>	171.58	-0.46	2.28
<i>Acarinina matthewsae</i>	171.70	-0.23	2.37
<i>Acarinina matthewsae</i>	172.30	-0.07	2.56
<i>Acarinina matthewsae</i>	172.51	0.05	2.41
<i>Acarinina matthewsae</i>	172.72	0.01	2.49

APPENDIX 1. Continued.

APPENDIX 1. Continued.

Species	Depth (m.b.s.f.)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Acarinina matthewsae</i>	173.08	-0.09	2.45
<i>Acarinina matthewsae</i>	173.20	0.21	2.34
<i>Acarinina matthewsae</i>	173.44	-0.24	2.37
<i>Acarinina matthewsae</i>	173.60	-0.16	2.29
<i>Acarinina matthewsae</i>	173.80	-0.09	2.30
<i>Acarinina matthewsae</i>	181.64	-0.23	2.75
<i>Acarinina matthewsae</i>	181.80	-0.23	2.59
<i>Acarinina matthewsae</i>	182.00	-0.11	2.47
<i>Acarinina matthewsae</i>	182.10	-0.11	2.48
<i>Acarinina matthewsae</i>	182.32	0.01	2.47
<i>Acarinina matthewsae</i>	182.52	-0.05	2.45
<i>Acarinina matthewsae</i>	183.80	-0.27	2.68
<i>Acarinina matthewsae</i>	183.98	-0.33	2.69
<i>Acarinina matthewsae</i>	184.20	-0.14	2.73
<i>Acarinina matthewsae</i>	184.41	-0.21	2.74
<i>Acarinina matthewsae</i>	184.60	-0.11	2.82
<i>Acarinina matthewsae</i>	185.10	-0.29	2.55
<i>Acarinina matthewsae</i>	185.96	-0.12	2.53
<i>Acarinina matthewsae</i>	186.07	-0.21	2.49
<i>Acarinina matthewsae</i>	186.22	-0.28	2.71
<i>Acarinina matthewsae</i>	186.50	0.12	2.57
<i>Acarinina matthewsae</i>	186.70	-0.36	2.53
<i>Acarinina matthewsae</i>	189.22	-0.25	2.37
<i>Acarinina matthewsae</i>	189.42	-0.20	2.42
<i>Acarinina matthewsae</i>	189.58	0.06	2.30
<i>Acarinina matthewsae</i>	189.72	-0.08	2.31
<i>Acarinina pseudotopilensis</i>	157.70	-0.12	3.30
<i>Acarinina pseudotopilensis</i>	157.93	-0.05	3.25
<i>Acarinina pseudotopilensis</i>	158.13	-0.17	3.19
<i>Acarinina pseudotopilensis</i>	158.24	0.02	3.29
<i>Acarinina pseudotopilensis</i>	158.81	0.01	3.37
<i>Acarinina pseudotopilensis</i>	159.22	0.00	3.21
<i>Acarinina pseudotopilensis</i>	159.74	-0.01	3.43
<i>Acarinina pseudotopilensis</i>	159.98	0.04	3.18
<i>Acarinina pseudotopilensis</i>	160.50	0.04	3.13
<i>Acarinina pseudotopilensis</i>	160.71	-0.10	3.16
<i>Acarinina pseudotopilensis</i>	161.22	-0.17	3.20
<i>Acarinina pseudotopilensis</i>	161.44	0.00	3.26
<i>Acarinina pseudotopilensis</i>	161.59	-0.05	3.31
<i>Acarinina pseudotopilensis</i>	161.80	-0.16	3.18
<i>Acarinina pseudotopilensis</i>	162.02	-0.17	3.15
<i>Acarinina pseudotopilensis</i>	162.39	0.18	3.28
<i>Acarinina pseudotopilensis</i>	162.40	-0.23	3.28
<i>Acarinina pseudotopilensis</i>	162.83	0.16	3.40
<i>Acarinina pseudotopilensis</i>	163.74	0.31	3.33
<i>Acarinina pseudotopilensis</i>	164.12	0.02	3.41
<i>Acarinina pseudotopilensis</i>	164.33	0.23	2.85
<i>Acarinina pseudotopilensis</i>	164.49	0.17	3.35
<i>Acarinina pseudotopilensis</i>	164.68	0.12	3.09
<i>Acarinina pseudotopilensis</i>	166.87	-0.12	3.24
<i>Acarinina pseudotopilensis</i>	167.27	0.18	3.06
<i>Acarinina pseudotopilensis</i>	167.88	0.36	3.26
<i>Acarinina pseudotopilensis</i>	168.08	0.25	3.11
<i>Acarinina pseudotopilensis</i>	168.20	0.10	3.12
<i>Acarinina pseudotopilensis</i>	171.01	0.12	3.09
<i>Acarinina pseudotopilensis</i>	171.38	-0.02	3.21
<i>Acarinina pseudotopilensis</i>	173.80	0.10	3.00
<i>Acarinina pseudotopilensis</i>	181.80	0.16	2.98
<i>Acarinina pseudotopilensis</i>	182.52	0.03	2.72
<i>Acarinina pseudotopilensis</i>	185.10	-0.16	2.74
<i>Acarinina pseudotopilensis</i>	185.96	-0.09	2.88
<i>Acarinina pseudotopilensis</i>	186.07	-0.01	2.91
' <i>Morozovella</i> ' <i>broedermanni</i>	157.93	-0.49	4.07
' <i>Morozovella</i> ' <i>broedermanni</i>	166.87	0.13	3.63
' <i>Morozovella</i> ' <i>broedermanni</i>	171.22	0.12	3.45
' <i>Morozovella</i> ' <i>broedermanni</i>	171.38	-0.10	2.95
' <i>Morozovella</i> ' <i>broedermanni</i>	172.30	-0.25	2.96
' <i>Morozovella</i> ' <i>broedermanni</i>	172.51	-0.07	3.05
' <i>Morozovella</i> ' <i>broedermanni</i>	172.72	-0.37	2.86

Species	Depth (m.b.s.f.)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
' <i>Morozovella</i> ' <i>broedermanni</i>	173.08	-0.20	2.66
' <i>Morozovella</i> ' <i>broedermanni</i>	173.80	0.08	3.33
<i>Morozovella crassata</i>	159.74	-0.42	3.86
<i>Morozovella crassata</i>	171.22	0.12	2.93
<i>Morozovella aragonensis</i>	183.80	-0.19	3.00
<i>Morozovella aragonensis</i>	183.98	-0.17	3.05
<i>Morozovella aragonensis</i>	184.20	-0.18	3.16
<i>Morozovella aragonensis</i>	186.91	-0.22	2.75
<i>Muricoglob. esnehensis</i>	171.01	-0.06	2.84
<i>Muricoglob. esnehensis</i>	171.70	-0.14	2.36
<i>Muricoglob. esnehensis</i>	172.30	-0.11	2.51
<i>Muricoglob. esnehensis</i>	172.51	0.03	2.46
<i>Muricoglob. esnehensis</i>	181.64	-0.60	2.69
<i>Muricoglob. esnehensis</i>	182.52	-0.12	2.83
<i>Muricoglob. esnehensis</i>	186.91	-0.14	2.15
<i>Muricoglobigerina angulosa</i>	147.10	0.04	3.07
<i>Muricoglobigerina angulosa</i>	154.60	-0.62	3.34
<i>Muricoglobigerina angulosa</i>	154.80	-0.32	3.80
<i>Muricoglobigerina angulosa</i>	155.20	-0.59	3.54
<i>Muricoglobigerina angulosa</i>	155.40	-0.62	3.38
<i>Muricoglobigerina angulosa</i>	155.80	-0.31	3.22
<i>Muricoglobigerina angulosa</i>	156.20	-0.20	3.43
<i>Muricoglobigerina angulosa</i>	156.43	-0.53	3.70
<i>Muricoglobigerina angulosa</i>	156.70	-0.34	3.10
<i>Muricoglobigerina angulosa</i>	156.92	-0.49	3.38
<i>Muricoglobigerina angulosa</i>	157.11	-0.68	3.44
<i>Muricoglobigerina angulosa</i>	157.47	-0.31	3.42
<i>Muricoglobigerina angulosa</i>	157.70	-0.37	3.40
<i>Muricoglobigerina angulosa</i>	157.93	-0.59	3.37
<i>Muricoglobigerina angulosa</i>	158.13	-0.40	3.28
<i>Muricoglobigerina angulosa</i>	158.24	-0.43	3.51
<i>Muricoglobigerina angulosa</i>	158.81	-0.53	3.36
<i>Muricoglobigerina angulosa</i>	158.98	-0.50	3.34
<i>Muricoglobigerina angulosa</i>	159.22	-0.58	3.40
<i>Muricoglobigerina angulosa</i>	159.74	-0.43	3.33
<i>Muricoglobigerina angulosa</i>	160.50	-0.46	3.28
<i>Muricoglobigerina angulosa</i>	160.71	-0.26	2.98
<i>Muricoglobigerina angulosa</i>	161.22	-0.33	3.25
<i>Muricoglobigerina angulosa</i>	161.44	-0.50	3.42
<i>Muricoglobigerina angulosa</i>	161.59	-0.56	3.49
<i>Muricoglobigerina angulosa</i>	161.80	-0.53	3.32
<i>Muricoglobigerina angulosa</i>	162.02	-0.64	3.08
<i>Muricoglobigerina angulosa</i>	162.20	-0.54	3.23
<i>Muricoglobigerina angulosa</i>	162.39	-0.40	3.21
<i>Muricoglobigerina angulosa</i>	162.70	0.04	3.07
<i>Muricoglobigerina senni</i>	153.50	-0.35	2.32
<i>Muricoglobigerina senni</i>	153.70	-0.28	2.56
<i>Muricoglobigerina senni</i>	154.10	-0.30	2.63
<i>Muricoglobigerina senni</i>	154.60	-0.32	2.56
<i>Muricoglobigerina senni</i>	154.80	-0.28	2.61
<i>Muricoglobigerina senni</i>	155.00	-0.34	2.71
<i>Muricoglobigerina senni</i>	155.20	-0.26	2.75
<i>Muricoglobigerina senni</i>	155.40	-0.44	2.54
<i>Muricoglobigerina senni</i>	155.64	-0.42	2.58
<i>Muricoglobigerina senni</i>	155.80	-0.27	2.28
<i>Muricoglobigerina senni</i>	156.20	-0.20	2.38
<i>Muricoglobigerina senni</i>	156.43	-0.45	2.42
<i>Muricoglobigerina senni</i>	156.63	-0.54	2.70
<i>Muricoglobigerina senni</i>	156.70	-0.65	2.39
<i>Muricoglobigerina senni</i>	156.92	-0.83	2.43
<i>Muricoglobigerina senni</i>	157.11	-0.45	2.36
<i>Muricoglobigerina senni</i>	157.70	-0.42	2.59
<i>Muricoglobigerina senni</i>	157.93	-0.64	2.42
<i>Muricoglobigerina senni</i>	158.13	-0.49	2.45
<i>Muricoglobigerina senni</i>	158.81	-0.19	2.42
<i>Muricoglobigerina senni</i>	158.98	-0.15	2.27
<i>Muricoglobigerina senni</i>	159.22	-0.23	2.30
<i>Muricoglobigerina senni</i>	159.74	-0.36	2.82

APPENDIX 1. Continued.

Species	Depth (m.b.s.f.)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Muricoglobigerina senni</i>	160.20	0.02	2.38
<i>Muricoglobigerina senni</i>	160.71	-0.47	2.27
<i>Muricoglobigerina senni</i>	161.22	-0.57	2.48
<i>Muricoglobigerina senni</i>	161.44	-0.41	2.60
<i>Muricoglobigerina senni</i>	161.59	-0.69	2.52
<i>Muricoglobigerina senni</i>	161.80	-0.57	2.41
<i>Muricoglobigerina senni</i>	162.02	-0.85	2.33
<i>Muricoglobigerina senni</i>	162.39	-0.49	2.40
<i>Muricoglobigerina senni</i>	162.40	-0.37	2.78
<i>Muricoglobigerina senni</i>	162.63	0.07	2.26
<i>Muricoglobigerina senni</i>	162.70	-0.51	2.30
<i>Muricoglobigerina senni</i>	163.74	-0.34	2.16
<i>Muricoglobigerina senni</i>	163.92	-0.53	2.39
<i>Muricoglobigerina senni</i>	164.33	-0.20	2.41
<i>Muricoglobigerina senni</i>	164.88	-0.39	2.11
<i>Muricoglobigerina senni</i>	165.08	-0.45	2.54
<i>Muricoglobigerina senni</i>	166.87	-0.22	2.16
<i>Muricoglobigerina senni</i>	167.07	-0.13	2.11
<i>Muricoglobigerina senni</i>	167.27	-0.07	2.04
<i>Muricoglobigerina senni</i>	167.47	-0.33	1.92
<i>Muricoglobigerina senni</i>	167.67	-0.13	1.91
<i>Muricoglobigerina senni</i>	167.87	-0.18	2.04
<i>Muricoglobigerina senni</i>	168.08	-0.02	2.12
<i>Muricoglobigerina senni</i>	168.20	-0.27	1.96
<i>Muricoglobigerina senni</i>	170.40	-0.27	1.96
<i>Muricoglobigerina senni</i>	170.60	-0.37	1.98
<i>Muricoglobigerina senni</i>	170.80	-0.21	1.90
<i>Muricoglobigerina senni</i>	171.10	-0.39	1.65
<i>Muricoglobigerina senni</i>	171.22	-0.08	1.90
<i>Muricoglobigerina senni</i>	171.38	-0.26	1.98
<i>Muricoglobigerina senni</i>	171.59	-0.35	1.78
<i>Muricoglobigerina senni</i>	172.10	-0.18	1.93
<i>Muricoglobigerina senni</i>	172.30	-0.04	2.08
<i>Muricoglobigerina senni</i>	172.51	-0.08	2.30
<i>Muricoglobigerina senni</i>	172.72	-0.41	2.04
<i>Muricoglobigerina senni</i>	173.08	-0.27	2.00
<i>Muricoglobigerina senni</i>	173.20	-0.26	1.92
<i>Muricoglobigerina senni</i>	173.44	-0.41	1.89
<i>Muricoglobigerina senni</i>	173.60	-0.55	1.84
<i>Muricoglobigerina senni</i>	173.80	-0.13	1.97
<i>Muricoglobigerina senni</i>	182.00	-0.11	2.04
<i>Muricoglobigerina senni</i>	182.32	-0.17	2.03
<i>Muricoglobigerina senni</i>	183.80	-0.29	2.00
<i>Muricoglobigerina senni</i>	183.98	-0.30	2.01
<i>Muricoglobigerina senni</i>	184.41	-0.29	2.16
<i>Muricoglobigerina senni</i>	184.60	-0.36	2.08
<i>Muricoglobigerina senni</i>	185.10	-0.18	2.13
<i>Muricoglobigerina senni</i>	185.96	-0.39	2.07
<i>Muricoglobigerina senni</i>	186.07	-0.13	2.00
<i>Muricoglobigerina senni</i>	186.22	-0.44	1.90
<i>Muricoglobigerina senni</i>	186.50	-0.19	2.29
<i>Muricoglobigerina senni</i>	186.91	-0.28	1.77
<i>Muricoglobigerina senni</i>	187.10	-0.33	2.06
<i>Muricoglobigerina senni</i>	189.22	-0.55	1.86
<i>Muricoglobigerina senni</i>	189.42	-0.54	2.15
<i>Muricoglobigerina senni</i>	189.58	-0.59	2.14
<i>Muricoglobigerina senni</i>	189.72	-0.41	2.06
<i>Globigerinatheka index</i>	156.20	-0.17	3.10
<i>Globigerinatheka index</i>	156.43	-0.26	2.85
<i>Globigerinatheka index</i>	156.63	-0.16	2.92
<i>Globigerinatheka index</i>	156.92	-0.34	3.01
<i>Globigerinatheka index</i>	158.81	-0.31	3.11
<i>Globigerinatheka index</i>	159.22	-0.08	3.20
<i>Globigerinatheka index</i>	160.20	-0.26	2.64
<i>Globigerinatheka index</i>	160.71	-0.41	2.76
<i>Globigerinatheka index</i>	161.22	-0.16	2.94
<i>Globigerinatheka index</i>	161.44	-0.28	3.00
<i>Globigerinatheka index</i>	161.59	-0.23	3.01
<i>Globigerinatheka index</i>	161.80	-0.20	3.00
<i>Globigerinatheka index</i>	162.02	-0.54	2.66

APPENDIX 1. Continued.

Species	Depth (m.b.s.f.)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Globigerinatheka index</i>	162.39	-0.14	2.99
<i>Globigerinatheka index</i>	162.40	-0.32	3.19
<i>Globigerinatheka index</i>	162.63	-0.37	2.91
<i>Globigerinatheka index</i>	162.70	-0.31	2.63
<i>Globigerinatheka index</i>	162.83	-0.41	3.14
<i>Globigerinatheka index</i>	163.92	-0.45	2.83
<i>Globigerinatheka index</i>	164.12	-0.24	3.10
<i>Globigerinatheka index</i>	164.33	-0.25	2.94
<i>Globigerinatheka index</i>	164.49	-0.37	2.88
<i>Globigerinatheka index</i>	164.68	-0.40	2.95
<i>Globigerinatheka index</i>	164.88	-0.51	2.66
<i>Globigerinatheka index</i>	165.08	-0.58	2.81
<i>Globigerinatheka index</i>	166.87	-0.21	3.18
<i>Globigerinatheka index</i>	167.07	-0.34	3.32
<i>Globigerinatheka index</i>	168.20	-0.29	2.84
<i>Globigerinatheka index</i>	170.40	-0.27	2.60
<i>Globigerinatheka index</i>	181.64	-0.22	2.91
<i>Globigerinatheka index</i>	181.80	-0.22	2.83
<i>Globigerinatheka index</i>	182.00	-0.22	2.77
<i>Globigerinatheka index</i>	185.10	-0.19	2.95
<i>Globigerinatheka index</i>	185.96	-0.17	2.54
<i>Globigerinatheka index</i>	186.07	-0.08	2.84
<i>Globigerinatheka sp.</i>	153.7	-0.37	2.76
<i>Globigerinatheka sp.</i>	154.8	-0.41	3.13
<i>Globigerinatheka sp.</i>	155.00	-0.23	2.96
<i>Guembelitrionides higgins</i>	154.80	0.03	3.01
<i>Guembelitrionides higgins</i>	155.80	0.25	2.52
<i>Guembelitrionides higgins</i>	156.63	-0.02	2.89
<i>Guembelitrionides higgins</i>	156.70	0.02	2.40
<i>Guembelitrionides higgins</i>	160.20	0.15	2.05
<i>Guembelitrionides higgins</i>	160.71	0.03	2.45
<i>Guembelitrionides higgins</i>	161.59	0.17	2.05
<i>Guembelitrionides higgins</i>	161.80	-0.15	2.64
<i>Guembelitrionides higgins</i>	162.02	-0.13	2.13
<i>Guembelitrionides higgins</i>	163.74	0.54	2.29
<i>Guembelitrionides higgins</i>	164.33	-0.07	2.54
<i>Guembelitrionides higgins</i>	164.49	0.09	2.31
<i>Guembelitrionides higgins</i>	166.87	0.27	2.52
<i>Guembelitrionides higgins</i>	167.07	0.14	2.65
<i>Guembelitrionides higgins</i>	170.80	0.24	2.22
<i>Guembelitrionides higgins</i>	171.01	0.26	2.16
<i>Guembelitrionides higgins</i>	171.22	0.20	2.02
<i>Guembelitrionides higgins</i>	171.38	0.29	1.97
<i>Guembelitrionides higgins</i>	172.51	0.26	2.42
<i>Guembelitrionides higgins</i>	172.72	0.31	2.36
<i>Guembelitrionides higgins</i>	173.08	0.17	1.98
<i>Guembelitrionides higgins</i>	173.60	0.11	1.97
<i>Guembelitrionides higgins</i>	173.80	0.22	2.27
<i>Guembelitrionides higgins</i>	181.80	0.21	2.15
<i>Guembelitrionides higgins</i>	182.00	0.11	2.20
<i>Guembelitrionides higgins</i>	182.52	0.43	2.02
<i>Guembelitrionides higgins</i>	186.07	0.30	1.82
<i>Guembelitrionides higgins</i>	186.91	0.34	1.75
<i>Subbotina eocaena</i>	171.01	0.51	1.63
<i>Subbotina eocaena</i>	173.08	0.44	1.65
<i>Subbotina eocaena</i>	173.80	0.39	1.63
<i>Subbotina eocaena</i>	181.80	-0.07	2.37
<i>Subbotina eocaena</i>	182.32	0.57	1.60
<i>Subbotina eocaena</i>	182.52	0.79	1.46
<i>Subbotina eocaena</i>	184.41	0.46	1.72
<i>Subbotina eocaena</i>	185.10	0.63	1.51
<i>Subbotina eocaena</i>	186.07	0.25	2.00
<i>Subbotina eocaena</i>	186.22	0.40	1.64
<i>Subbotina eocaena</i>	187.10	0.47	1.66
<i>Subbotina eocaena</i>	189.58	-0.07	2.13
<i>Subbotina linaperta</i>	153.30	0.29	2.05
<i>Subbotina linaperta</i>	153.70	0.33	2.12
<i>Subbotina linaperta</i>	154.60	0.29	2.12

APPENDIX 1. Continued.

Species	Depth (m.b.s.f.)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Subbotina linaperta</i>	154.80	0.44	2.17
<i>Subbotina linaperta</i>	155.00	0.32	2.05
<i>Subbotina linaperta</i>	155.20	0.35	2.02
<i>Subbotina linaperta</i>	155.40	0.32	2.16
<i>Subbotina linaperta</i>	155.64	0.43	2.28
<i>Subbotina linaperta</i>	155.80	0.38	1.90
<i>Subbotina linaperta</i>	156.20	0.28	2.23
<i>Subbotina linaperta</i>	156.43	0.30	2.23
<i>Subbotina linaperta</i>	156.63	0.56	2.19
<i>Subbotina linaperta</i>	156.70	0.36	1.92
<i>Subbotina linaperta</i>	156.92	0.40	1.96
<i>Subbotina linaperta</i>	157.11	0.20	2.22
<i>Subbotina linaperta</i>	157.70	0.24	2.02
<i>Subbotina linaperta</i>	157.93	0.38	2.08
<i>Subbotina linaperta</i>	158.13	0.18	2.46
<i>Subbotina linaperta</i>	158.24	0.34	2.18
<i>Subbotina linaperta</i>	158.81	0.41	2.40
<i>Subbotina linaperta</i>	158.98	0.40	2.53
<i>Subbotina linaperta</i>	159.22	0.69	1.99
<i>Subbotina linaperta</i>	159.74	0.48	2.01
<i>Subbotina linaperta</i>	160.20	0.63	1.94
<i>Subbotina linaperta</i>	161.22	0.58	1.94
<i>Subbotina linaperta</i>	161.44	0.52	1.89
<i>Subbotina linaperta</i>	161.59	0.92	1.64
<i>Subbotina linaperta</i>	161.80	0.47	1.92
<i>Subbotina linaperta</i>	162.02	0.43	1.92
<i>Subbotina linaperta</i>	162.39	0.80	1.85
<i>Subbotina linaperta</i>	162.40	0.45	2.23
<i>Subbotina linaperta</i>	162.63	0.65	1.97
<i>Subbotina linaperta</i>	163.74	0.56	1.68
<i>Subbotina linaperta</i>	163.92	0.51	1.76
<i>Subbotina linaperta</i>	164.33	0.55	1.81
<i>Subbotina linaperta</i>	164.68	0.39	1.89
<i>Subbotina linaperta</i>	166.87	0.33	1.82
<i>Subbotina linaperta</i>	167.07	0.63	1.69
<i>Subbotina linaperta</i>	167.27	0.42	1.73
<i>Subbotina linaperta</i>	167.47	0.51	1.87
<i>Subbotina linaperta</i>	167.67	0.45	1.89
<i>Subbotina linaperta</i>	167.88	0.40	1.67
<i>Subbotina linaperta</i>	171.01	0.64	1.32
<i>Subbotina linaperta</i>	171.22	0.71	1.61
<i>Subbotina linaperta</i>	172.30	0.18	1.66
<i>Subbotina linaperta</i>	173.08	0.64	1.77
<i>Subbotina linaperta</i>	173.20	0.44	1.59
<i>Subbotina linaperta</i>	173.44	0.19	1.67
<i>Subbotina linaperta</i>	173.60	0.30	1.53
<i>Subbotina linaperta</i>	173.80	0.50	1.64
<i>Subbotina linaperta</i>	181.64	0.58	1.88
<i>Subbotina linaperta</i>	182.10	0.49	1.74
<i>Subbotina linaperta</i>	182.32	0.60	1.33
<i>Subbotina linaperta</i>	182.52	0.60	1.57
<i>Subbotina linaperta</i>	183.80	0.54	1.76
<i>Subbotina linaperta</i>	183.98	0.75	1.82
<i>Subbotina linaperta</i>	184.20	0.57	1.79
<i>Subbotina linaperta</i>	186.07	0.47	1.69
<i>Subbotina linaperta</i>	186.50	0.44	1.69
<i>Subbotina linaperta</i>	186.91	0.47	1.50
<i>Subbotina linaperta</i>	187.10	0.54	1.56
<i>Subbotina frontosa</i>	153.70	0.32	2.18
<i>Subbotina frontosa</i>	156.20	0.53	2.17
<i>Subbotina frontosa</i>	156.43	0.75	2.05
<i>Subbotina frontosa</i>	156.63	0.38	1.98
<i>Subbotina frontosa</i>	156.70	0.48	2.02
<i>Subbotina frontosa</i>	156.92	0.36	2.08
<i>Subbotina frontosa</i>	158.13	0.23	2.09
<i>Subbotina frontosa</i>	159.22	0.42	1.80
<i>Subbotina frontosa</i>	159.74	0.21	2.06
<i>Subbotina frontosa</i>	160.50	0.66	2.10
<i>Subbotina frontosa</i>	160.71	0.43	1.83
<i>Subbotina frontosa</i>	161.22	0.57	2.01

APPENDIX 1. Continued.

Species	Depth (m.b.s.f.)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Subbotina frontosa</i>	161.44	0.05	1.83
<i>Subbotina frontosa</i>	161.59	0.43	2.06
<i>Subbotina frontosa</i>	161.80	0.35	2.03
<i>Subbotina frontosa</i>	162.40	0.38	2.02
<i>Subbotina frontosa</i>	162.63	0.54	1.98
<i>Subbotina frontosa</i>	162.83	0.40	2.02
<i>Subbotina frontosa</i>	163.74	0.28	1.97
<i>Subbotina frontosa</i>	164.12	0.30	2.00
<i>Subbotina frontosa</i>	164.33	0.49	1.99
<i>Subbotina frontosa</i>	164.49	0.36	1.95
<i>Subbotina frontosa</i>	164.88	0.37	1.87
<i>Subbotina frontosa</i>	165.08	0.28	1.91
<i>Subbotina frontosa</i>	166.87	0.39	1.82
<i>Subbotina frontosa</i>	167.07	0.27	1.79
<i>Subbotina frontosa</i>	167.27	0.29	1.81
<i>Subbotina frontosa</i>	167.88	0.20	1.76
<i>Subbotina frontosa</i>	168.08	0.36	1.73
<i>Subbotina frontosa</i>	168.20	0.24	1.72
<i>Subbotina frontosa</i>	170.40	0.13	1.48
<i>Subbotina frontosa</i>	170.60	0.27	1.73
<i>Subbotina frontosa</i>	170.80	0.27	1.76
<i>Subbotina frontosa</i>	171.01	0.38	1.79
<i>Subbotina frontosa</i>	171.22	0.61	1.98
<i>Subbotina frontosa</i>	171.38	0.77	1.97
<i>Subbotina frontosa</i>	171.70	0.14	1.57
<i>Subbotina frontosa</i>	172.10	0.17	1.51
<i>Subbotina frontosa</i>	172.51	0.32	1.85
<i>Subbotina frontosa</i>	172.72	0.46	1.81
<i>Subbotina frontosa</i>	173.08	0.27	1.64
<i>Subbotina frontosa</i>	173.20	0.13	1.62
<i>Subbotina frontosa</i>	173.44	0.03	1.61
<i>Subbotina frontosa</i>	173.60	0.18	1.54
<i>Subbotina frontosa</i>	173.80	0.31	1.79
<i>Subbotina frontosa</i>	181.64	0.40	1.75
<i>Subbotina frontosa</i>	181.80	0.34	1.84
<i>Subbotina frontosa</i>	182.00	0.46	1.70
<i>Subbotina frontosa</i>	182.10	0.44	1.63
<i>Subbotina frontosa</i>	182.32	0.62	1.80
<i>Subbotina frontosa</i>	182.52	0.80	1.64
<i>Subbotina frontosa</i>	183.80	0.40	1.86
<i>Subbotina frontosa</i>	184.20	0.42	1.85
<i>Subbotina frontosa</i>	184.60	0.33	1.72
<i>Subbotina frontosa</i>	185.10	0.35	1.68
<i>Subbotina frontosa</i>	185.96	0.48	1.69
<i>Subbotina frontosa</i>	186.07	0.44	1.76
<i>Subbotina frontosa</i>	186.50	0.32	1.73
<i>Subbotina frontosa</i>	186.91	0.37	1.62
<i>Subbotina frontosa</i>	187.10	0.50	1.74
<i>Subbotina frontosa</i>	189.42	-0.12	2.01
<i>Subbotina aff. inaequispira</i>	155.20	0.68	2.00
<i>Subbotina aff. inaequispira</i>	155.40	0.45	1.75
<i>Subbotina aff. inaequispira</i>	156.20	0.83	1.94
<i>Subbotina aff. inaequispira</i>	156.63	0.91	1.81
<i>Subbotina aff. inaequispira</i>	156.70	0.79	1.68
<i>Subbotina aff. inaequispira</i>	156.92	0.66	1.94
<i>Subbotina aff. inaequispira</i>	157.93	0.47	1.89
<i>Subbotina aff. inaequispira</i>	158.13	0.75	1.68
<i>Subbotina aff. inaequispira</i>	158.24	0.73	1.75
<i>Subbotina aff. inaequispira</i>	158.98	0.63	2.68
<i>Subbotina aff. inaequispira</i>	159.22	0.44	2.61
<i>Subbotina aff. inaequispira</i>	159.74	0.64	2.74
<i>Subbotina aff. inaequispira</i>	160.71	0.54	1.41
<i>Subbotina aff. inaequispira</i>	161.22	1.03	1.86
<i>Subbotina aff. inaequispira</i>	161.44	1.25	1.43
<i>Subbotina aff. inaequispira</i>	161.59	0.82	1.73
<i>Subbotina aff. inaequispira</i>	161.80	1.01	1.77
<i>Subbotina aff. inaequispira</i>	162.02	0.68	1.77
<i>Subbotina aff. inaequispira</i>	162.63	0.69	1.95
<i>Subbotina aff. inaequispira</i>	162.83	0.71	1.96
<i>Subbotina aff. inaequispira</i>	163.74	0.87	1.70

APPENDIX 1. Continued.

Species	Depth (m.b.s.f.)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Subbotina</i> aff. <i>inaequispira</i>	164.12	0.59	2.10
<i>Subbotina</i> aff. <i>inaequispira</i>	164.33	0.87	1.70
<i>Subbotina</i> aff. <i>inaequispira</i>	165.08	0.96	1.36
<i>Subbotina</i> aff. <i>inaequispira</i>	166.87	0.95	1.53
<i>Subbotina</i> aff. <i>inaequispira</i>	167.07	1.07	1.64
<i>Subbotina</i> aff. <i>inaequispira</i>	167.27	1.07	1.50
<i>Subbotina</i> aff. <i>inaequispira</i>	167.47	0.91	1.59
<i>Subbotina</i> aff. <i>inaequispira</i>	167.67	0.96	1.63
<i>Subbotina</i> aff. <i>inaequispira</i>	167.88	1.00	1.60
<i>Subbotina</i> aff. <i>inaequispira</i>	168.08	1.15	1.68
<i>Subbotina</i> aff. <i>inaequispira</i>	168.20	0.94	1.73
<i>Subbotina</i> aff. <i>inaequispira</i>	170.40	1.26	1.67
<i>Subbotina</i> aff. <i>inaequispira</i>	170.60	0.97	1.39
<i>Subbotina</i> aff. <i>inaequispira</i>	170.80	0.86	1.37
<i>Subbotina</i> aff. <i>inaequispira</i>	171.01	1.12	1.35
<i>Subbotina</i> aff. <i>inaequispira</i>	171.22	0.80	1.70
<i>Subbotina</i> aff. <i>inaequispira</i>	171.38	0.96	1.46
<i>Subbotina</i> aff. <i>inaequispira</i>	171.70	0.93	1.33
<i>Subbotina</i> aff. <i>inaequispira</i>	172.51	0.97	1.58
<i>Subbotina</i> aff. <i>inaequispira</i>	173.08	0.98	1.39
<i>Subbotina</i> aff. <i>inaequispira</i>	173.80	0.88	1.51
<i>Subbotina</i> aff. <i>inaequispira</i>	182.10	0.42	1.70
<i>Subbotina</i> aff. <i>inaequispira</i>	183.30	0.78	1.65
<i>Subbotina</i> aff. <i>inaequispira</i>	183.98	0.62	1.86
<i>Subbotina</i> aff. <i>inaequispira</i>	184.20	0.74	1.69
<i>Hantkenina</i> spp.	155.64	0.26	2.07
<i>Hantkenina</i> spp.	156.63	0.17	2.24
<i>Hantkenina</i> spp.	158.13	0.20	1.97
<i>Hantkenina</i> spp.	160.71	0.51	2.12
<i>Hantkenina</i> spp.	161.44	0.48	2.01
<i>Hantkenina</i> spp.	161.59	0.35	1.91
<i>Hantkenina</i> spp.	161.80	0.48	1.90
<i>Hantkenina</i> spp.	171.38	0.62	1.57
<i>Hantkenina</i> spp.	171.58	0.25	1.42
<i>Hantkenina</i> spp.	172.10	0.38	1.78
<i>Hantkenina</i> spp.	172.30	0.31	1.73
<i>Hantkenina</i> spp.	172.51	0.39	1.86
<i>Hantkenina</i> spp.	172.72	0.24	1.56
<i>Clavigerinella eocanica</i>	186.50	0.39	1.79

APPENDIX 2

ISOTOPE DATA BY SIZE FRACTION FOR FIG. 5

Species	Sample	Size fraction (μm)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Acarinina matthewsae</i>	155.40	125–150	–0.12	2.31
		180–212	0.33	2.07
		212–250	0.53	2.34
		250–300	0.32	2.16
		300–355	0.21	2.10
	156.70	150–180	–0.39	2.00
		180–212	0.10	1.87
		212–250	–0.11	2.38
		250–300	–0.47	2.55
		300–355	–0.45	2.88
	164.33	355–425	–0.39	3.15
		150–180	–0.25	2.21
		180–212	–0.15	2.41
		212–250	–0.41	2.55
		250–300	0.16	3.10
	167.07	300–355	–0.36	3.05
		355–425	–0.34	3.24
		125–150	–0.10	2.08
		150–180	–0.16	2.16
		180–212	–0.17	2.24
	172.12	212–250	–0.32	2.42
		250–300	–0.27	2.50
		300–355	–0.20	2.98
		150–180	0.09	2.06

APPENDIX 2. Continued.

Species	Sample	Size fraction (μm)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Acarinina triplex</i>	187.10	180–212	–0.28	2.06
		212–250	0.24	2.19
		250–300	–0.01	2.43
		125–150	0.10	1.92
		150–180	–0.64	1.92
	187.10	180–212	–0.50	2.13
		212–250	–0.56	2.29
		125–150	0.24	2.19
		150–180	0.06	2.18
		180–212	–0.16	2.42
<i>Acarinina pseudotopilensis</i>	155.40	212–250	–0.06	2.56
		250–300	–0.11	2.77
		300–355	–0.23	3.16
		355–425	–0.18	3.17
		150–180	0.02	2.98
	156.70	180–212	0.07	2.81
		212–250	0.00	3.10
		250–300	–0.08	3.31
		300–355	–0.18	3.55
		125–150	–0.14	2.20
<i>Muricoglobigerina senni</i>	163.74	180–212	–0.17	2.54
		250–300	–0.10	3.19
		300–355	–0.15	3.38
		212–250	0.18	2.17
		250–300	0.31	3.33
	167.07	150–180	0.06	3.07
		180–212	0.01	2.58
		212–250	–0.01	2.88
		250–300	–0.02	3.04
		125–150	–0.27	1.52
'Morozovella' broedermanni	167.07	150–180	–0.14	1.63
		180–212	–0.27	1.90
		212–250	–0.18	1.98
		250–300	0.00	2.26
		150–180	0.23	3.01
	155.40	180–212	–0.12	3.75
		212–250	–0.41	3.78
		180–212	0.46	2.10
		212–250	0.24	2.17
		250–300	0.37	2.08
<i>Subbotina frontosa</i>	156.70	300–355	0.36	2.01
		355–425	0.07	1.85
		125–150	0.09	2.26
		150–180	0.19	1.69
		180–212	0.35	1.87
	163.74	180–212	0.43	1.83
		180–212	0.60	2.13
		212–250	0.23	2.04
		300–355	0.49	1.99
		425–530	0.43	2.07
<i>Subbotina linaperta</i>	167.07	150–180	0.50	1.82
		180–212	0.56	1.72
		212–250	0.46	1.90
		250–300	0.28	1.97
		300–355	0.31	1.90
	155.40	125–150	0.37	2.46
		180–212	0.33	2.07
		212–250	0.53	2.34
		250–300	0.32	2.16
		300–355	0.21	2.10
<i>Subbotina aff. inaequispira</i>	167.07	125–150	0.53	2.05
		150–180	0.53	2.07
		180–212	0.76	1.71
		212–250	0.42	1.78
		250–300	0.40	1.77
	155.40	300–355	0.28	1.90
		150–180	0.69	2.29
		212–250	0.72	2.16
		250–280	0.45	1.75
		212–250	1.01	1.52
	167.07	250–300	0.91	1.69
		300–355	1.03	1.80