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Distribution and Taxonomy of *Globigerina pachyderma* (Ehrenberg) off the Sanriku Coast, Northeast Honshu, Japan

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ABSTRACT

In order to work out taxonomic problems of the generic assignment of *Globigerina pachyderma-Globoquadrina dutertrei* plexus in the light of ecology, investigations have been conducted on taxonomy and ecologic distribution of planktonic foraminifera using material collected by towing. The material was sampled through the use of simultaneous horizontal tows at two stations of the subarctic (St. 1; May 27, 1978) and perturbed areas (St. 2; June 29, 1977) off Northeast Honshu, Japan.

Based on specimens from the two stations, studied are both the distribution pattern of a species in different ontogenetic stages and those of different species (intra- and interspecific distribution patterns in this paper) in water column. Each of the patterns appears to be peculiar to a water mass where foraminifera live, which are specified by the measured physicochemical properties.

The daily vertical movement of foraminifera has also been inspected, particularly for *G. pachyderma*, using specimens collected both by the sediment traps (collector) and nets at St. 1 in the subarctic area. Laying stress on wall structure, the ontogenetic development of various forms has been detected under the scanning electron microscope. A gross shape of each species has been examined based on the population which relates to a distinct distribution pattern in water column.

As a result, in the upper 200 m layer, the intra-and interspecific distribution patterns of planktonic foraminifera reflect characters of water masses sensitively even in the perturbed water mass, where the hydrographic setting is complicated due to a mixture of different water masses.

The distribution patterns are basically characterized by two maximum concentration layers related to life cycles in the water column at both stations. Planktonic foraminifera descend distances of less than 50 m at night, and in the early morning, they reproduce daughters synchronously in a depth range of 150–250 m, where is the lower maximum concentration layer of the populations. After then, they put off empty shells which settle down according to a settling velocity peculiar to each species with no remarkable dispersion. Encrustation of *G. pachyderma* is closely connected with reproduction, and the specimens in bottom sediments appear to be mostly those after reproduction.

It is quite possible, on the basis of living populations, that the left-coiled *G. pachyderma* belongs to the genus *Globigerina*, meanwhile the so-called right-coiled variety of *G. pachyderma* is synonymous with *Globoquadrina dutertrei* (d'Orbigny). They inhabit respectively different niches (water masses) and the boundary between those realms is defined by water temperatures around 8°C at St. 2 (perturbed area).

Correspondence of the position of 7.2°C isotherm of surface water in April to the boundary between the distributions of the so-called left- and right-coiled populations of *G. pachyderma* in bottom sediments, as shown by Ericson (1959), can be explained by large populations and a brief turnover time of the populations of left-coiled *G. pachyderma* during their blooming in spring in the subpolar region.

CONTENTS

INTRODUCTION

Since Ehrenberg (1861) originally described *Globigerina pachyderma* under the name of *Aristerospira pachyderma* from sediments of the Arctic Ocean, this species has attracted much attention of investigators in the fields of paleontology and paleoceanography for its peculiar ecologic distribution and taxonomy.

Fundamental matters with this species are as follows.

(1) Contrary to wide distribution of the typical form of *Globigerina pachyderma* in bottom sediments of the polar region (Bé, 1960b; Bé and Tolderlund, 1971), only few specimens of it have been collected by plankton-nets (Brady, 1884; Uchio, 1960; Cifelli, 1973; Cifelli and Smith, 1970). It is generally accepted that surface dwelling thin-shelled specimens are the counterparts of thick-shelled specimens on the bottom (Bé, 1960b; Parker, 1962; Jenkins, 1967; Cifelli, 1973). The taxonomic relationship between these two forms and the process of encrustation are, however, still unclear, since the life history of planktonic foraminifera in water column is not understood mainly due to unreliable sampling techniques (Phleger, 1976).

(2) It is well known that the population of *Globigerina pachyderma* includes two forms with the opposite coiling directions; the left-coiled form dominates the polar-subpolar region and the right-coiled one the subpolar-temperate region. The boundary between those two realms roughly coincides with the present 10°C surface isotherm (Ericson, 1959; Bé,

1959a; Bé and Hamlin, 1967; Bé and Tolderlund, 1971; Boltovskoy, 1969, 1971b; Tolderlund and Bé, 1971; Bé and Hutson, 1977).

Disputant is that whether a change in coiling direction represents a phenotypic variation, as caused by water temperature, of a species, or two different species or subspecies (Cifelli, 1961, 1971, 1973; Parker, 1962, 1971; Parker and Berger, 1971; Bé, 1969; Bé and Hamlin, 1967; Bé and Tolderlund, 1971).

As *Globigerina pachyderma* (Ehrenberg) shows a remarkable morphological variation and renders a possible gradation with other species such as *Globoquadrina dutertrei* (d'Orbigny), there are also glaring discrepancies among investigators in its taxonomical criteria and generic assignment, which remain unsettled yet; for example, *Globigerina* (Parker, 1962), *Globorotalia* (Jenkins, 1967), *Turborotalia* (Bandy et al., 1969), *Globigerina* (Bé and Tolderlund, 1971), *Neogloboquadrina* (Collen and Vella, 1973) and *Globoquadrina* (Bé, 1977).

In pursuit of the taxonomic problem there are two principal approaches; one incorporates phylogenetic lineage and the other ecology. Because these two approaches are closely related with each other and *Globigerina pachyderma* was originally described on the basis of the material from Recent bottom sediments, ecological research on the modern populations collected by plankton-nets may give a feasible way to natural classification as discussed by Parker (1962) and Bé and Hamlin (1967).

If there is a vertical habitat segregation of planktonic foraminifera in water column according to varieties of ontogenetic stages and species, the specimens collected by simultaneous horizontal tows (Motoda Horizontal Net) may be suitable for taxonomic work from an ecological point of view.

This type of nets enable us to collect enough specimens for the study of the vertical distribution of planktons over a long lateral distance at each depth layer which may equate a patchy distribution and make quantitative analysis possible. Therefore, the distribution pattern of planktonic foraminifera can be verified in association with the measured physicochemical properties of water masses from which specimens were gathered.

Specimens collected by this type of nets have additional merits:

(1) Naturally, living specimens collected by simultaneous horizontal tows are from a restricted water in space and time, which possess great merit not only in an ecological interpretation but also in taxonomic work from an ecological point of view, as compared with specimens from bottom sediments which accumulated from a variety of water masses for a long time. Therefore, it is probable to distinguish a series of phenotypic variations resulted from physicochemical conditions, and to substantiate a specific classification for most of the ontogenetic stages with accuracy.

(2) Samples collected by plankton-nets are free from solution effect. This is another merit when a taxonomic examination is conducted ontogenetically on species which live in high latitudes, where solution effect is severe especially on delicate-shelled juveniles (Berger, 1970a, 1971a; Parker and Berger, 1971).

If the taxonomy of *Globigerina pachyderma-Globoquadrina dutertrei* complex be established on specimens from the convergence area, the results may be applicable to all the populations of this complex from different areas. Because many problems are largely associated with converging morphoclines of the two species in those areas.

Taking all the above-mentioned into consideration, the study was made employing samples collected by simultaneous horizontal tows at two stations in the Northwest Pacific, off the Sanriku Coast, Northeast Japan, part of a limited area

where the left-coiled *Globigerina pachyderma-Globoquadrina dutertrei* complex is distributed (Bradshaw, 1959). This complex was examined, giving prime importance on wall structure on an ontogeny basis, with the scanning electron microscope at high magnification, and also on gross shape on a population basis under an optical microscope.

The process of shell thickening related to life cycle in water column was observed on the specimens, mainly of *Globigerina pachyderma*, from the subarctic station.

ACKNOWLEDGEMENTS

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The plankton collection discussed here was obtained on the KT–77–8 and KT–78–7 cruises of the research vessel "Tansei-maru" of the Ocean Research Institute of the University of Tokyo, directed by Professor Satoshi Nishizawa of the Department of Fishery Science, Faculty of Agriculture, Tohoku University. I participated in those cruises and had the use of part of tow samples for this study. The physicochemical properties of waters were measured by members of that department. Dr. Akira Taniguchi, Associate Professor of the same department, kindly informed me of the oceanography of this area. Dr. Hiroshi Sasaki of the Department of Fishery Science, Tohoku University placed foraminiferal specimens collected by collectors at my disposal. I express my sincere thanks to that scientific party and the crew for their consideration and helpfulness.

METHODS OF COLLECTION AND PREPARATION

A. Simultaneous Horizontal Tows (Motoda Horizontal Net abbreviated to MTD Horizontal Net)

This type of net has a peculiarity in that its mouth ring is fixed to a triangular frame. The mouth is kept open upward when the net is lowered, and kept vertical during horizontal towing at a wire angle 45°. After towing, the net mouth is closed by dropping a messenger so that no contamination occurs during hauling up and down. The volume of water filtered by the net can be calculated from the records of the flow meter suspended in the center of the mouth.

The construction and usage are detailed by Motoda (1971). The MTD (Motoda) horizontal towing net used in this study is 56 cm in mouth diameter and 180 cm long from the front to the collecting bag. Bolting cloth and the collecting bag are made of Pylen No. 200 with 0.10 mm mesh apertures. When wire made an angle of about 45° with water surface the nets were horizontally towed for about half an hour at 2 knots to get enough specimens for the study.

Sampling was made at two stations during daytime in order to keep out of the effect of daily migration. At KT–77–8 Station 2 (hereafter referred to as St. 2), net towing was conducted on June 29, 1977, in a depth range from the surface down to 2,000 m, and at KT–78–7 Station 1 (hereafter referred to as St. 1) on May, 27, 1978 from the surface down to 1,000 m, respectively. The net-out times are as follows: 1) St. 1, 1,000–

200 m (12:43–13:10), 150–0 m (14:25–14:39); 2) St. 2, 2,000–1,000 m (11:48–12:22), 800–200 m (14:54–15:10), 150–0 m (18:01–18:20), respectively. Because the populations of planktonic foraminifera may change their habitats particularly within surface water, nets were towed at closer intervals for the upper 200 m water column than for greater depths. A vertical series of towing of nets are: at St. 2, seven layers for intervals of 2,000–1,000 m, six layers for 800–200 m, and seven layers for 150–0 m; at St. 1, six layers for 1,000–200 m and seven layers for 150–0 m, respectively.

Samples were preserved in a 5 percent solution of formalin, neutralized with hexamethylene tetramine (hexamine) and sodium carbonate.

In the laboratory, foraminiferal tests were extracted from the samples following the undermentioned procedure.

1) For the convenience of treatment, all the samples are divided into appropriate-sized aliquot parts by a plankton splitter.
2) The foraminiferal tests in the samples are condensed by the density separation method described by Bé (1959b) in a saturated sodium chloride solution.
3) Before the condensation, a preservative (sea water with buffered formalin solution) is drained to avoid dilution of the saturated sodium-chloride solution.
4) Tests gathered on the bottom of a buret are removed together with the sodium-chloride solution into a beaker through the stopcock.
5) The solution contained foraminiferal tests is passed through a black-membrane filter (# 0.8).
6) All the foraminiferal tests on the filter paper are picked up with a fine brush under an optical binocular microscope.
7) The floating residues in the solution are poured into the beaker. From this part, all the foraminiferal tests are also picked up by the plankton-picker described by Hamlin and Bé (1963).
8) The same procedure is repeated for another aliquot part until specimens of more than 200 are obtained.
9) After then, all the specimens prepared were stained with a heated saturated solution of Sudan Black B after Walkers et al. (1974) to discriminate live specimens from empty ones.
10) After all, the live and empty specimens on an assemblage slide were identified separately and calibrated for their diameters under an optical binocular microscope.

B. Collectors (Sediment Traps)

Vertical flux patterns of the planktonic foraminiferal tests were obtained for the upper 500 m water column at St. 1 by using sediment traps (collectors) in the daytime (09:30–19:00, May 27, 1978) and night (21:00–09:00, May 27–28, 1978) separately. The device is simply a bottomed cylindrical tube of 150 mm in diameter. Inside the cylinder, fine glass tubes, 15 mm in inner diameter and 50 mm high, are banded in a honeycomb manner in order to keep the collected material from water agitation. The traps were connected with rope in a series for a simultaneous sampling in eight layers from 50 to 500 m. These traps were suspended in water for 10 to 12 hours and then recovered. All the foraminiferal specimens on filter paper were picked up and were soaked in sea water with a 5 percent buffered formalin solution for a day. Then the specimens were stained by the aforementioned Sudan Black B method. The identification and calibration of specimens were made in the same way as the specimens collected by the nets.

HYDROGRAPHY

A. General Setting

The study area is a portion of the Northwest Pacific off the Sanriku Coast, Northeast Honshu, Japan, where the warm Kuroshio current meets the cold Oyashio current. Each current extends

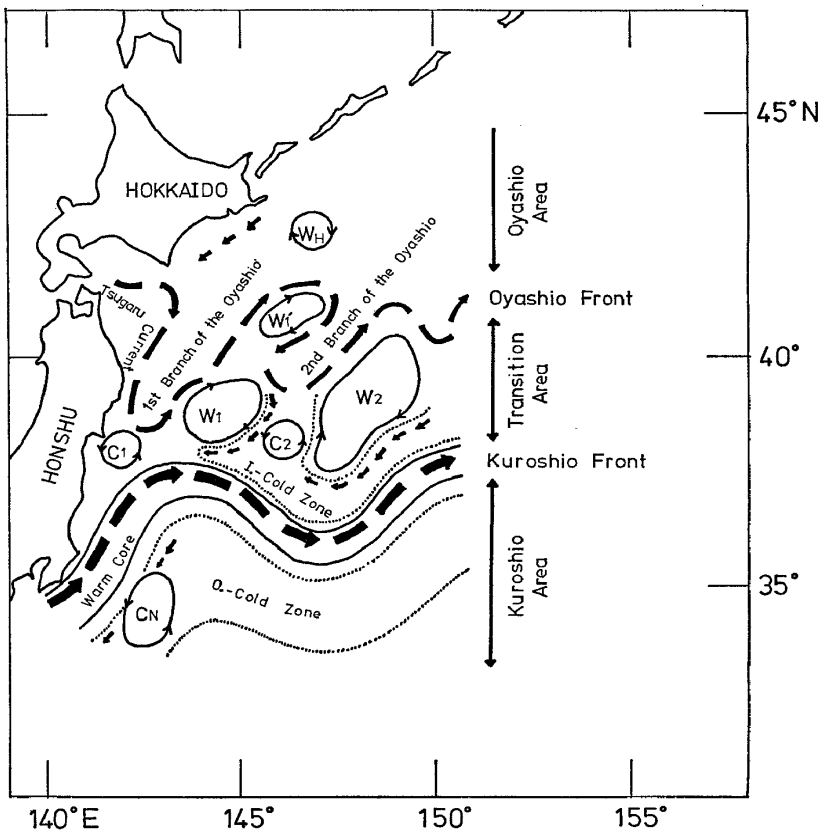

Fig. 1. Scheme of hydrography off Northeast Japan (Kawai, 1972).

eastward to compose part of the subtropical and subarctic gyres (Kawai, 1972). Kawai (*op. cit.*) divided this area hydrographically into three areas by two fronts of the Oyashio and Kuroshio, namely Oyashio area, perturbed or transitional area and Kuroshio area from north to south (Fig. 1).

The studied specimens were taken at two stations (Fig. 2): St. 1 is located in the Oyashio area (subarctic water mass) and St. 2 in the perturbed area. The measured physicochemical properties of the water can help to discriminate water masses on the basis of criteria standardized by Sverdrup et al. (1942), Kawai (1972) and Masuzawa (1972). Most of the terms used here in respect to the oceanography are designated by those authors.

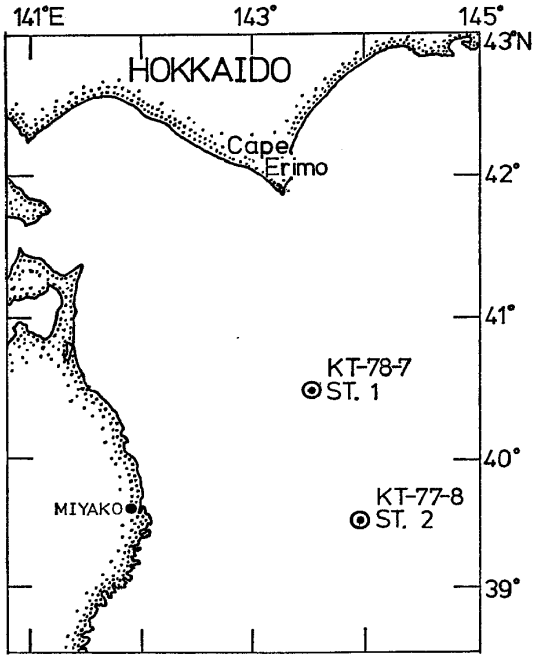

Fig. 2. Locations of plankton collection off Sanriku area. KT–78–7 Station 1: (40°28.5′N, 143°28.1′E); KT–77–8 Station 2: (39°31.0′N, 143°58.2′E)

B. Station 1

Station 1 is located within the Oyashio

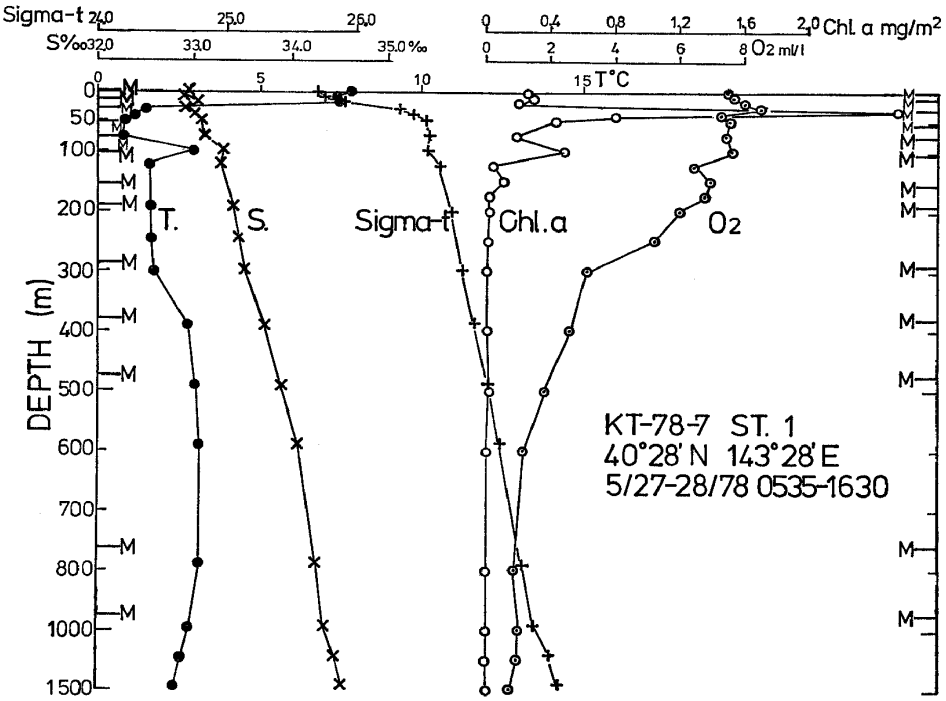

Fig. 3a. Hydrography of the upper 1500 m of water at KT–78–7 Station 1. Sampling depths of simultaneous horizontal tows (MTD nets) are indicated by letter M.

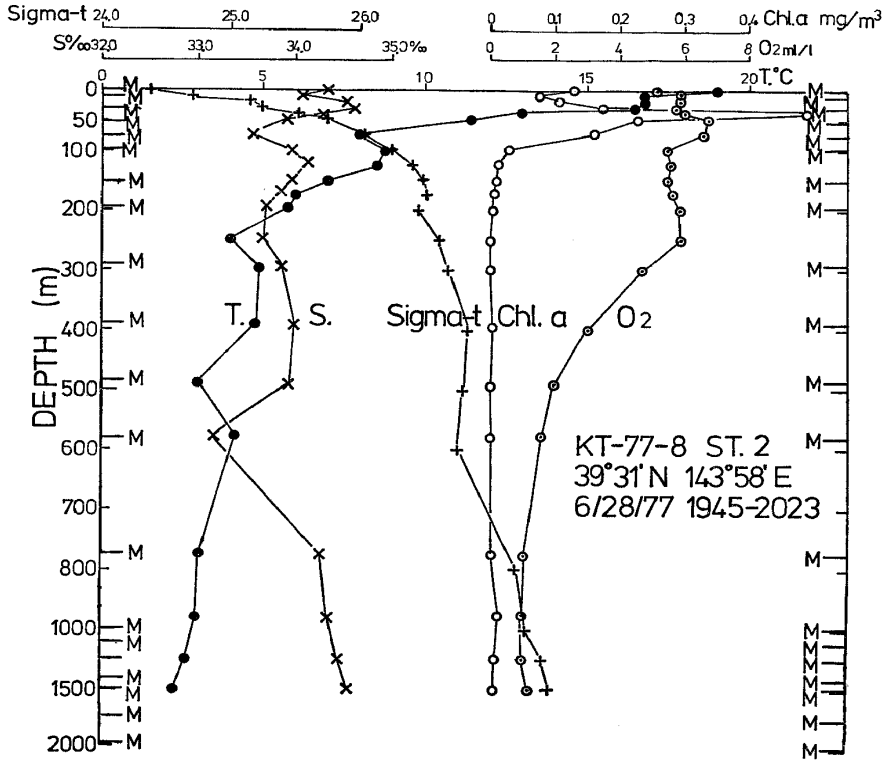

Fig. 3b. Hydrography of the upper 1500 m of water at KT–77–8 Station 2. Sampling depths of simultaneous horizontal tows (MTD nets) are indicated by letter M.

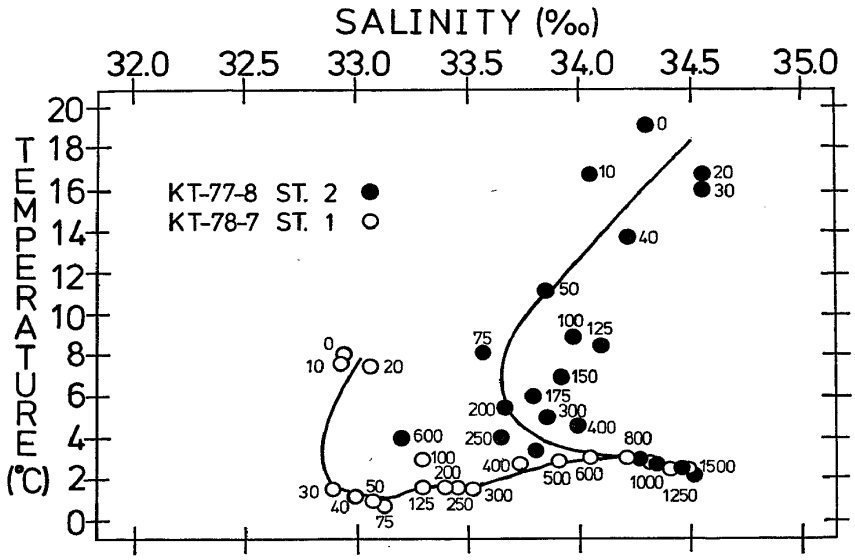

Fig. 4. T-S diagram of waters at KT–78–7 Station 1 and KT–77–8 Station 2. Numerals associated indicate water depth.

area (subarctic region). Therefore no subsurface salinity minimum is present nor is a permanent thermocline distinct (Fig. 3a). A vague and broad halocline is located at depths of 200 to 600 m.

In the upper 300 m, the water shows the lowest temperature and salinity values, and the highest oxygen content. The T-S diagram (Fig. 4) shows that the water at depths of 30–300 m belongs to the original Oyashio water (Kawai, 1972). The inter-cool and inter-warm water layers (Uda, 1938) exist as a temperature inversion layer in thermocline (Fig. 3a). The occurrence of a shallow temperature minimum at 30–75 m depth is probably due to the summer heating at the surface of the winter-mixed layer (Uda, 1935). The warm water is located at a depth of 100 m beneath the cold mixed water (Masuzawa, 1972). There is a slight increae of temperature at 400–800 m depth, and salinity increases gradually toward the deeps. At a depth of 30 m the concentration of chlorophyll *a* is highest and the water is saturated with oxygen (Fig. 3a). Correspondence of the maximum of chlorophyll *a* content to that of oxygen at depths of 30 m and 100 m apparently shows increased biological activities. Oxygen content reaches to minimum as low as 1 ml/l at a depth of 800 m.

C. Station 2

This station is located in the northern limit of the subtropical convergence (between 35°N and 40°N) and also the limits of surface-formative area of the western North Pacific Central Water (Sverdrup et al., 1942. p. 742). In more detail, St. 2 is located in a warm-core eddy floating as a lens on the bulk of cold water. The warm-core eddies are large lenses of subtropical water wandering through a cooler area. The warm-core eddies in this area are shed by the Kuroshio Current. In eddy water, a thorough mixing of water masses takes place, and the Kuroshio water is diluted by the Oyashio water (Sverdrup et. al., *op. cit.*).

The upper 400 m is occupied by a diluted subtropical water and shows high temperature and salinity (Kawai, *op. cit.*) (shown in Figs. 3b, 4). Underlying layers deeper than 500 m show the common properties of temperature-salinity-oxygen to those at St. 1 (Figs. 3b, 4).

Fig. 4 shows that the water at depths

of 125 to 400 m bears the character of a fresh North Pacific Intermediate Water (Kawai, *op. cit.*). Cold-water intrusion into the warm water is also clear in Fig. 3b at depths of about 75 m (shallow cool water) and 250 m (deep cool water), the both are characterized by the salinity and temperature minima and oxygen maximum. This cold water probably originated in the Oyashio region, then moved into the perturbed area, and spread extensively at an intermediate depth. The chlorophyll *a* and oxygen contents in the water correspond to each other in the same manner with St. 1 (Fig. 3b).

DISTRIBUTION OF PLANKTONIC FORAMINIFERA

A. General Distribution Pattern

1. *Absolute abundance*

As the studied samples were taken by plankton nets (XX 13) with 0.1 mm opening, examinations were restricted to specimens larger than 100 μm. The smallest identifiable specimens were, however, actually found.

At. St. 1 (Fig. 5a), six species occurred. All are cool water or cosmopolitan species. In decreasing order, *Globigerina pachyderma*, *Globigerina bulloides* and *Globigerina quinqueloba* dominate, occupying more than 90 percent of the total population.

At St. 2, 12 subarctic-temperate-warm water species occurred (Fig. 5b). The populations of *G. pachyderma* and *Globoquadrina dutertrei* in the sense of this paper including *G. dutertrei* s.s., *Globigerina incompta* and *G.* aff. *G. pachyderma*

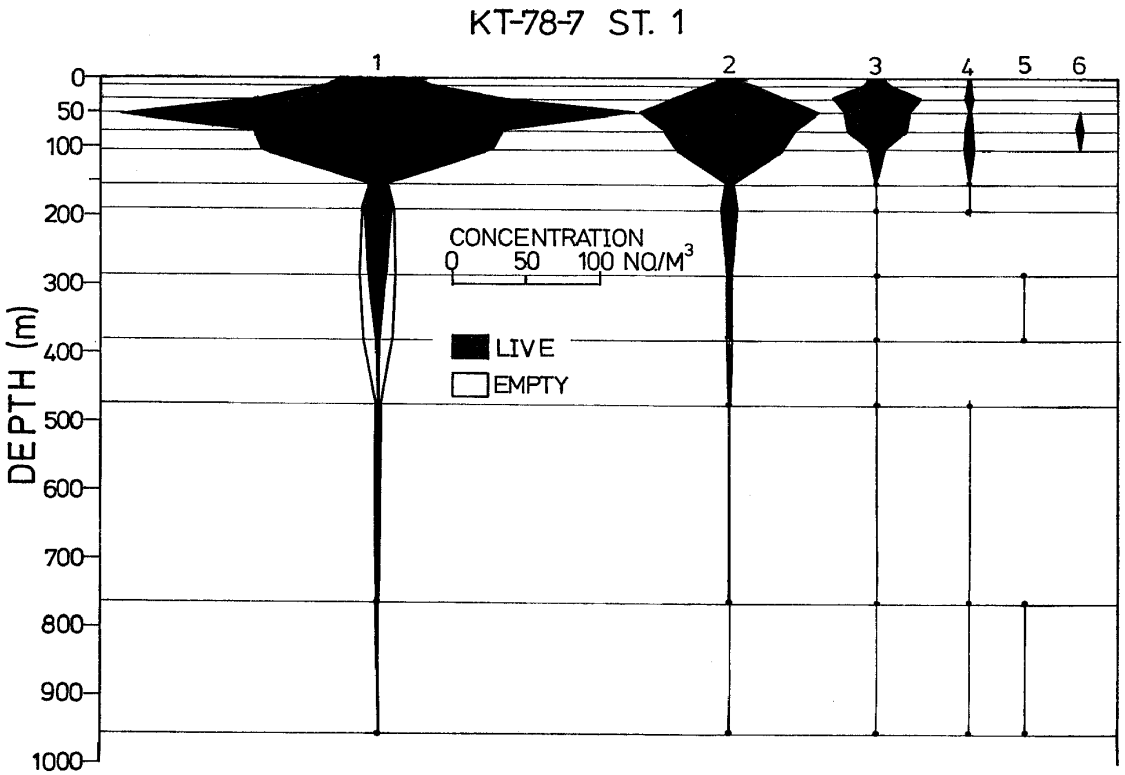

Fig. 5a. Concentration of planktonic foraminiferal species in the water column at KT–78–7 Station 1. Horizontal lines indicate sampling horizons of simultaneous horizontal tows (MTD nets). 1, *Globigerina pachyderma* (Ehrenberg); 2, *Globigerina bulloides* d'Orbigny; 3, *Globigerina quinqueloba* Natland; 4, *Globigerinita uvula* (Ehrenberg); 5, *Globorotalia scitula* (Brady); 6, *Hastigerinella riedeli* Rögl and Bolli.

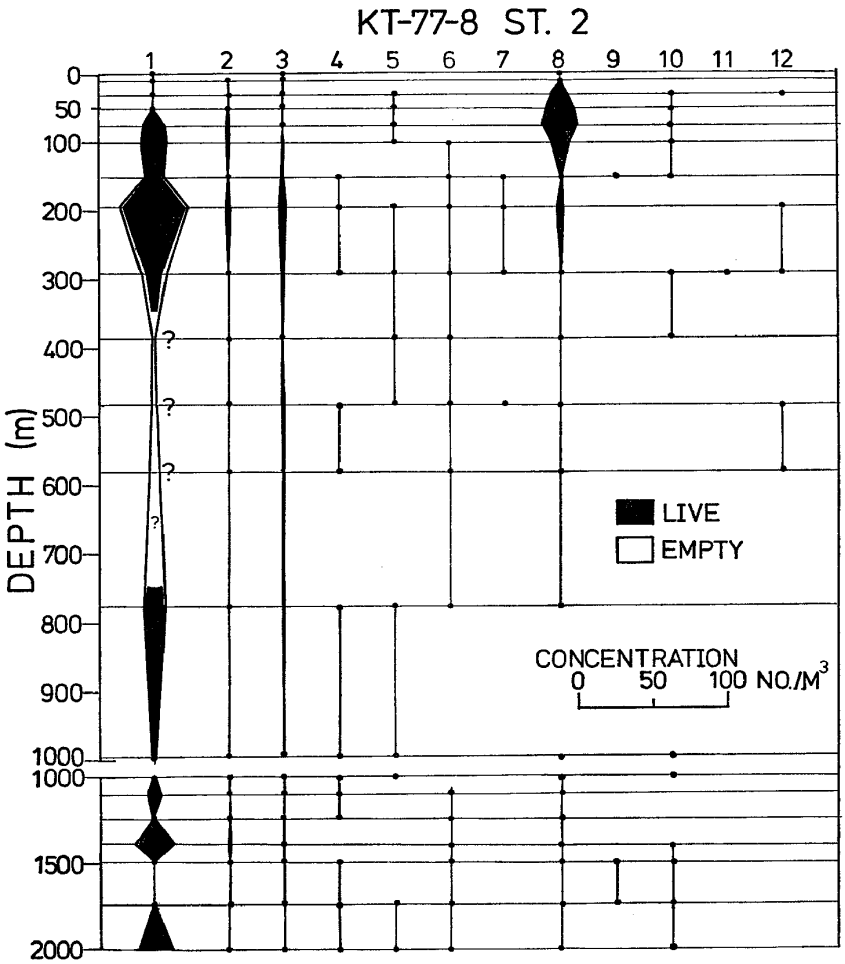

Fig. 5b. Concentration of planktonic foraminiferal species in the water column at KT–77–8 Station 2. Horizontal lines indicate sampling horizons of simultaneous horizontal tows (MTD nets). 1, *Globigerina pachyderma* (Ehrenberg); 2, *Globigerina bulloides* d'Orbigny; 3, *Globigerina quinqueloba* Natland; 4, *Globigerinita uvula* (Ehrenberg); 5, *Globigerinita glutinata* (Egger); 6, *Globorotalia scitula* (Brady); 7, *Hastigerinella riedeli* Rögl and Bolli; 8, *Globoquadrina dutertrei* (d'Orbigny); 9, *Globorotalia truncatulinoides* (d'Orbigny); 10, *Globorotalia inflata* (d'Orbigny); 11, *Orbulina universa* d'Orbigny; 12, *Globigerinoides ruber* (d'Orbigny).

as in the case with Cifelli and Smith (1970) occupy more than 90 percent of the total.

It is noteworthy that only two to three species dominate the total populations at the two stations irrespective of the number of species and faunal composition. This trend agrees with the observations by Tolderlund and Bé (1971), Bradshaw (1959) and Cifelli (1973) in various oceans.

The species composition at each station is consistent with that of the faunas described by previous workers. The assemblage at St. 1 is equal to the cold water fauna of Bradshaw (1959) or the subarctic fauna of Bé and Tolderlund (1971), and that of St. 2 corresponds to the transition fauna of the same authors, respectively. The fact shows that the faunal zones, defined by those authors to be in harmony with various water masses in world oceans, are approved even on a local scale as exemplified by completely different faunas at St. 1 and 2, only 120 km apart from each other.

At each station, the population density of each species in water columns broadly corresponds to the value of chlorophyll *a*, which indicates a standing crop of phytoplankton, producer. At both stations, the shallower maximum concentration of each species exists at depths of 50 m and 75 m (around or just below the maximum of chlorophyll *a* concentration) and minimum exists at a depth of 150 m where the chlorophyll *a* minimum is located. A pronounced decrease in number with depth occurs between 50 m and 150 m. The total population is ten times higher at St. 1 than St. 2, corresponding to the concentration of chlorophyll *a* which is about five times larger at St. 1 than St. 2.

At St. 1, specimens of all the species gather and are mostly living in the upper 150 m layer, the euphotic layer or the first production layer or the epipelagic layer. The first maximum concentration layer of *Globigerinita uvula* (Ehrenberg) is slightly shallower than that of other species. This concentration pattern matches with those observed in world ocean (Jones, 1967; Bradshaw, 1959; Bé 1960a; Bé and Hutson, 1977). The second maximum concentration layer is at a depth of 200 m, where empty shells initially appear.

Although a similar tendency of concentration is observed at St. 2, the concentration pattern of each species is somewhat distorted in response to a complicated hydrography.

At St. 2, the cold-water species such as *G. pachyderma*, *G. bulloides* and *G. quinqueloba* gather more densely in the lower part of the upper layer, and are particularly scarce in the upper 50 m. *G. uvula* is absent in the upper layer. This phenomenon is probably related to the intrusion of the cold water from the Oyashio into the intermediate layer of the perturbed area. After the intrusion, they probably descended due to the effect of high temperature.

In the upper 150 m layer at St. 2, *G. pachyderma* mostly lacks juveniles as contrasted with its high concentration in the upper 30 m layer at St. 1. This phenomenon probably shows that high temperature inhibits reproduction or the growth of juveniles of cold water species. At depths of 50 to 150 m, a negative correlation is seen between *G. dutertrei* and *G. pachyderma* in the declines of their individual number. This profile is apparently related to a temperature depression from 11.2°C to 6.9°C along the thermocline as discussed later.

At St. 2, *G. dutertrei* dominates the upper 150 m layer and only this species bears many juveniles, especially at a depth of 30 m, the upper pelagic layer. Considering the low concentration of other temperate-warm water species, these distributions appear to indicate that *G. dutertrei* encounters concentrations near the optimum for its flourish in warm water masses mixed with cold water. This results in a good agreement with the latitudinal distribution pattern of *G. dutertrei* being dominant in the transitional area (Bradshaw, 1959; Bé and Tolderlund, 1971; Tolderlund and Bé, 1971). The fact that the population of *G. dutertrei* dominates the subsurface layer and is scarce in the surface layer agrees with the observations by Jones (1967) and Bé and Hamlin (1967).

In addition, at St. 2, there are four high concentration layers of *G. pachyderma* within a depth range of 200 m to 2,000 m at increments of 600 m. This profile is probably related to the daily and synchronous descending of the population from the upper layer as discussed later.

In short, the populations of planktonic foraminifera have two maxima and one minimum layers of concentration in the upper 200 m at two stations, and they primarily predominate the epipelagic zone. Planktonic foraminifera may be carried into another water mass from the inherent one, and thereafter they will

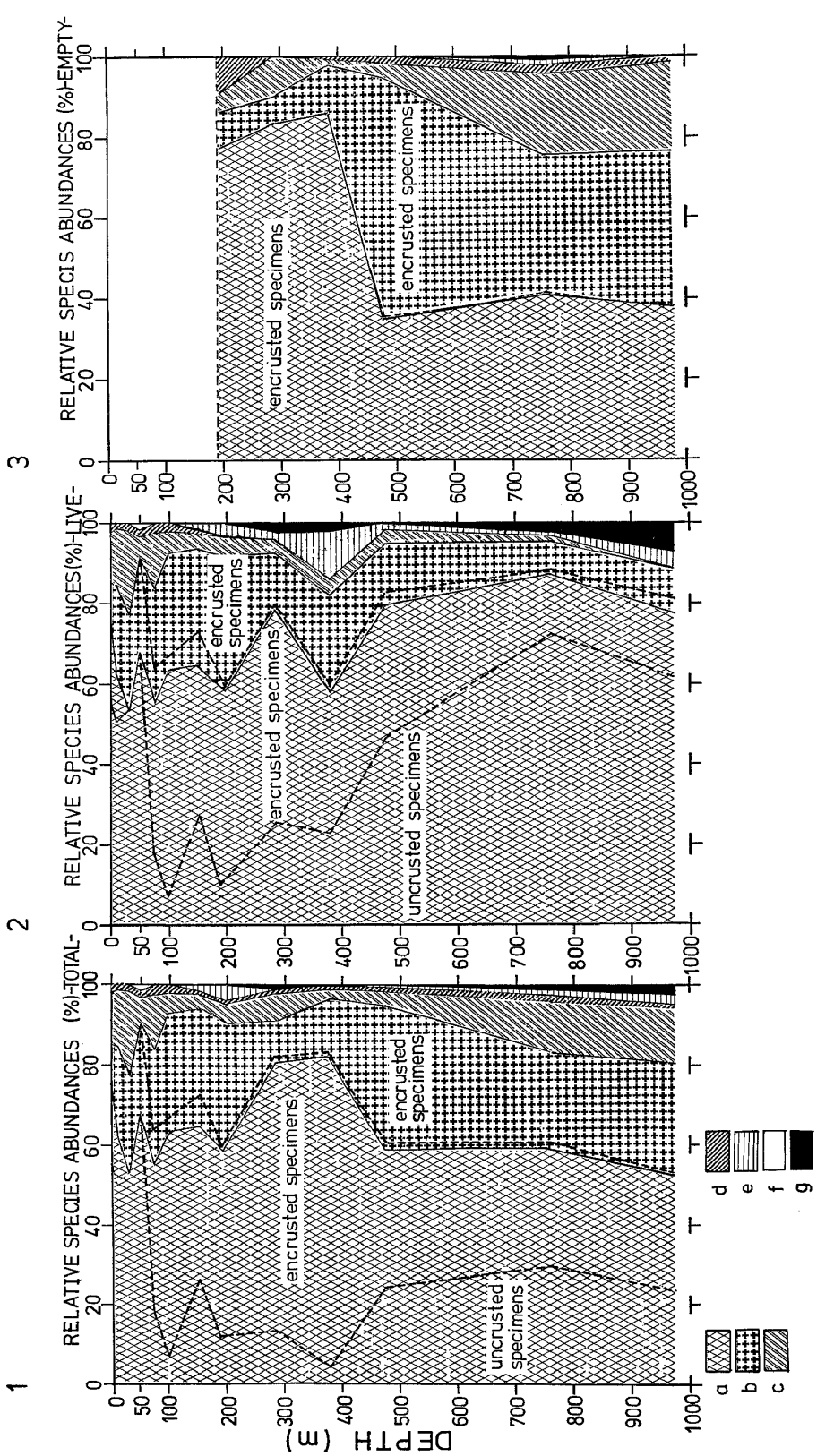

Fig. 6. Relative abundance of planktonic foraminiferal species in the water column at KT-78-7 Station 1. 1, total specimens (live plus empty); 2. live specimens; 3, empty specimens; a, *Globigerina pachyderma*; b, *Globigerina bulloides*; c. *Globigerina quinqueloba*; d, *Globigerinita uvula*; e, *Globigerinita glutinata* f, *Hastigerinella riedeli*; g, *Globorotalia scitula*.

find their optimum layer and form a series of vertical segregations in the water column as a whole. According to the definition by Sverdrup et al. (1942), the population of St. 1 represents the *individual population succession*, while that of St. 2 primarily the *local sequence*, composed of a variety of populations particular to different water masses, although that in each water mass suggests the appearance of the *individual population succession* in a distorted shape by a mixing of water masses and the vertical migration of planktonic foraminifera.

The density of planktonic foraminifera in water column agrees basically with the concentration pattern of each species, which well corresponds to water masses. Therefore, it will be a good indicator for recognition of the shape and dimension of the water masses in the upper 200 m.

2. *Relative abundance*

a) Station 1: Figure 6 shows that *Globigerina pachyderma*, *Globigerina bulloides* and *Globigerina quinqueloba* all dominate throughout the water column in this station. The profile of live assemblage concentrations (Fig. 6) shows that *Globigerinita glutinata* and *Globorotalia scitula* are, respectively, intermediate and deep water species. Figures 5a and 6 show that *Globigerinita uvula* is a comparatively surface dweller.

It is noteworthy that, of both *G. pachyderma* and *G. bulloides*, empty shells are all heavily encrusted and occur below 200 m in depth (Fig. 6). It is unnatural that any plankton feeders selectively eat only protoplasm of encrusted specimens. Therefore, it is construed that empty specimens represent a stage after reproduction, and the encrustation of test stands for a terminal facies or preparation for reproduction. The process of reproduction of *G. pachyderma* and other species is discussed later in more detail.

The concentration of the empty shells of *G. pachyderma* is relatively low at depths of 500–1,000 m (Fig. 6). It is inferred that most of the encrusted specimens reproduced a day ago at depths of about 200 to 300 m, and then descended down to deeper than 1,000 m.

b) Station 2: Owing to a failure in staining the samples from depths of 400 m, 500 m and 600 m, a discrimination between empty and live shells is not capable for these depths (Fig. 7).

At this station, as shown in Fig. 7, *G. pachyderma* also dominates the water column, but significant is the dominance of *G. dutertrei* particularly in the upper layer. *G. scitula* is a deep-water dweller as is at St. 1, but the cold water species such as *G. uvula*, *G. pachyderma*, *G. bulloides* and *G. quinqueloba* are not shallower inhabitants as discussed previously.

A peculiar phenomenon is that, although temperature is comparatively high in the upper 10 m layer, the percentage of *G. dutertrei* is low there. This can be explained from the following assumption: 1) *G. dutertrei* is a species that dominates the subsurface layer as previously discussed, and 2) as St. 2 is located in the perturbed area, the lateral and vertical mixing processes of water masses should carry specimens from the deeper to upper layers. This will be favored by such observations that, in the upper 50 m layer, there are some encrusted specimens of *G. pachyderma* native to the deeper layer at St. 1 as discussed later. Considering a low concentration of planktonic foraminifera in the surface layer, these two factors may play an important role in forming a peculiar distribution pattern in the upper layer at St. 2.

It is also curious that most of the specimens of *G. dutertrei* and other species in the deeper layer possess protoplasm. It seems unnatural that specimens, particularly of warm water species, succeed in living in the deeper layer of low temperature. Those specimens with proto-

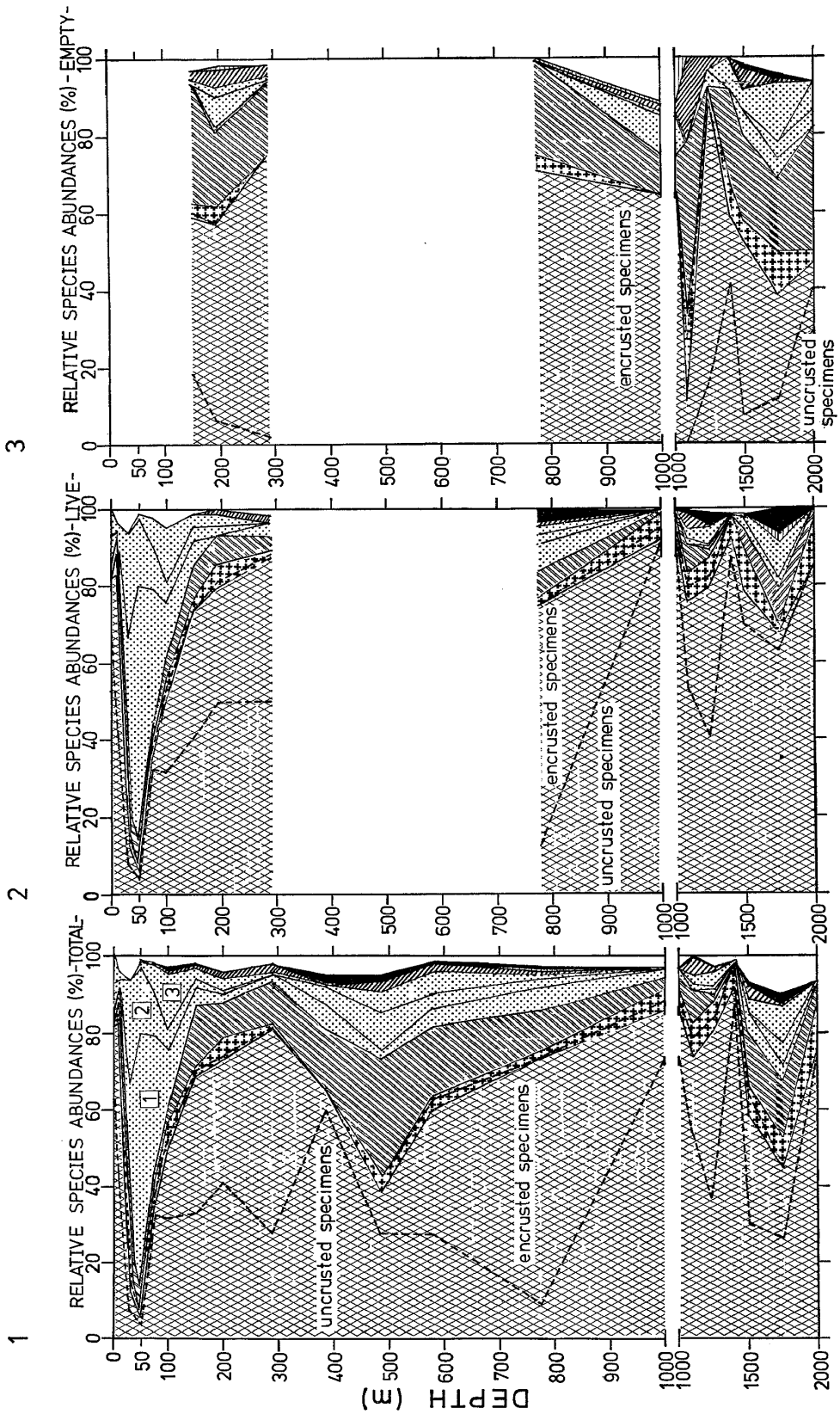

Fig. 7. Relative abundance of planktonic foraminiferal species in the water column at KT-77-8 Station 2. 1, total specimens (live plus empty); 2, live specimens; 3, empty specimens; a, *Globigerina pachyderma*; b, *Globigerina bulloides*; c, *Globigerina quinqueloba*; d-1, *Globoquadrina dutertrei* s.s.; d-2, *Globigerina incompta*; d-3, *Globigerina* aff. *G. pachyderma*; e, *Globigerinita uvula*; f, *Globigerinita glutinata*; g, *Globorotalia scitula*; h, others.

plasm may not represent live specimens but ones settled down from the upper layer without decomposition of their protoplasm. These phenomena imply slow decomposition of protoplasm as compared with settling velocity in water column. This does not, however, exclude utterly the possibility that planktonic foraminifera dwell or reproduce in the deep layer or near the sea bottom.

Although *G. dutertrei* dominates the upper layer, its relative frequency, for both live and empty assemblages, is not so high in the deep layer. Such a distribution pattern shows a reciprocal relation to that of *G. pachyderma*; the high concentration of this species appears in the intermediate layer (200 m) and from this or the overlying layer its tests descend down to the deeper layer.

Fluctuations in relative frequency of species in the water column reflect a periodic descent of shells from the upper layer. Moreover, marked fluctuations in the ratio of encrusted specimens to uncrusted ones are probably due to differences in settling velocity between uncrusted and empty shells.

Another important observations are that the concentration of *G. dutertrei* s.s. is high at depths of 30–50 m (in the upper layer), the high temperature layer, and *G.* aff. *G. pachyderma* predominates at depths of 75 to 100 m, the relatively low temperature layer. This is also discussed later.

Specimens in the upper 150 m layer are mostly live; empty shells, encrusted specimens after reproduction, initially appear at a depth of 200 m as in the case of St. 1 (Fig. 6). The specific composition in the upper layer has some resemblance to that in the underlying layer.

B. Ontogenetic Change of Planktonic Foraminifera in Vertical Distribution

Ontogenetic changes in vertical distribution were examined intensively on *G. pachyderma*, mainly using the specimens collected from St. 1. For this sort of study, the specimens from this station have the advantage of that an ecologic distribution pattern remains unmodified because of the simplicity of the environments, higher concentrations of individuals and less numbers of species, as compared with those of St. 2.

It is generally concerned that the size of tests represents ontogenetic stages. In this study at the first step, the maximum dimensions of the specimens were taken for each water depth layer under a binocular microscope equipped with micrometer (Fig. 8). The thickness of test wall was also measured on the specimens fixed on a slide glass with Caedax under an optical microscope at magnifications of $\times 400$ or 600 (Fig. 9). For this measurement, the specimens were randomly picked up from the live samples collected at each water depth.

As a result, juveniles dominate the upper 30 m layer, and adults predominate depths of more than 50 m (Fig. 8), showing no appreciable change in the shape of frequency curve. In the upper 50 m layer, however, the modes gradually move toward the larger side with depths from the surface to a depth of 50 m. This trend implies a gradual growth of individuals within a depth range of 0 to 50 m.

Shell thickening from the surface to a depth of 50 m is probably not related to encrustation but a natural result of ontogenetic development (Fig. 9). On the other hand, a clear tendency of encrustation is seen at depths of 50 m to 150 m. The encrustation at this depth interval results in a bimodal frequency distribution of shell thickness in layers deeper than 150 m. Hence, except for the specimens from depths of 75–100 m which show a transitional stage of encrustation, encrusted specimens are easily distinguished from uncrusted ones under a binocular microscope. From the

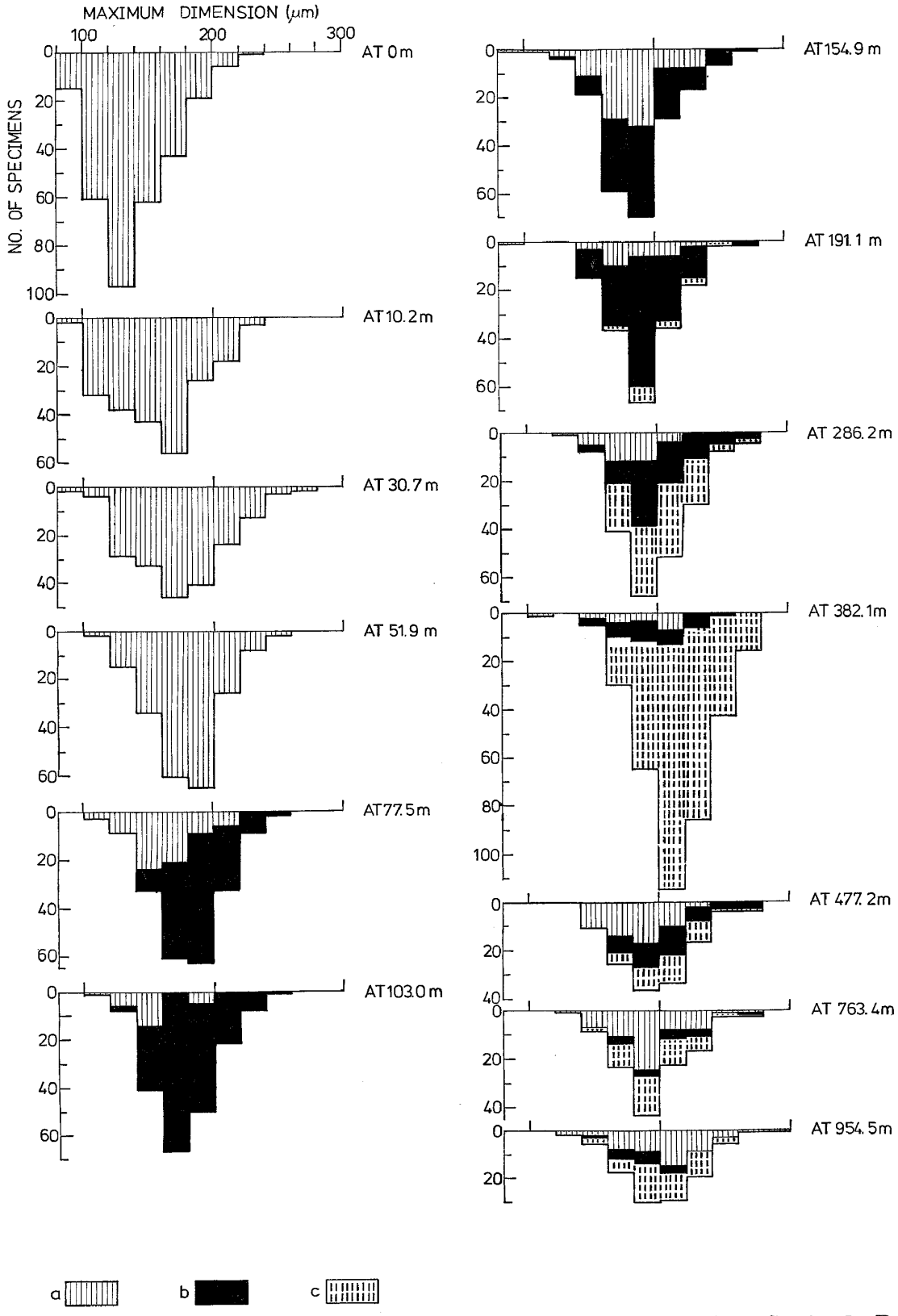

Fig. 8. Maximum dimension frequency of *Globigerina pachyderma* at KT–78–7 Station 1. Depths indicate sampling horizons of simultaneous horizontal tows (MTD nets). a, uncrusted specimens (live); b, encrusted specimens (live) c, encrusted specimens (empty).

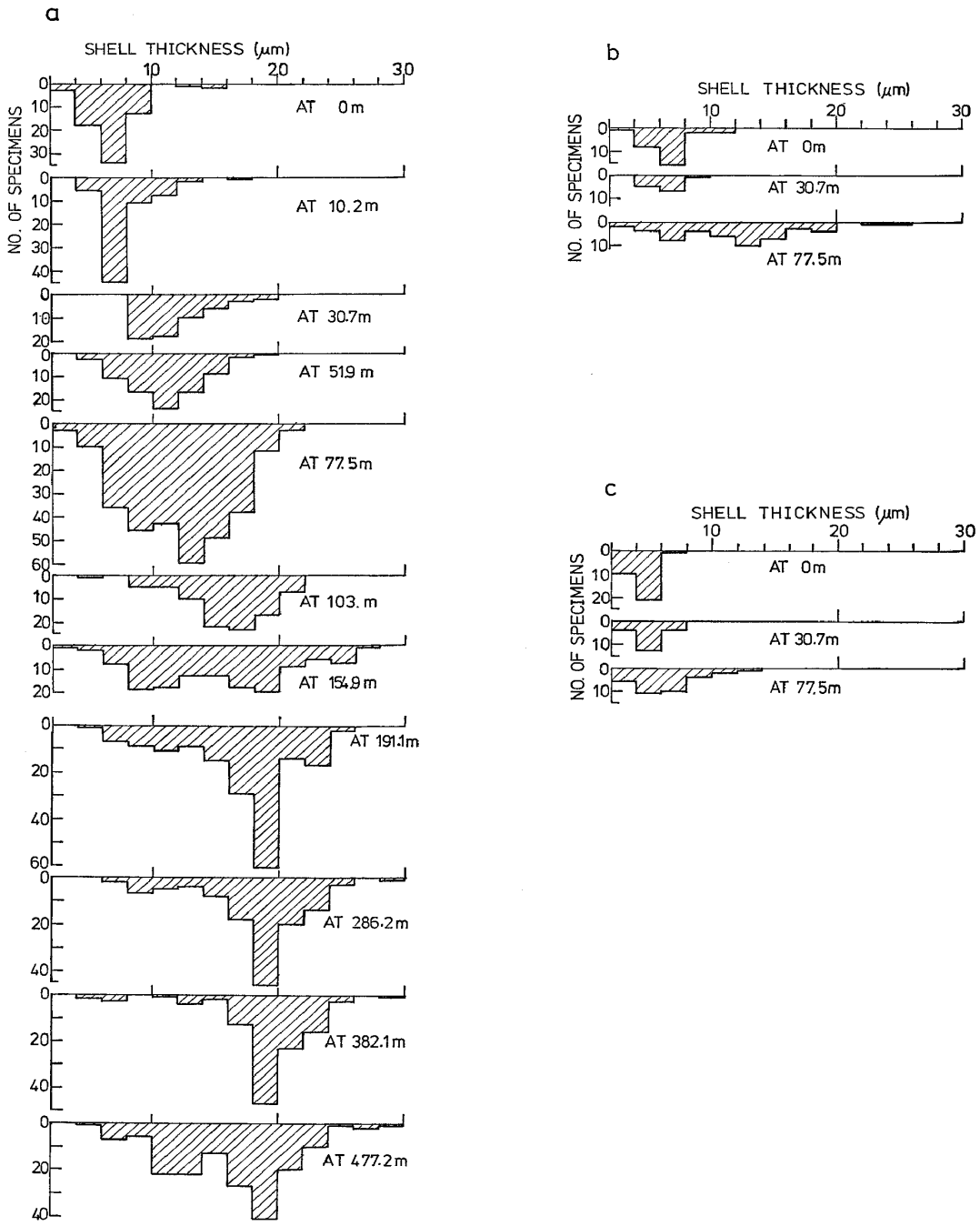

Fig. 9. Frequency of shell thickness of foraminiferal species at KT–78–7 Station 1. Depth indicates sampling horizon of simultaneous horizontal tows (MTD nets). a, *Globigerina pachyderma*; b, *Globigerina bulloides*; c, *Globigerina quinqueloba*.

observation on encrusted specimens under an optical microscope and on dissected specimens by the scanning electron microscope, it is clear that encrustation takes place in the last stage of growth after all the chambers are constructed.

Encrusted specimens predominate over uncrusted specimens at depths of 75 m to 400 m (Fig. 8). The empty shells of all species initially appear at a depth

of 200 m, and the empty tests of *G. pachyderma* predominate over the uncrusted ones at depths of 200–400 m.

This result indicates that encrustation of tests takes place in the 50–150 m layer in preparation for producing offspring at depths of 200–400 m.

Except for the 75–150 m layer, there are few specimens intermediate between encrusted and uncrusted ones. Such an occurrence indicates a rapid encrustation, and suggests that the process will not stop on the way of the encrustation.

Kummerforms, specimens with a smaller ultimate chamber than penultimate one, initially appear at a depth of 75 m where the test begins to encrust (Fig. 10). Through the water column between 75 m and 500 m, uncrusted specimens contain a small percentage of kummerforms (0–10%), but encrusted ones do 25–40 percent no matter whether they are live or empty and completely encrusted or not. The record indicates that both the addition of a small ultimate chamber and encrustation are of reproductive phase, and the kummerform stage precedes the encrusting one.

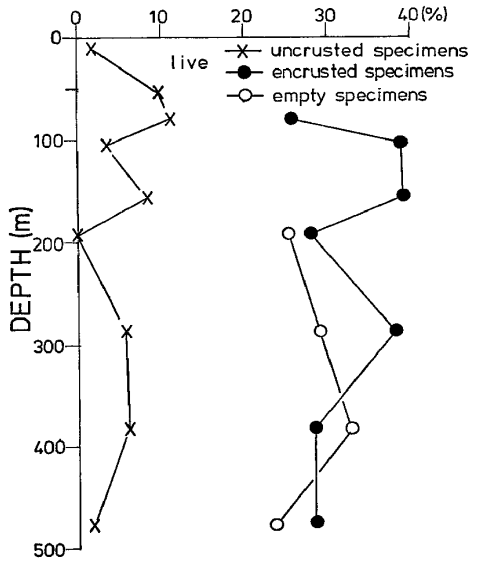

Fig. 10. Percentage of kummerforms of *Globigerina pachyderma* in the water column at Station 1.

Since Sigma-t values (specific gravity of water) at depths between 50 m and 100 m are almost constant (Fig. 3a), the Berger's view (1969a), as it is called, which explains encrustation by floating adaptability to water, is not applicable to this depth interval.

Compared with St. 1, the tendency of encrustation of *G. pachyderma* is not so clear at St. 2, but there is still an increasing encrustation from the upper layer to a depth of 150 m (Fig. 11a). A bimodal frequency distribution of shell thickness also exists at depths greater than 150 m. The existence of empty shells at depths from 150 m to 300 m at St. 2 (Fig. 12) suggests that this depth layer is also favorable for reproduction.

At St. 1, *G. bulloides* and some of the specimens of *G. quinqueloba* begin encrustation at the same depth as *G. pachyderma* (Fig. 9b, c). At St. 2, many of the specimens of *Globoquadrina dutertrei* complete encrustation at a depth of 75 m (Fig. 11b).

Another criterion implicit in growth stages is the chamber numbers from the proloculus to the last chamber. Figure 13 shows a linear correlation between the shell diameter and chamber numbers within each of various classes of the proloculus diameter. In this study, the diameter of tests is represented by the maximum inner diameter to avoid the effects of anomalous shell thickening. The results clearly show that specimens with larger proloculus diameter are larger in test diameter even when the chamber number is same (Fig. 13). On the other hand, in adults, the test diameter is nearly constant regardless of the proloculus diameter, and, of the chamber number at the last stage (Fig. 14b-e).

The observed growth indicates that the chamber number at the last stage depends on the proloculus diameter. It is, therefore, not reasonable to assume

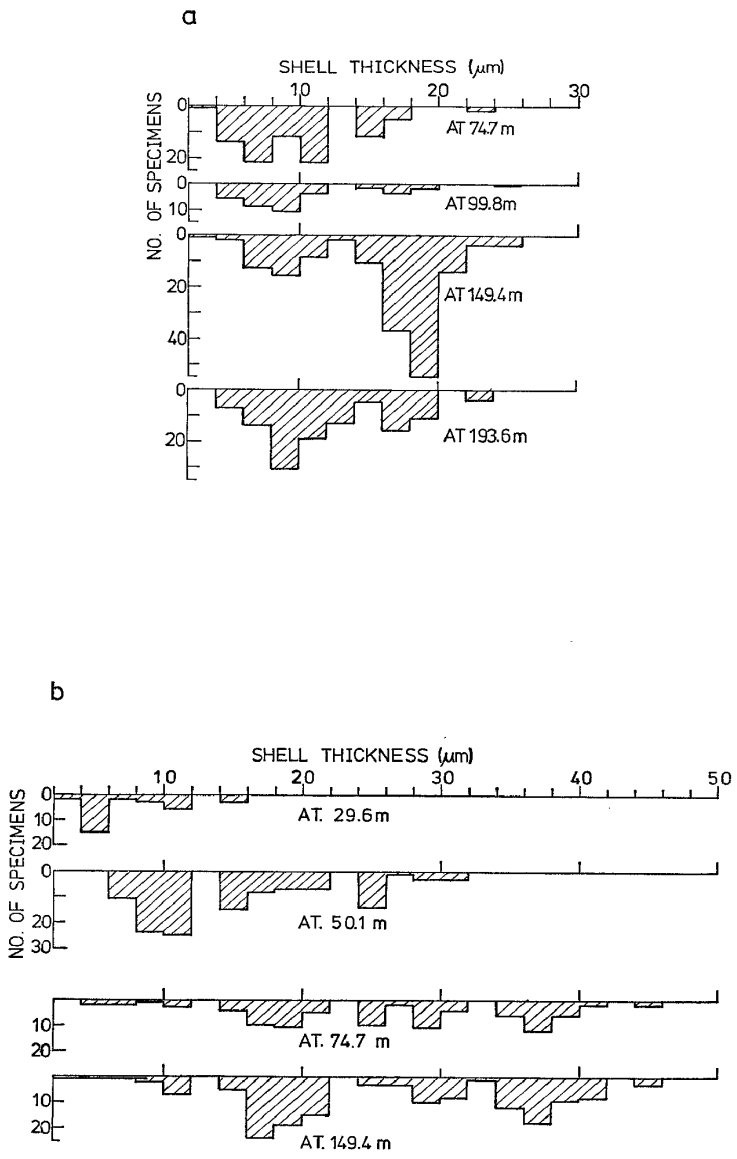

Fig. 11. Frequency of shell thickness of foraminiferal species at KT–77–8 Station 2. Depths indicate sampling horizons of simultaneous horizontal tows (MTD nets). a, *Globigerina pachyderma*; b, *Globoquadrina dutertrei* s.s.

that the chamber number always reflects growth stages of planktonic foraminifera. Consequently, it is most desirable in investigations to determine growth stages by means of both the average chamber number and the maximum dimension within each of various classes of the proloculus diameter, and then to compare those values with each other. The results are shown in Fig. 14.

Figure 14a shows in comparison with Figs. 14b-e that the upper 30 m layer is dominated by juveniles as judged by both chamber number and maximum dimension. In more detail, among the upper 0, 10 and 30 m layers, differences in the mean diameters of the specimens with a smaller proloculus are smaller than those with a larger proloculus.

On the other hand, the chamber number and the diameter of specimens at depths of 50 m to 500 m mostly match

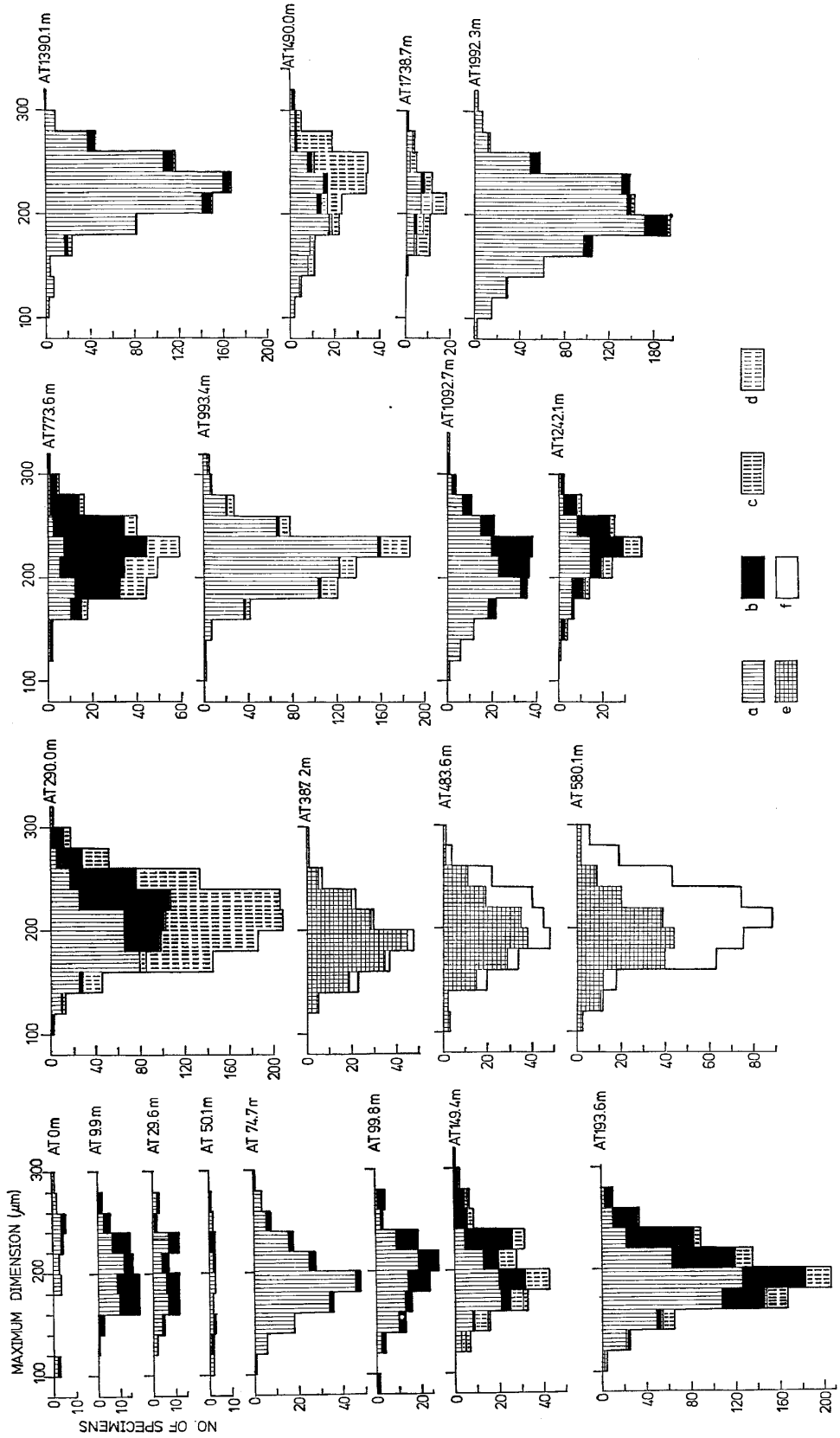

Fig. 12. Maximum dimension frequency of *Globigerina pachyderma* at KT-77-8 Station 2. Depths indicate sampling horizons of simultaneous horizontal tows (MTD nets). a, uncrusted specimens (live); b, encrusted specimens (live); c, encrusted specimens (empty); d, uncrusted specimens (empty). e, uncrusted specimens (live plus empty); f, encrusted specimens (live plus empty).

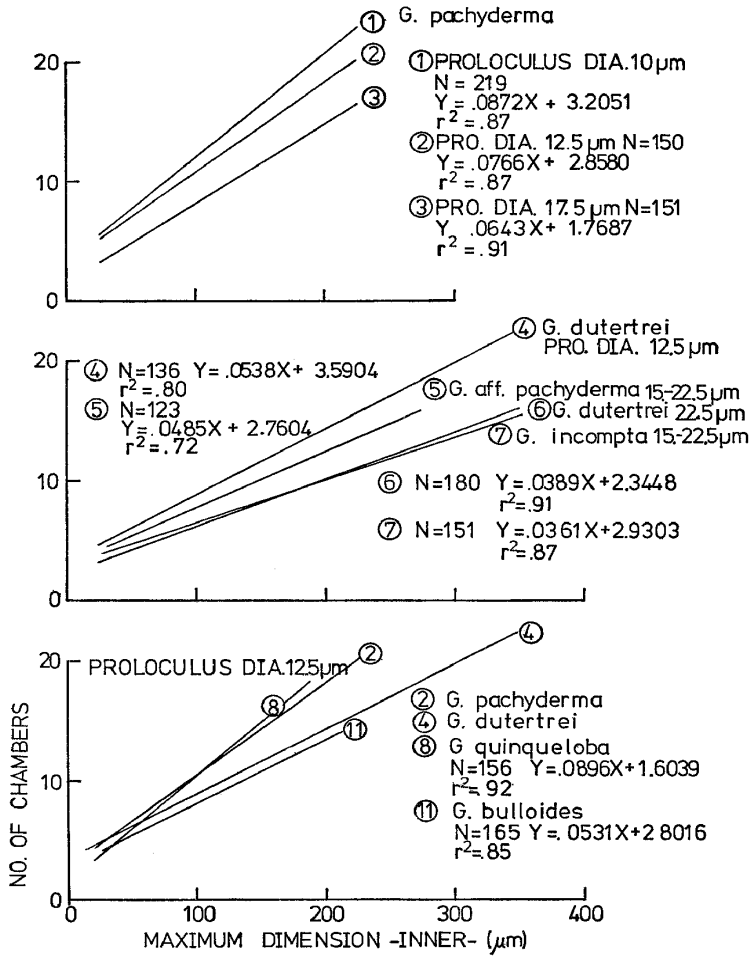

Fig. 13. Growth curves of planktonic foraminiferal species with the same proloculus diameter, except for *Globigerina incompta* and *Globigerina* aff. *G. pachyderma*.

with each other (Figs. 14b–e). In more detail, at a depth of 500 m the chamber number of uncrusted specimens fits that of encrusted ones, but the maximum dimension of encrusted specimens are about 20 μm larger than that of uncrusted ones (Fig. 14e). In addition, the maximum dimension and the chamber number of uncrusted specimens at a depth of 500 m match well with those at 50 m (Figs. 14b, e). A difference of 20 μm is twice that of the shell thickness between encrusted specimens and uncrusted ones (Fig. 14e).

This shows that most of the uncrusted specimens below a depth of 50 m are also adults without crusts. The shells of *G. pachyderma* without crusts are thus constructed mainly in the upper 50 m layer.

In addition, empty specimens at St. 1 range in maximum dimension from 140 μm to 280 μm and chamber number from 11 to 19. Hence, the shell diameter and the chamber number do not necessarily indicate growth stages; *G. pachyderma* reproduces at various growth stages as suggested by shell diameter and number of chambers.

In short, juveniles of planktonic foraminifera, particularly of *G. pachyderma*, dominate the populations in the upper 30 m layer and adults below a depth of 50 m. Adults begin encrustation at depths around 50–75 m which sometimes proceeds from attaching of a small ultimate

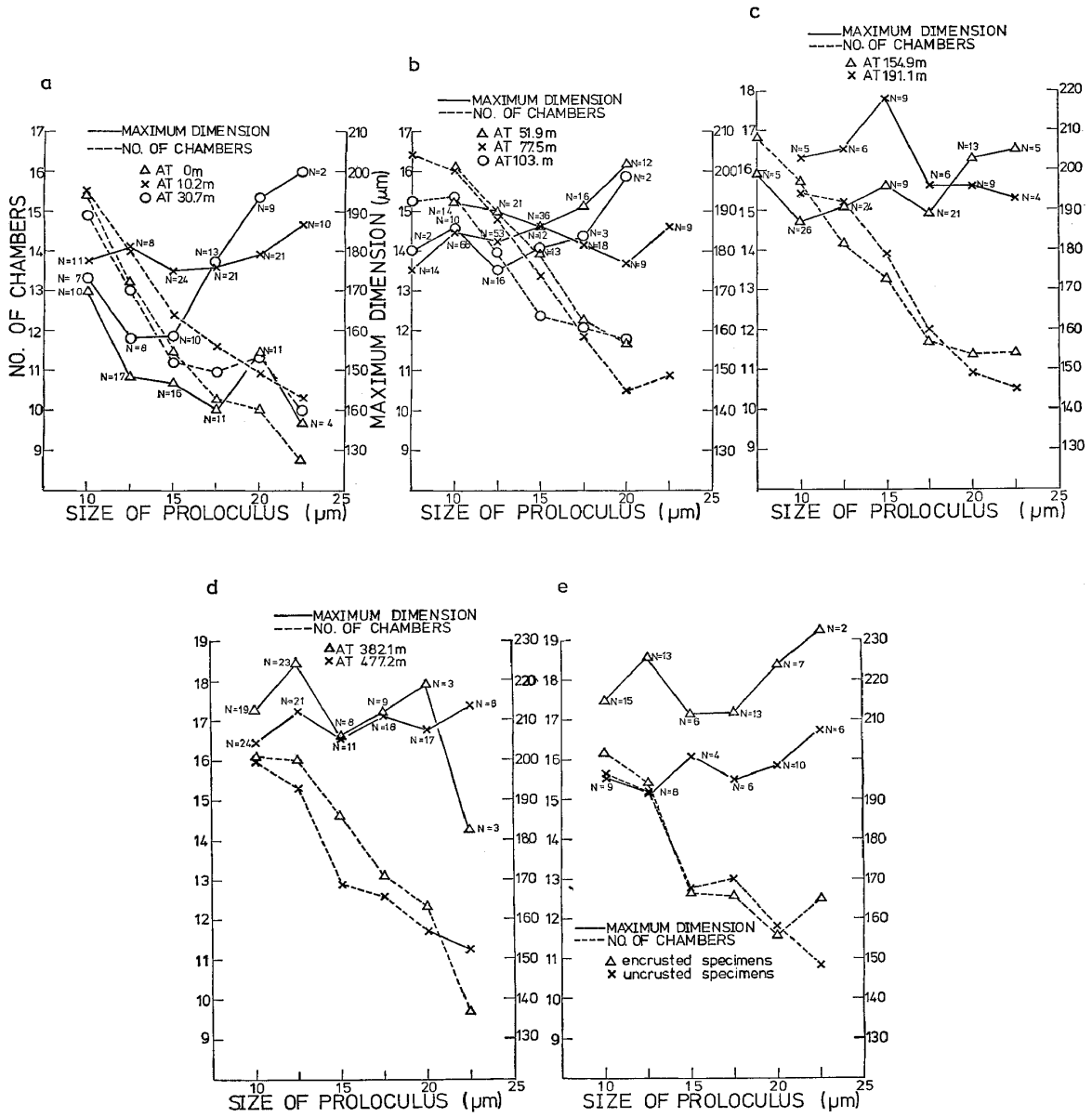

Fig. 14. Variation in proloculus size of *Globigerina pachyderma* in relation to the number of chambers and maximum dimensions in samples collected by simultaneous horizontal towing at various depths. a-d, total specimens (encrusted plus uncrusted); e, encrusted specimens vs. uncrusted ones at a depth of 500 m.

chamber and finishes at a depth of 150 m. Encrusted specimens reproduce and put off empty shells at depths of 150 m to 250 m. The above-mentioned facts possibly indicate that planktonic foraminifera needs water depths more than 200 m to complete their life cycle. This may be one of the factors that appear to be responsible for planktonic foraminifera being indigenous to the pelagic realm.

C. Proloculus Diameter

Through examinations on the specimens collected by the filtration-system from the water column in the equatorial Atlantic, Bishop et al. (1977) first mentioned that planktonic foraminifera also have microspheric and megalospheric

individuals as do benthic foraminifera. According to them, the megalospheric specimens dominate the upper layer and the microspheric ones exist in the deep layer. Further, they suggested the possibility of alternation of generations of planktonic foraminifera at different water depths.

The writer examined frequency distribution of live specimens in each of various classes of the proloculus diameter at each layer (Figs. 15–17). However, a direct comparison with the result of Bishop et al. (*op. cit.*) is improper, since the specimens collected by tows are largely adults, on the other hand, specimens collected by filtration system involve many juveniles. Proloculus diameter was measured mainly on the specimens collected at St. 1 by the same method with the shell thickness (magnifications are ×400 or 600).

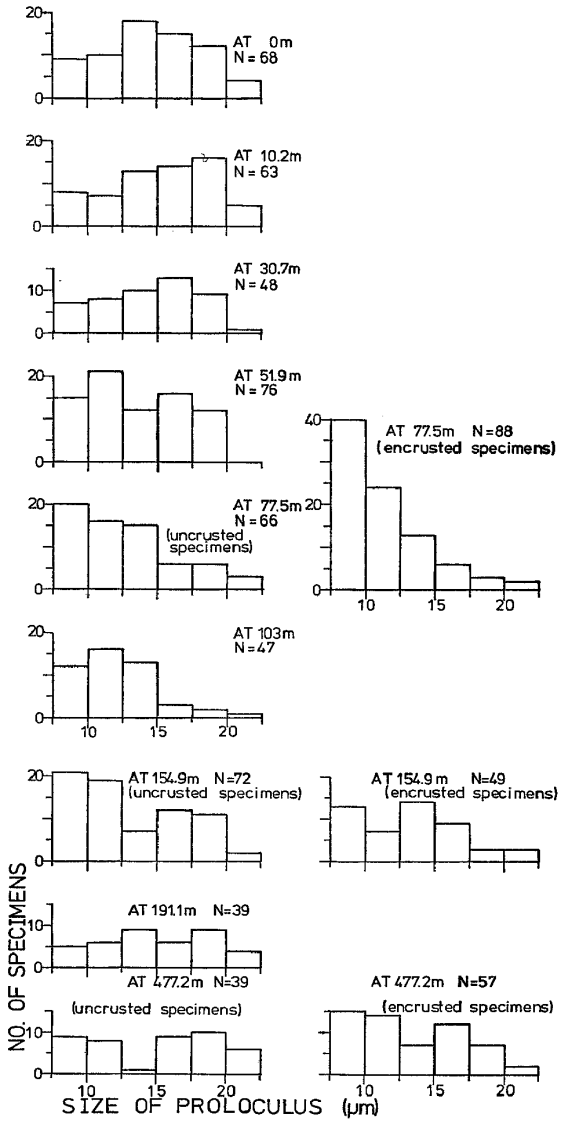

Fig. 15. Frequency diagram of proloculus size of *Globigerina pachyderma* at different depths of KT–78–7 Station 1.

The proloculus diameter of *G. pachyderma* ranges from 6.5 μm to 26.3 μm. Fig. 15 shows that specimens in the upper 30 m have a large proloculus, and specimens with a small proloculus dominate at depths of 50 m to 100 m. Water temperatures at each depth are: 7.9°C to 1.5°C at 0–30 m and 0.8°C to 0.75°C at 50–75 m (Fig. 3a). This fact probably shows that the proloculus diameter of *G. pachyderma* is closely related to water temperature. In waters colder than 1°C, the specimens with a small proloculus dominate, but in the warmer water so do the ones with a large proloculus.

A minor contradiction to this presumption is: (1) a slight but apparent high frequency of the specimens with a large proloculus at a depth of 50 m and (2) the predominance of the specimens with a small proloculus at a depth of 100 m (inter-warm water). This may be explained by the presence of descending specimens from the upper layer.

On the contrary, at St. 2, the specimens of *G. pachyderma* with a large proloculus dominate the upper 200 m (Fig. 16a). This may be resulted from high temperatures exceeding 5.76°C at this station (Fig. 3b).

At St. 1, *G. bulloides* and *G. quinqueloba* largely have a small proloculus which ranges 7.5–17.5 μm in the former and 7.5–22.5 μm in the latter, respectively, in the upper 75 m layer of comparatively high temperature (Figs. 17a, b).

At St. 2, *G. dutertrei* also shows a clear correspondence between the proloculus diameter and water temperature in a

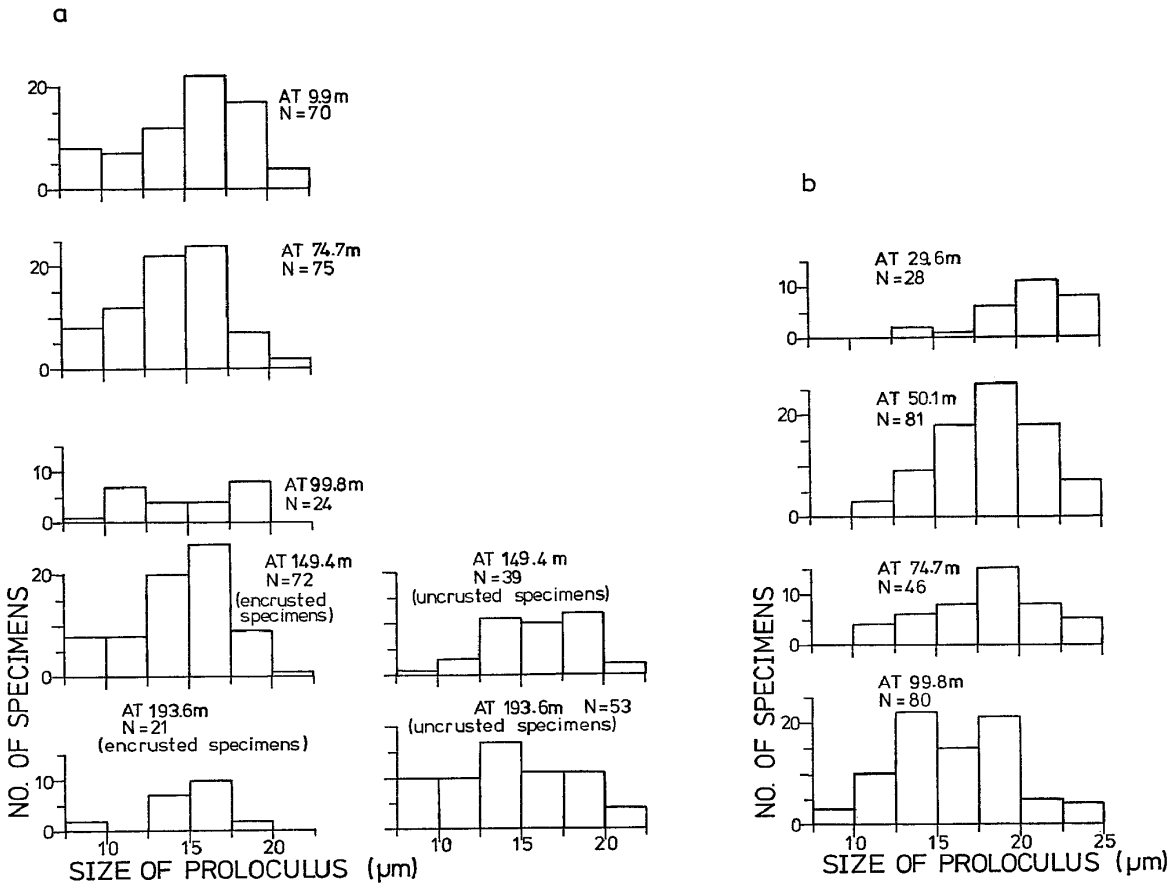

Fig. 16. Frequency diagram of proloculus size of *Globigerina pachyderma* and *Globoquadrina dutertrei* at different depths of KT–77–8 Station 2. a, *Globigerina pachyderma*; b, *Globoquadrina dutertrei*.

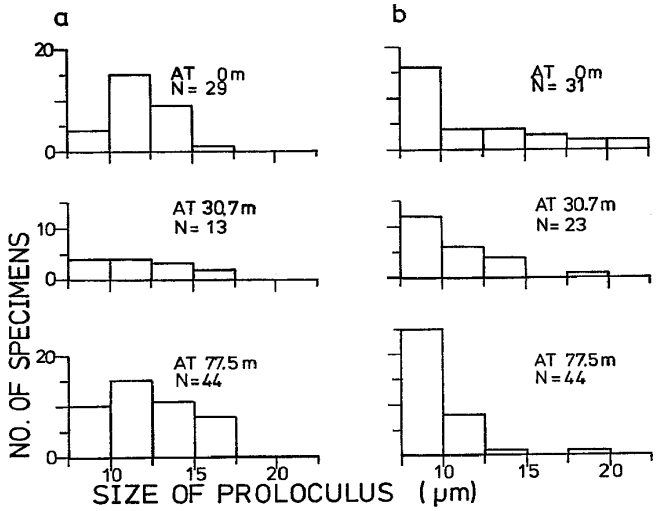

Fig. 17. Frequency diagram of proloculus size of *Globigerina bulloides* and *Globigerina quinqueloba* at different depths of KT–78–7 Station 1. a, *Globigerina bulloides*; b, *Globigerina quinqueloba*.

range of the proloculus diameter 10–27.5 μm (Fig. 16b). For example, the specimens with a large proloculus dominate the upper 75 m layer, and those with a small proloculus at depth greater than 100 m. Temperature at a depth of 75 m is 8.12°C and that of 100 m 8.73°C, respectively. Because these layers exist in a prominent thermocline, the above-mentioned phenomenon appears to correspond to lowering temperature. At depths of 75–100 m, the declining absolute abundance of *G. dutertrei* occurs as discussed previously, and the dominance of *G. pachyderma* exchanges for that of *G. dutertrei*.

The above-mentioned signs indicate that planktonic foraminifera also have specimens with microspheric and megalospheric proloculi that may correspond to the sexual and asexual generations, respectively, which alternate with each other in different layers or seasons.

The benthic species in the microspheric stage generally can tolerate unfavorable conditions (Hofker, 1930) and dominate at the cold season (Myers, 1943). As planktonic foraminifera inhabit the water column whose deeper layer has ordinarily lower temperature and chlorophyll *a* value and is deficient in oxygen, the microspheric specimens exist in the deeper layer and megalospheric ones gather in its upper layer.

Examinations of the proloculus diameter may lead to a conclusion that *G. pachyderma* has proficiency in cold water environments, and water temperatures of around 8°C is a critical point for the existence of *G. dutertrei*.

D. Flux of Tests

1. *Live specimens*

Sediment traps were set in the daytime and night separately, and nets were towed at noon when the daytime sediment traps were being suspended. It is then possible to clarify the daily vertical

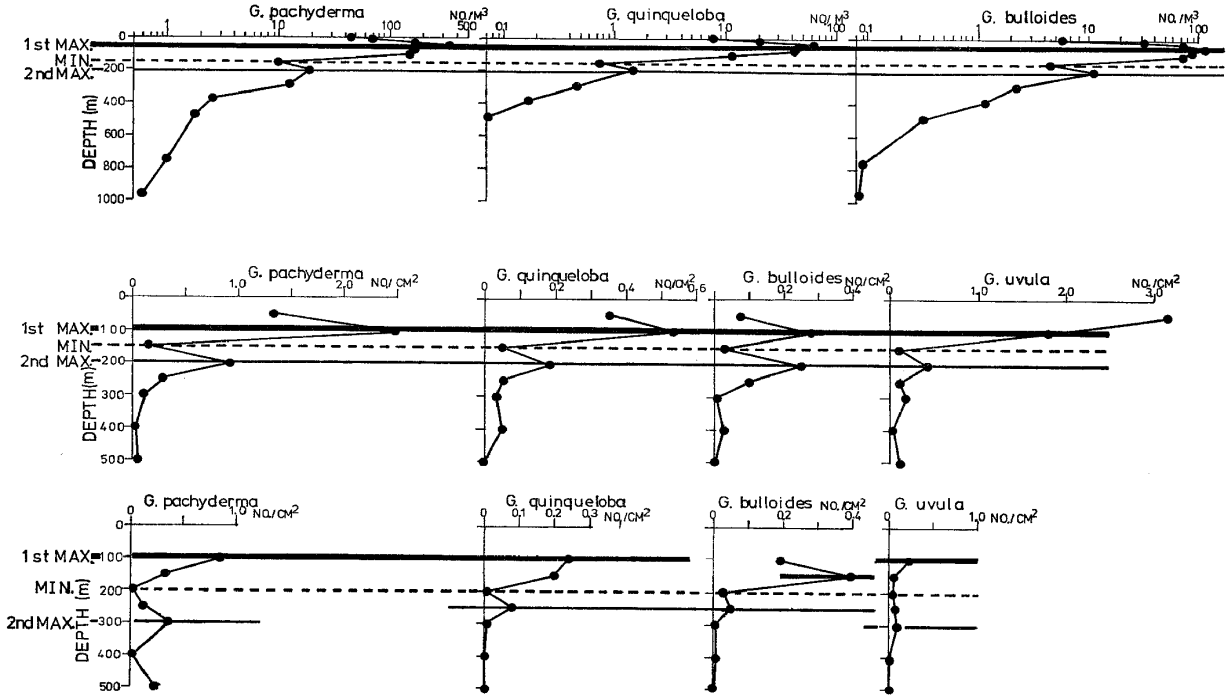

Fig. 18. Populations and flux of the live specimens of planktonic foraminiferal species at KT–78–7 Station 1. Upper, samples collected by the nets (13:00–15:00, May 27, 1978); middle, flux density in sediment traps (collector) in the night (21:00, May 27– 9:00, May 28, 1978); lower, flux density in sediment traps (collector) in the daytime (9:30–19:00, May 27, 1978).

movement of foraminifera from the flux and concentration pattern determined in temporal sequence.

The empty specimens of *G. pachyderma* both in sediment traps and tows are almost adult tests after reproduction. This is also true in *G. quinqueloba*, *G. bulloides* and *G. uvula*. For the study of daily dynamics, live and empty specimens should be treated separately, since empty tests are specimens settled down after reproduction following specific gravity, while live specimens may move in their own ways not only downward but also upward.

Sediment traps (collector) store specimens coming down. Once stored in cylindrical glass tubes, most of the specimens probably never get out of them.

The results are shown in Figs. 18 and 19. Figure 18 shows that the density profiles of all the species both in the daytime and night denote two maxima and a minimum as does the case of concentration. In the density profile of the night traps, the upper maximum exists at a depth of 100 m, and a minimum at 150 m, and the second (lower) maximum at 200 m for all species.

In the daytime traps, the upper maximum exists at a depth of around 100 m, and the minimum at a depth of 200 m for all species except for *G. bulloides* that has the upper maximum at a depth of 150 m. The lower maximum exists at a depth of 300 m both for *G. pachyderma* and *G. uvula*, and at 250 m for *G. bulloides* and *G. quinqueloba*, respectively.

Accordingly, in the daytime, the minimum density layer shifts about 50 m

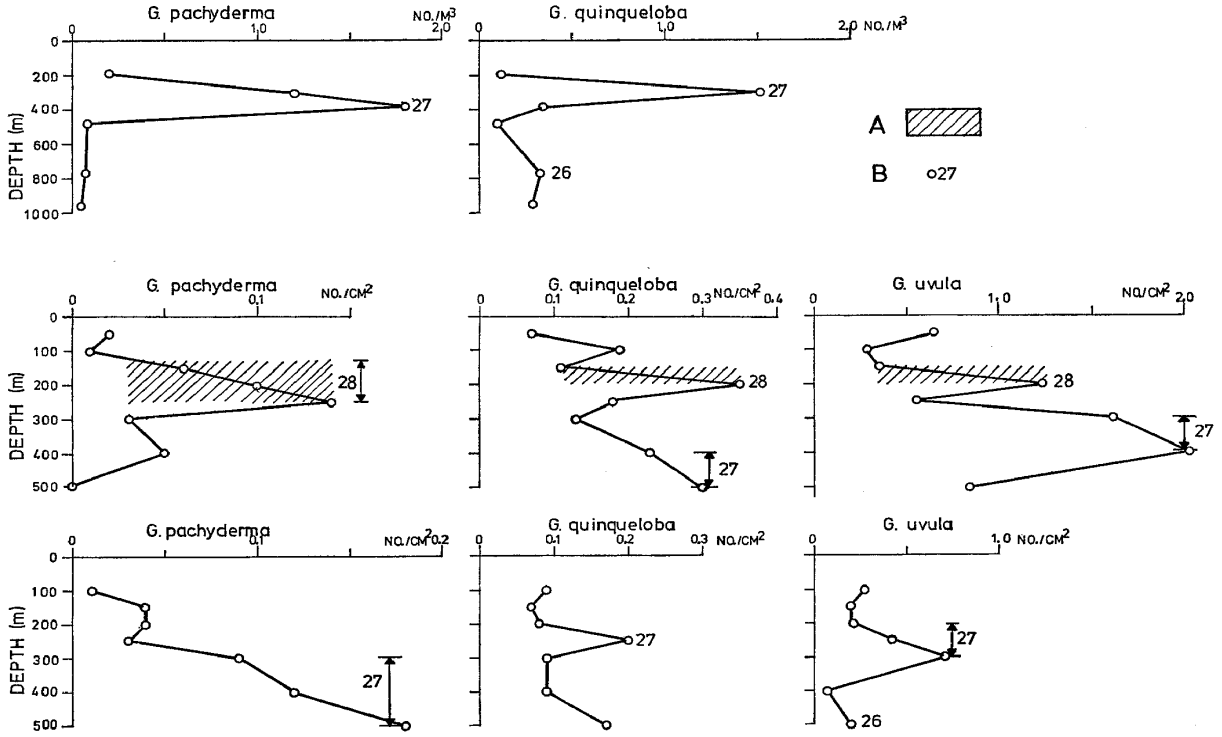

Fig. 19. Flux of empty specimens. Upper, samples collected by nets (13:00–15:00, May 27, 1978); middle, flux density in sediment traps (collector) in the night (21:00, May 27–9:00, May 28, 1978); lower, flux density in sediment traps (collector) in the daytime (9:30–19:00, May 27, 1978).
A, reproduction zone; B, specimens started reproduction early in the morning on May 27, 1978.

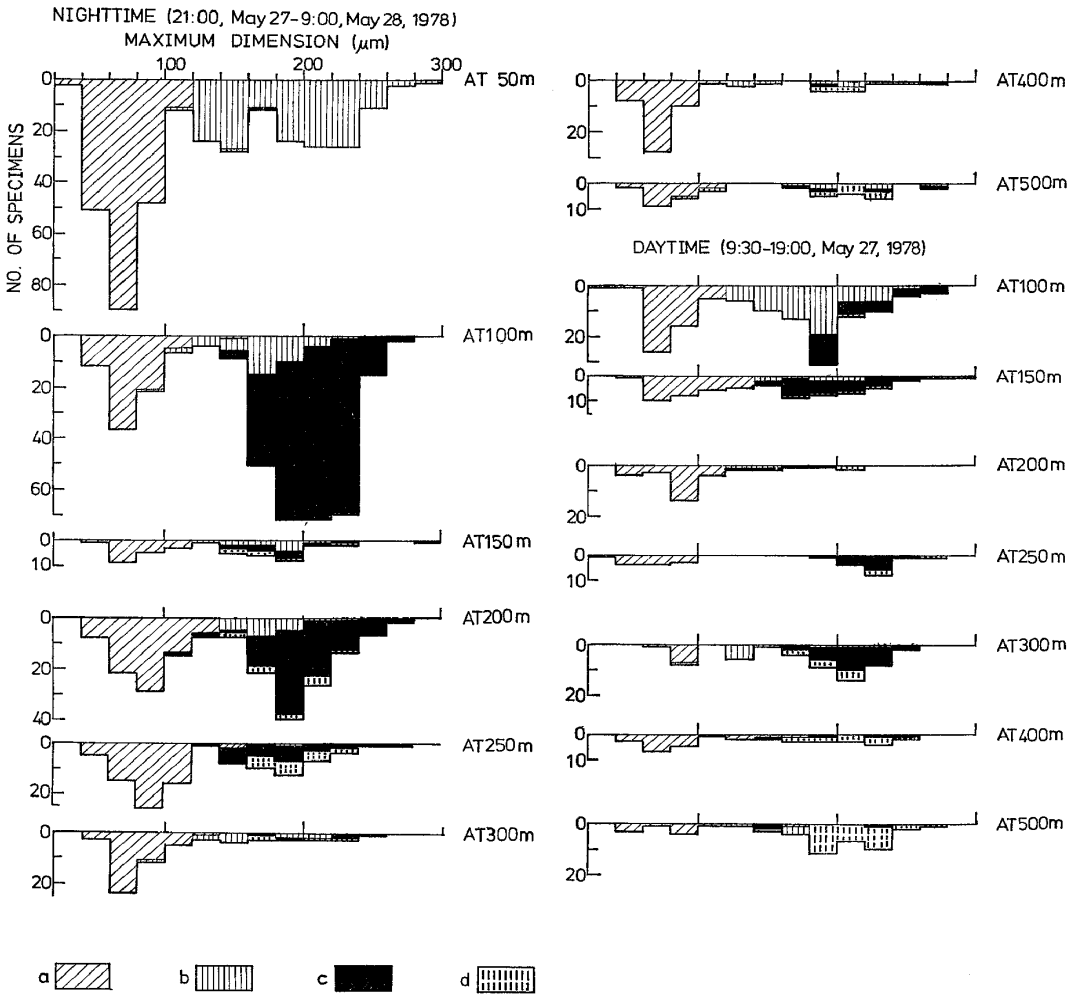

Fig. 20. Flux of *Globigerina pachyderma* sampled by sediment traps (collector). a, juveniles of *Globigerina pachyderma*, *Globigerina bulloides* and *Globigerina quinqueloba*; b, uncrusted specimens (live); c, encrusted specimens (live); d, encrusted specimens (empty).

downward for all species, and the lower maximum also shifts about 50 to 100 m downward, but the upper maximum layer stays at a depth of 100 m or so except for *G. bulloides*.

When the concentration of *G. pachyderma* which may represent an intraspecific structure *in situ* and that from the sediment traps are compared, the ratio of encrusted or uncrusted specimens to the total *G. pachyderma* agrees well with each other at depths of 50 m, 100 m and 200 m, during the night (Fig. 20).

On the other hand, the calculated density in sediment traps, particularly in the night, is significantly greater than the real concentration of the specimens in water column on the stipulation that specimens simply descend in water column. In detail, a water column of 0–150 m (150 m^3) contains 6,800 specimens of *G. pachyderma*, larger than 120 μm in diameter. On the other hand, the night trap at a depth of 50 m received 12,800 specimens of a size per m^2: The measured concentration from the traps in the night is several times higher than that in the daytime.

Such discrepancies may indicate that the specimens in water column do not simply come down but possibly move up

and down frequently during their descent. The movement in this manner takes place both in the upper and lower layers. Nocturnal vertical oscillations are several times over those of the daytime. In the daytime most of the specimens probably move up, especially early in the morning, so that no clear descending processes are shown. The distance of vertical migration in a day is up to 50 m.

Encrusted specimens are supplied from the 75–150 m layer into the 200 m layer after sunset (19:00–21:00) and some of them may go up again early in the morning.

The high density of juveniles (Fig. 20) accords with the observations by Bé (1977) that these specimens are carried downward in the shape of pellets without any destruction by feeders. A depth around 150 m is a passage through which ontogenetic migration takes place from the pelagic layer down to the lower maximum concentration layer.

2. *Empty specimens*

a) *Globigerina pachyderma* (Ehrenberg): The empty specimens in the sediment traps at night (21:00–09:00, May 27–28) shows that density steeply increases from depths of 150 m to 250 m, and there is a minimum of density at a depth of 300 m (Fig. 19). On the profile of concentration (13:00, May 27), a maximum exists at a depth of 400 m. Thus it is concluded that empty specimens descend from 250 to 400 m in depth for 4 hrs. (09:00–13:00). A given settling velocity of the empty specimens of *G. pachyderma* is 1.04 cm/sec or 900 m/day. Figure 20 shows that the maximum concentration of live specimens composed almost entirely of encrusted specimens exist at a depth of 200 m.

Those facts show that the encrusted specimens of *G. pachyderma* reproduce simultaneously once a day early in the morning at a depth of around 200 m, the second maximum layer of concentration, and after then the encrusted empty shells settle down at their own speed, 900 m/day, without much disparity. If this settling velocity be valid, the empty shells, reproduced early in the morning of the preceding day, are present at a depth of around 1,300 m (400 m+900 m) at the time when the simultaneous horizontal tow was conducted (13:00, May 27).

The settling velocity of *G. pachyderma* can also be calculated in the following premises:

(1) The tests of *G. pachyderma* settle following the Stokes' Law as discussed by Berger and Piper (1972).

(2) As the encrusted specimens of this species are nearly spherical, the test can be approximated to a sphere with an average density struck by the weight of calcified test and inner cavity filled with sea water.

Settling velocity is calculated by the formula

$$V = \frac{2a^2(\rho_0-\rho)g}{9\eta}$$

where a: the radius of test, the mode of frequency in diameter, in this case 0.01 cm,

g: gravitational acceleration,

η: viscosity of water. In the case of sea water of 35‰ salinity at 0°C and 5°C, the viscosities are read from the table given by Sverdrup et al. (1942, p. 69) (18.9×10^{-3} c.g.s. at 0°C and 16.1×10^{-3} c.g.s. at 5°C, respectively), and

$(\rho_0-\rho)$: the density contrast of particles with sea water.

On these bases, the settling velocity was calculated at: 0.96 cm/sec or 830 m/day at 0°C and 1.12 cm/sec or 970 m/day at 5°C. The settling velocities agree well with the value obtained from an analysis of flux (1.04 cm/sec or 900 m/day).

The shell thickness of encrusted specimens is about 20 μm irrespective of the shell diameters, most of which range from

180 μm to 250 μm. The settling velocity of the specimens with those minimum and maximum diameters is also calculated: When the shell diameter is 250 μm, 1.25 cm/sec or 1,083 m/day at 0°C and 1.47 cm/sec or 1,271 m/day at 5°C, and when shell diameter is 180 μm, 0.83 cm/sec or 717 m/day at 0°C or 861 m/day at 5°C. Those values show that the empty specimens do not exhibit much disparity in their settling velocity. After reproduction, the empty specimens will descend without remarkable dispersion in a highly viscous cold water.

b) *Globigerina quinqueloba* Natland: A marked increase of empty specimens exists at depths of 150 m to 200 m in the night density (Fig. 19). This shows that the population around depths of the lower maximum concentration layer reproduces in the morning. In the case of *Globigerina quinqueloba*, the encrustation of empty specimens is not so marked as compared with *C. pachyderma* and *C. bulloides*. The reproduction zone of *G. quinqueloba* is narrower than that of *G. pachyderma*. This may imply that the settling velocity of the specimens, in reproduction, of the former is slower than that of *G. pachyderma*.

If a maximum of concentration shifts from depths of 200 m to 300 m in 4 hrs. (09:00–13:00) in the observation time, the settling velocity of empty specimens comes at 0.69 cm/sec or 600 m/day.

On the other hand, the concentration of empty specimens shows two maxima at depths of 300 m and 800 m. If the lower maximum is represented by specimens reproduced on the preceding day, the settling velocity is calculated at 0.52 cm/sec or 500 m /day. These values substantially agree with the former estimate.

The flux density in the night shows that empty specimens increase in number at depths of 300 m to 500 m (Fig. 19). This suggests the addition of specimens produced early in the morning on the day when the nighttime traps were set (When the nighttime traps were set, the empty specimens produced early in the morning on that day were located at a depth around 450 m (200 m+500/2 m)).

c) *Globigerinita uvula* (Ehrenberg): In the night density profile (Fig. 19), the empty specimens of *G. uvula* increase in number rapidly at depths of 150 m to 200 m. This indicates that reproduction takes place at depths of 150 m to 200 m. This layer corresponds to the second maximum of live specimens in the night profile (Fig. 18). There are two maxima of the density of empty specimens at depths of 200 m and 400 m. This profile probably reflects a decrease of settling velocity of the empty specimens of *G. uvula*, and the second maximum at a depth of 400 m would manifest the specimens reproduced on the preceding day.

When the night traps were set, the maximum layer which includes only the specimens reproduced early in the morning before probably at a depth of 300 m have sunk to a depth of 400 m, and the subsequent empty specimens were newly produced at depths of 150 m to 200 m. From these values the settling velocity of the empty specimens of *G. uvula* is calculated at about 0.23 cm/sec or 200 m/day.

In short, planktonic foraminifera migrate daily forming the concentration profile characterized by two maxima and one minimum. In the night they descend up to 50 m as a result of up- and downward movements. The specimens in the lower maximum concentration layer reproduce simultaneously at a depth around 200 m early in the morning. The specimens in reproduction and after the release of the daughter cells settle down following the species' own settling velocity. The reproduction layer corresponds to the secondary maximum concentration layer or the oxygen minimum layer. Specimens of the secondary

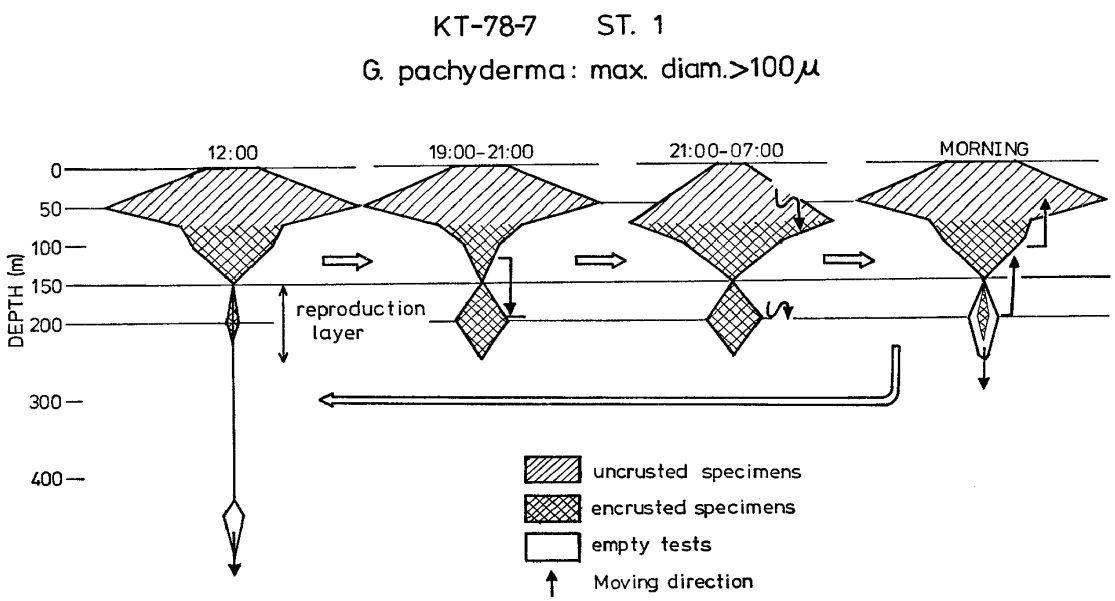

Fig. 21. Schematic diagram of daily vertical migration.

maximum layer were probably supplied from the upper layer after sunset.

Therefore, specimens in the deeper layer are not independent but mutually related to those in the upper layer through the process of daily or ontogenetic migration. Daily vertical movement of *Globigerina pachyderma* is schematically shown in Fig. 21.

3. *Turnover time*

A knowledge of the turnover time of planktonic foraminifera enables one to appraise the flux of foraminiferal specimens to the sea bottom and provides paleontologists with a clue to understand fossil assemblages.

The turnover time or the reproduction rate of planktonic foraminifera was calculated from the method described by Berger (1967). The empty specimens in this study are probably tests after reproduction. So, the turnover time can be expressed by the ratio of empty specimens to live ones. The live specimens are all adult, larger than 150 μm in diameter, and their numbers are calculated from the concentration in the upper 150 m of water column except for the case of *G. pachyderma* in which the concentration in sediment traps was also used.

The results and the measured thickness of the layer in which empty specimens gathered are:

	Thickness (and depths) of layer in which empty shells cluster	Turnover time	
		nets	sediment traps
G. pachyderma	100 m (300 m to 400 m)	14 days	15 days
G. bulloides	200 m (300 m to 500 m)	24 days	
G. quinqueloba	50 m (275 m to 325 m)	22 days	

Generally, the turnover time in this study is shorter than that recorded by Berger (1967) at the Santa Barbara Basin in August. Compared with the summer in the Santa Barbara Basin, the Oyashio water, where St. 1 is located, is marked by a high productivity especially in bloom during the spring. So accelerated may be the reproduction by fertility of the water of St. 1.

RELATIONSHIP BETWEEN 'TYPICAL' AND 'THIN-SHELLED' FORMS OF *GLOBIGERINA PACHYDERMA* (EHRENBERG)

Cifelli (1973) reported an enigma concerning the left-coiled *Globigerina pachyderma*: Specimens are entirely 'typically' encrusted in the bottom sediments of the subarctic and temperate areas, but their counterparts are absent in surface water. Bé and Hamlin (1967) and others also reported the same fact except for the specimens from the sea bottom on the continental shelf in the Ross Sea (Kennett, 1968) and Beaufort Sea (Vilks, 1975) where the sedimentary basins are shallower than 200 m.

The encrusted form of *G. pachyderma* at St. 1 may be equated to the Cifelli's (1973) compact form on the sea bottom of subarctic-temperate areas. In this study, it is concluded that encrustation and kummerforms represent a reproductive phase. Encrustation will never stop in the transitional stages. Both the concentration and flux indicate that the vertical flux of *G. pachyderma* is mainly the result of reproduction except for juveniles (smaller than 100 μm in shell diameter) (Figs. 18–20). The above-mentioned view explains the enigma that the specimens of *G. pachyderma* on the sea bottom are entirely 'typical' forms.

As the encrustation of *G. pachyderma* takes place in the course of a descent, beginning at depths of 50 m–75 m and ending at a depth around 200 m, sediments on the sea bottom shallower than 200 m contain the uncrusted specimens of *G. pachyderma* or the transition of encrustation of Kennett (*op. cit.*) and Vilks (*op. cit.*).

The above discussion implies that the samples collected by vertical or oblique tows, especially in the upper layer, may not contain the 'typical' forms existing in a comparatively deep layer and compose only a minority of the total population of *G. pachyderma*. This may explain the enigma of the absence of 'typical' forms of *G. pachyderma* in the plankton tows as in the case of Brady (1884), Uchio (1960) and Cifelli and Smith (1970).

An additional explanation is that, because the 'typical' forms of *G. pachyderma* represent a reproductive stage, they are possibly absent in the water column depending on the time of day and year.

The appearance of 'typical' forms of *G. pachyderma* in the tow samples in the temperate area, as reported by Cifelli and Smith (*op. cit.*), may be referable to the presence of that form in the upper layer at St. 2 (Fig. 12). At this station, *G. pachyderma* including the 'typical' form, which descended to the intermediate layer, is carried up to the upper layer through a mixing of water masses.

TAXONOMY OF *GLOBIGERINA PACHYDERMA* (EHRENBERG)

A. Taxonomic Problems on *Globigerina pachyderma* (Ehrenberg)

G. pachyderma has been considered to be useful for paleoceanographic investigations and stratigraphic correlation since Ericson (1959) and Bandy (1960) emphasized the significance of the ratio of left to right coiled forms of this species. Since then, the oppositely coiled variety of *G. pachyderma* has been considered to be intraspecific phenotypic variations depending on changes in temperature, which are also related to latitudes within the range of its distribution.

Previous studies indicate that the left-coiled form dominates the subpolar regions and lives exclusively in the polar region, while the right-coiled form dominates both waters and bottom sediments of the subpolar and transitional regions,

and extends to the subtropical to tropical regions. Within the realm where these two forms dominate, a comparatively sharp boundary is recognized in the subtropical convergent area between cold and warm water masses (Bé, 1969; Bé and Hamlin, 1967; Blair, 1965; Boltovskoy, 1966, 1967, 1971b; Bradshaw, 1959; Kennett, 1968; Kipp, 1976; Vella, 1974).

It is generally considered that the right-coiled variety of *G. pachyderma* in the subpolar and transitional waters grades morphologically into *Globoquadrina dutertrei* living in the major warm currents of the subtropical and tropical areas (Bé and Tolderlund, 1971; Kipp, *op. cit.*; Vella, *op. cit.*). On account of correspondence of geographical distributions to morphological changes, many investigators have considered that the left-coiled *G. pachyderma* and *G. dutertrei* latitudinally make complete morphological clines and they may be genetically linked together closely.

As a natural consequence, it followed that *G. pachyderma* was assigned to *Globoquadrina* or *Neogloboquadrina* by some workers.

On the other hand, some investigators hold different views of the taxonomy of *G. pachyderma* based on a variety of morphologic criteria for its generic assignment.

Parker (1962) gave importance of natural classification to the taxonomy of planktonic foraminifera. She considered that a phenotypic variation and intergradation are within the range of a species and wall structure is the most important criterion for classification. She assigned in this way *G. pachyderma* to the family Globigerinidae, and *Globoquadrina dutertrei* to the Globorotaliidae, respectively. At the same time, she recognized *G. incompta* Cifelli as right-coiled phenotypic variants or subspecific form of the left-coiled *G. pachyderma.*

Parker (1971) and Parker and Berger (1971) suggested, however, that all or part of the right-coiled variety of *G. pachyderma* may be environmentally stressed specimens of *G. dutertrei* and polyphyletic from the left-coiled ones.

Cifelli and Smith (1970) taxonomically examined the live population of the right-coiled *Globigerina pachyderma-Globigerina dutertrei* complex from the North Atlantic in view of the ontogenetical development. They separated this complex into three end members, such as *Globigerina* aff. *Globigerina pachyderma, Globigerina incompta* and *Globigerina dutertrei,* and considered the so-called right-coiled *G. pachyderma* to span the first two taxa. From close similarities in the gross shape, they placed *G. pachyderma-G. dutertrei* complex in a single genus, but allowed that a slight difference may exist in their phylogenetical development.

After then, Cifelli (1973) taxonomically investigated in great detail the specimens of the left-coiled *Globigerina pachyderma* and *Globigerina incompta,* which were collected both from bottom sediments and plankton tows in the North Atlantic. He regarded them as different species having their own histories within a single genus.

Olsson (1973, 1974) offered constructive opinion based on analyses of the ontogenetic growth of the so-called *Globigerina pachyderma* employing the specimens from core samples ranging from early Pliocene to Recent in age. He pointed out that the right- and left-coiled populations of *G. pachyderma* of the Pliocene-lowermost Pleistocene and the right-coiled population of the Pleistocene-Holocene are different from the left-coiled ones of the Pleistocene-Holocene. He assumed only the last-mentioned ones to be *G. pachyderma.*

Further, Olsson (1976) afforded explicit evidence, which supports his former view, from the study of wall ultrastructure on the oppositely coiled form from bottom sediments. Scanning

electron micrographs show that the wall structure of the left-coiled *Globigerina pachyderma* has strong affinities with the type species of the genus *Globigerina*, while that of the right-coiled one to the turborotaliids. Hence, he concluded that *G. pachyderma* has never had right-coiled form in the course of its evolution.

As discussed above, the taxonomic problems of *G. pachyderma* are focused on whether the left- and right-coiled forms of *G. pachyderma* are both temperature dependents of a single species or they are separate taxa.

If *G. dutertrei* and *G. pachyderma* were closely related in genetics with each other, the populations of these two will be distributed in a world-wide range from the tropical to arctic areas. This stipulation is unrealistic because, as described by Bé and Tolderlund (1971), the distribution of planktonic foraminifera is generally confined to particular water masses which they inhabit.

On the other hand, the left-coiled *G. pachyderma* changes its morphology remarkably in the distribution especially between the Northern and Southern Hemispheres as discussed by Kennett (1970a) and Bandy and Theyer (1971). Because *G. dutertrei* and the right-coiled *G. pachyderma* make a geographical morphocline latitudinally, left-coiled *G. pachyderma-G. dutertrei* plexus makes two morphoclines within the range of their distribution. From the biogeographical understanding that there exists only one morphological cline for single species in relation to the environmetal gradation, the above-mentioned fact is not easily explained.

Tolderlund and Bé (1971), Jones (1967) and Kipp (1976) showed that *G. dutertrei* dominates major warm currents, and intermediate forms and the right-coiled *G. pachyderma* dominate high latitudes where the warm currents extend. In addition, specimens of the right-coiled *G. pachyderma* or *G. incompta* Cifelli are probably of uniform morphology in the world (Parker, 1962; Cifelli and Smith, 1970).

It is, therefore, possible to venture some working hypotheses: (1) *G. dutertrei* and *G. pachyderma* are different in genetics, and live in different water masses. (2) *G. dutertrei* in lower latitudes spreads over the cooler area with major warm currents, gradually changing its morphology; and near the extremity of the extention of warm current, where the warm and cold current converge, the test of *G. dutertrei* becomes smaller in size and increases in wall thickness, and morphologically converges to that of *G. pachyderma* which lives in cold water. (3) As right-coiled specimens dominate the population of *G. dutertrei* and the left-coiled ones do that of *G. pachyderma*, the so-called *G. pachyderma* changes its coiling direction in the convergent area depending on a mixing of water masses or temperature.

On these hypotheses the phylogenetic distance between *G. dutertrei* and *G. pachyderma* may not be comprehended too short. The evolvement from parent species into new taxa needs a geographical isolation of populations. The distribution patterns of *G. pachyderma* s.s. and *G. dutertrei* s. l., however, appear contradictory to the requisite (Bé, 1959a; Bradshaw, 1959).

To test those hypotheses, it is necessary to substantiate that, in the convergence area where different water masses exist in a short distance, the left-coiled population of *G. pachyderma* inhabits only cold water and the so-called right-coiled one of *G. pachyderma-G. dutertrei* complex in the water affected by warm current.

This sort of work should be done by using living populations as discussed by Parker (1962). Classification must be conducted on the population basis in the light of natural classification that allows

for ecophenotypic variation, intergradation and ontogenetic stages.

In addition, Lipps (1966) and Steineck and Fleisher (1978) discussed thoroughly the gross morphologic characters related to the floatation of planktonic foraminifera, such as the mode of coiling, aperturral position, wall projections and spines, all tend to converge polyphyletically by reason of 'multiple evolution of mechanical optimum' (Steineck and Fleisher, *op. cit.*). On the contrary, wall structures are probably unaffected by environments and are persistent. Subsequently, differences in wall structures may be important for the determination of phylogenetical distances in natural classification.

In this study, because sampling was made only at two stations, phenotypic variations depending on geographical factors can not be described sufficiently, but the morphology of each species in different ontogenetic stages can be recognized with the support of ecological information particularly on ontogenetic migration in water column. In fulfillment of natural classification, the wall structures on each ontogenetic stages should be examined.

B. Classification of *Globigerina pachyderma-Globoquadrina dutertrei* plexus

1. *Methods of investigation*

In this study, as discussed previously, samples from the water column at St. 1 contain only the left-coiled *G. pachyderma* of this complex and those at St. 2 yield the left-coiled one together with the *G.* aff. *G. pachyderma-G. incompta-G. dutertrei* complex in the sense of Cifelli and Smith (1970) with the record of a complete ontogeny and inter-gradation. Therefore, the definition of species is primarily based on those samples in this investigation.

The procedure of taxonomic investigations is as follows:

Firstly, the range of variations and ontogenetic development of the populations of the left-coiled *G. pachyderma*, *G. bulloides* and *G. quinqueloba* are established using the specimens from the water column at St. 1. The process of shell construction is also examined by the scanning electron microscope.

Secondly, the specimens of *G.* aff. *G. pachyderma-G. incompta-G. dutertrei* complex are picked up from the samples at St. 2 to deal with their ontogeny according to the criteria described by Cifelli and Smith (*op. cit.*). Wall structure or the process of wall construction and changes in gross shapes with ontogenetic development were investigated by the scanning electron microscopy and compared with those of *G. pachyderma*. The range of variations of those attributes of each taxon can be determined through examinations of a great number of specimens.

Thirdly, tendencies of shell enlargements of all taxa were compared with each other based on the measurements under an optical microscope.

Fourthly, the distribution pattern of each taxon in water column is discussed from an ecological point of view with the support of taxonomical investigations of this complex.

2. *Gross shapes and shell structure in ontogenetic stages*

a) *Globigerina pachyderma* versus *Globigerina bulloides* and *Globigerina quinqueloba*: As already described, juveniles predominate the upper 30 m, and adults, which show the trend toward encrustation, exclusively dominate at depths of 50 to 150 m. Hence, the morphology and wall structure of *G. pachyderma* on each ontogenetic stage can be examined using the specimens from the surface to a depth of 150 m.

G. pachyderma at 0 m (Pl. 26, figs. 1–3).

This form is probably equated to that described by some workers (e.g. Uchio, 1960; Phleger, 1952; and Banner and Blow, 1960) as *G. bulloides* on the basis of gross shapes. As discussed previously,

it is generally considered to be the surface-water counterpart of the typical *G. pachyderma* in bottom sediments, as exemplified by some authors (Bé, 1960b; Kennett, 1968; Cifelli, 1973; Boltovskoy, 1971a; and Parker, 1962).

This form has rounded and inflated chambers gradually increasing in size through its development. On the spiral side chambers in early whorls conspicuously protrude. Sutures are distinctly depressed and radiate on the spiral and umbilical sides so that the outline of the equatorial periphery is lobulated. An aperture is large and high-arched and exists in the umbilical to extraumbilical area, although customarily in the umbilical area. An apertural lip extends through around the margin of the aperture as a belt perpendicular to the chamber surface.

On the other hand, *G. bulloides* at St. 1 (subarctic form) is identified with *G. bulloides* forma *trilocularis* described by Boltovskoy (1971b) from the Antarctic Ocean (Pl. 28, figs. 1–5). A discrimination between those two taxa is not so difficult. *G. pachyderma* has 4 to $4^1/_2$ chambers (in umbilical view) enlarging gradually in the last whorl and a high-arched, semicircular broad aperture with a distinct lip. However, *G. bulloides* at St. 1 has 3 to $3^1/_2$ chambers (in umbilical view) in the last whorl in which the chambers enlarge rapidly, and an aperture, which is small and low-arched, with a poorly developed lip. *G. pachyderma* does not have spines at all even in the early stage, on the contrary, *G. bulloides* does have long spines except for the last stage in which it bears an encrusted test. Compared with specimens of the same diameter, the test wall of *G. pachyderma* is explicitly thicker than that of *G. bulloides*.

G. pachyderma is also distinguishable from *G. quinqueloba* at St. 1 which has a delicate shell and dense spines on the surface of test wall except for the last stage in which it sometimes possesses encrusted tests (Pl. 29, figs. 1–3). The chambers in the last whorl of *G. quinqueloba* elongate tangentially to the coiling axis, contrasting to *G. pachyderma* which has rounded chambers. *G. quinqueloba* has a low-arched small aperture in the umbilical area and has lips, if not so distinct, in a similar way to that of *G. pachyderma*. Both in *G. pachyderma* and *G. quinqueloba*, however, the axial periphery is broadly rounded.

The test surface of *G. pachyderma* is shown in Pl. 26, fig. 3 at high magnification. The surface of test wall is covered with tubercles, which have a tendency to connect with one another to compose ridges, except for the ultimate chamber on which discrete tubercles are developed.

Under a binocular microscope, the surface of test wall in the initial stage is seen to be hispid, as described by Parker (1962), nearly the same as in the other globigerine species. Imperfectly circular pores exist on the smooth flat surface as holes without a depression in pore areas. The pores are not uniform in diameter, and are unevenly distributed, but there are none near or on the ridges or tubercles. Ridges show no tendency to make a pore area as do those of the species of the genus *Globoquadrina* (Steineck and Fleisher, 1978).

G. bulloides and *G. quinqueloba* have a wall structure similar to that of *G. pachyderma* (Pl. 28, figs. 3, 5; Pl. 29, fig. 3), particularly in the shape and distribution of pores. Minor differences are that, in *G. bulloides* and *G. quinqueloba*, many of the typical tubercles of *G. pachyderma* exist as spine bases, and some of the pores are located near them.

G. pachyderma at 50 m (Pl. 26, figs. 4–6)

As already discussed, specimens in this layer are mostly adult. Judging from the number of chambers and test diameter, the illustrated specimen is also adult. The gross shape is similar to that of the surface specimens except

for bluntly incised sutures.

Examinations of the wall surface by scanning electron micrographs show that the ridges constructed by the connection of tubercles have enlarged their extents in both width and height. Consequently, the area around pores is comparatively restricted and narrower than that of the surface specimens. The pores are, however, kept detached from the ridges, and the pore area remains flat. The lip is strengthened by an addition of minute tubercles to show a ropy appearance. It is noteworthy that those structures are probably the consequence of growth, not necessarily of encrustation.

G. pachyderma at 75 m (Pl. 27, figs. 3, 4)

The specimens displaying a tendency toward encrustation initially appear at this depth. The connection of ridges has become accelerated, and width and height of ridges are more enlarged than before. As a natural consequence, the pores exist in a narrow furrow and some of the pores align along the furrow between ridges. The surface around the pore still remains flat. The pores thoroughly penetrate into the test as cylindrical holes. The apertural lip is thickened and almost buried under the chamber surface so that an aperture shows a slit-like appearance. A sutural depression becomes more blunt, and then the peripheral outline is insignificantly lobulate. The wall in this stage is made of microcrystals.

G. pachyderma at 150 m (Pl. 27, figs. 5, 6)

Encrustation is completely advanced to generate the so-called *G. pachyderma*. In this stage, the pore area is entirely lost, but the pore diameter on the test surface is broadened. An aperture is restricted and extends from the umbilical to extra-umbilical area as a slit, and shows the characteristic of the genus *Turborotalia*. The specimens at this depth lose sutural indentations entirely, and are sometimes endowed with a reduced ultimate chamber (kummerforms), so that the peripheral outlines become oval. The surface of encrusted specimens often has well-developed euhedral crystals.

In addition, Pl. 35, fig. 1 shows that no inconsistency caused by differences in crystal growth or lamellar structure occurs in the crust. This also indicates that the encrustation may not stop in a transitional stage but continue to the end without any interruption. This view may explain the fact that specimens on a transitional stage are really rare in samples from the bottom sediments.

Shell construction process both in *G. bulloides* and *G. quinqueloba* is substantially the same as *G. pachyderma* (Pl. 28, figs. 3, 5; Pl. 29, fig. 3). Encrustation in both species starts on the formation of ridges through the mutual connection of tubercles or spine bases, and progresses with increases in width and height of the ridges. Through the shell construction process, pores exist as cylindrical holes on the test as in the case of *G. pachyderma*. Slight differences of shell construction between *G. pachyderma* and *G. bulloides* are irregularities of the shell surface around pores, and pores that frequently exist near the spine bases or tubercles (Pl. 28, fig. 3).

In short, the shell construction process of *G. pachyderma* is primarily similar to that of the genus *Globigerina*, represented by *G. bulloides*. Slight, not essential, differences between them are that, in *G. pachyderma*, the spine bases are lost or reduced to tubercles without spines.

In addition, at both stations, more than 98 percent of *G. pachyderma* coils sinistrally, and about 60 percent of *G. bulloides* and as many *G. quinqueloba* coil sinistrally in the upper 300 m of the water column. No remarkable discrepancies, therefore, occur in changes of coiling directions among those taxa at both stations.

b) *Globoquadrina dutertrei* (d'Orbigny)

s.s.: As St. 2 is located in high latitudes, there exist no typical forms of *G. dutertrei* having well-developed teeth as already recognized in various regions (Parker, 1962; Bandy, Frerich and Vincent, 1967; Parker and Berger, 1971; and Srinivasan and Kennett, 1976).

According to Cifelli and Smith (1970), *G. dutertrei* s.s. is morphologically distinguished from other taxa (*G. incompta*, *G.* aff. *G. pachyderma*) mainly by a broad umbilicus throughout ontogeny.

In detail, the aperture of *G. dutertrei* s.s., a large opening, is restricted to the center of the whorl in the adult stage in contrast to that of *G. incompta* which remains in the umbilical-extraumbilical area throughout ontogeny. Its wall texture is finer than that of *G. incompta* in their early stages.

G. aff. *G. pachyderma* is distinguished from *G. dutertrei* s.s. without much difficulty, as the former has a small aperture confined to the umbilical area and markedly coarser wall texture particularly in its early stages.

Ontogenetic changes in the morphology and wall structure of *G. dutertrei* s.s. were examined based on the specimens in various stages, as determined by their shell diameter and the number of chambers. At. St. 2, juveniles and delicate-shelled specimens predominate at a depth of 30 m and encrustation takes place at a depth interval around 50 m to 75 m (Fig. 11b). Therefore, juveniles and delicate-shelled adults were picked up from the samples at a depth of 30 m and specimens showing the process of encrustation were from depths of 50 m to 100 m.

G. dutertrei with 7 chambers (Pl. 30, figs. 1–3)

Going back to the earlier stages, it is recognized that *G. dutertrei* has the appearance of the genus *Globorotalia* as does *Globoquadrina conglomerate* illustrated by Parker (1962).

The examined specimen is flattened on the spiral side and convex to moderately vaulted on the umbilical side. Chambers rapidly increase in size and coil in low trochospiral. The sutures are slightly curved and distinctly depressed on the umbilical side and tangentially slightly depressed on spiral side in the initial whorl. An aperture, surrounded by the apertural face to be slightly concave with the shoulder, is located in the umbilical-extraumbilical area. A triangular-crescent apparent lip, broadening its width toward the umbilicus to cover the umbilical area, is located at the apertural base. The lip is connected with the chamber surface with a linear joint. The wall is thin, shiny, and transparent. The wall surface is smooth, but studded with fine circular pores.

G. dutertrei with 9 to 15 chambers (Pl. 30, figs. 4–6)

With the ontogenetic development, the chambers become inflated and tend to conic. The wall surface gradually intensifies its relief to grow into papillae which tend to surround any pores. In the whorl, the specimens with 15 chambers have a coarser wall surface in the earlier chambers than the ultimate chamber. On the umbilical side, chambers adjoin each other leaving slight spaces behind the umbilical area to open an umbilicus.

G. dutertrei with 14 chambers (Pl. 31, figs. 1–3)

Apertures are furnished with triangular or crescent lips along the bases, which protrude into the umbilicus to show a weakly developed flap-like appearance, a feature of the genus *Globoquadrina*. The pores are 1) clearly circular, 2) mostly uniform in size, 3) distributed at a certain distance, and 4) situated in slightly but appreciably concaved pore areas.

G. dutertrei with 15 chambers (Pl. 31, figs. 4, 5)

A comparatively small globular ultimate chamber adjoins the preceding ones, disposing its apertural face toward the whorl axis. Consequently the aperture is confined to the center of the whorl and the peripheral outline becomes rounded. An umbilicus is markedly deep, and widely open. The papillae in the preceding stages develop to form ridges which completely confine each pore to the respective funnel-shaped pore area. Entirely circular pores are situated in the center of the pore pits. The junction of ridges is particularly emphasized in their height. Such a cancellate wall texture is a significant character of the genus *Globoquadrina* (Parker, 1962; Steineck and Fleisher, 1978). The wall structure of this specimen closely resembles that of '*Neogloboquadrina dutertrei dutertrei* group A' described by Srinivasan and Kennett (1976).

The above mentioned is mainly observations on wall structure and ontogenetic development at a water depth of 30 m. At greater depth, the test wall becomes encrusted. In contrast with *G. pachyderma*, *G. dutertrei* always retains funnel shaped pore areas which become aided with a steeper slope (Pl. 35). On the wall surface of specimens from the deeper tows, fully grown large rhombic crystals, showing growth lines paralell to a short diagonal of the rhombic cleavage planes, are well developed to cover the crest and slope of the ridges and encircle pore pits (Pl. 31, fig. 6). The early chambers of the last whorl, especially in the umbilical area, are covered with spine-like pustules of the rhombic crystals developed from the intersecting points of three facies normal to the test surface.

Plate 35, fig. 3 shows that the encrustation of *G. dutertrei* continues to the end without interruption as in the case with *G. pachyderma*. After the encrustation, the peripheral indentation of this species becomes less distinct than that of uncrusted forms in the upper layer, but because of its large size, sutural furrows of this species are not completely burried under the crust as is the case with *G. pachyderma*. In the last stage of the encrustation (Pl. 35, fig. 3), most of the specimens possess many features identical with the '*Neogloboquadrina dutertrei dutertrei* group B' of Srinivasan and Kennett (*op. cit.*).

In short, the pores of *G. dutertrei* s.s. are distributed at regular intervals, and the ridges encircle each pore, resulting in a polygonal appearance throughout the ontogenetic development. Therefore, under a binocular microscope unlike *G. pachyderma* or *G. bulloides*, the wall surface of *G. dutertrei* s.s. bears regularly arranged pores and ridges on the entire surface.

c) *Globigerina incompta* Cifelli: This species shows the same ontogenetic distribution pattern in water column as *G. dutertrei* s.s. Therefore, *G. incompta* was examined for its ontogenetic change in gross shape and the process of shell construction in the same way as *G. dutertrei* s.s.

G. incompta with 10 chambers (Pl. 32, figs. 3, 4)

Throughout its ontogenetic stages, *G. incompta* shows a globorotaliid appearance which is indicated by 1) the flat spiral side, 2) compressed chambers, 3) an aperture narrowly restricted to the umbilical-extraumbilical area, and 4) a crescent broad lip, which forms a linear junction with the chamber surface and tends to cover the umbilical area. In this specimen, the suture is slightly curved and depressed on the umbilical side, and tangentially slightly depressed on the spiral side. An equatorial profile is subrhombic to quadrate, and chambers rapidly increase in size as add. An umbilicus is narrow but deep.

Under a binocular microscope, the wall of this specimen is shiny and delicate,

but tenacious just the same with *G. dutertrei* s.s. is. The wall structure in this specimen (Pl. 32, fig. 4) is entirely the same as *G. dutertrei* s.s. in a little more advanced stage.

G. incompta with 10 to 12 chambers (Pl. 32, figs. 5, 6; Pl. 33, figs. 1–3)

Through ontogeny, this species does not change its gross shape remarkably, and keeps the character of the genus *Globorotalia*. The chambers in the last whorl increase in size more rapidly, so that the last two chambers take up an increasingly larger portion of the whole test than in *G. pachyderma*. A chamber attaches to the preceding one leaving a slight space behind as in the case of *G. dutertrei* s.s. from the tropical-subtropical area (Parker, 1962; Srinivasan and Kennett, 1976).

Shell construction process is entirely the same as in *G. dutertrei* s.s. Papillae have grown into ridges that surround each of the pores keeping or strengthening funnel-shaped pore areas to form a pitted wall surface ultimately.

In the last stage (Pl. 33, figs. 4–6), there exist usually euhedral rhombic crystals with growth facet mainly on ridges which encircle pores in the same way with *G. dutertrei* s.s. Consequently, peripheral lobulation is obscured to some extent. However, the suture is sometimes strongly depressed and almost incised toward umbilicus.

As a result, basic characters of the morphology of *G. incompta*, such as the shape and location of lips and wall structure are the same as those of *G. dutertrei* s.s. throughout ontogeny.

d) *Globigerina* aff. *G. pachyderma* (Ehrenberg): This form initially displays its appreciable appearance at water depths more than 75 m at St. 2.

The problem of taxonomy is with juveniles of this species which closely resemble those of *G. pachyderma* in gross shape. The young form of *G.* aff. *G. pachyderma* (Pl. 34, figs. 4, 5) also bears the same gross shape as that of *G. incompta* and *G. dutertrei* s.s. which is featured by a triangular lip showing a tendency to cover the umbilicus, and by a flat spiral side and subquadrate-subrhomboidal outline on the equatorial periphery. Chambers also enlarge rapidly as add.

Examination shows that the wall structure of *G.* aff. *G. pachyderma* in the 'early stage' is entirely the same as that of *G. dutertrei* s.s. and *G. incompta* (Pl. 34, figs. 5, 6 and Pl. 35, figs. 5, 6) in the advanced stages. Pores are spaced regularly and are located in the center of the pore area surrounded by rhombic crystals having lamellar striations on their surfaces. A dissected specimen clearly shows that, before encrustation, the wall surface has a funnel-shaped pore area which is entirely the same as that of *G. dutertrei* s.s. and *G. incompta*.

In short, in natural consequences of encrustation in the early stages, *G.* aff. *G. pachyderma* displays a *G. pachyderma*-like feature, although the primary features are entirely the same as that of *G. dutertrei* s.s. and *G. incompta*. Examination of fractured faces of the 'adult' specimens of *G.* aff. *G. pachyderma* shows that, in the early whorl, there are no thick-shelled juveniles but thin-shelled ones with pustules. Assuming that the encrustation of *G. pachyderma* with shell diameters of 140–280 μm represents a preparation facies for reproduction, the juvenile of *G.* aff. *G. pachyderma* should be a form in the last stage of their life cycles.

e) Summary: In basic morphological characters *G. pachyderma* is related to globigerine species, particularly *G. quinqueloba*, in the early stages. On the other hand, the gross shape of *G. dutertrei* s.s.-*G. incompta*-*G.* aff. *G. pachyderma* is entirely the same in basic characters, and displays complete clines throughout their ontogeny.

The wall structure of *G. pachyderma* has a great similarity to that of *G. bulloides* and *G. quinqueloba*. The wall structure

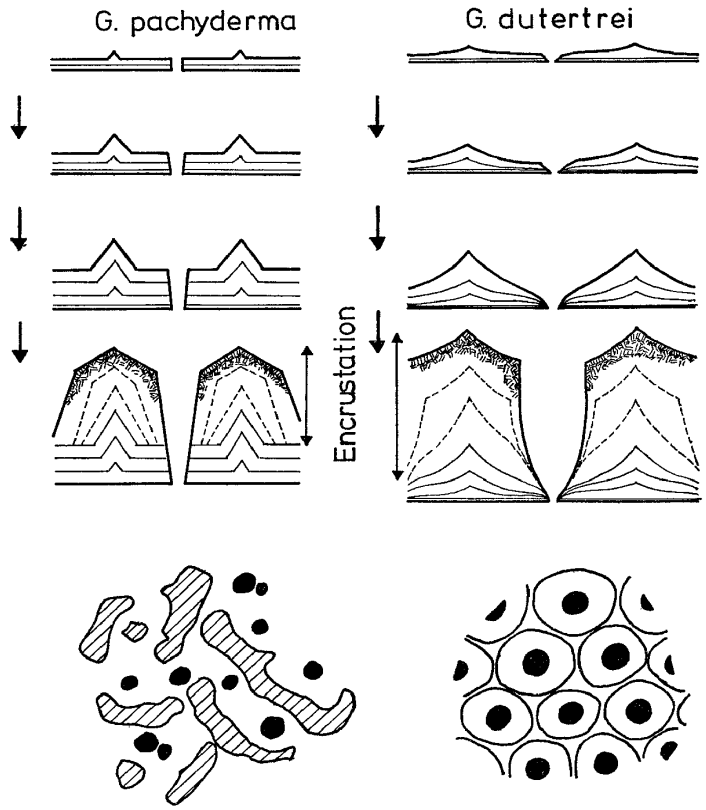

Fig. 22. Schematic diagram of the process of wall construction of *Globigerina pachyderma* in comparison with *Globoquadrina dutertrei*. A, cross section; B, wall surface texture. Arrow shows wall construction process.

of *G. dutertrei* s.s.-*G. incompta*-*G.* aff. *G. pachyderma* is entirely the same and shows a tendency to grow into a pitted-wall texture that is considered to be a prominent character of the genus *Globoquadrina* or the family Globorotaliidae (Parker, 1962; Steineck and Fleisher, 1978).

The juveniles of *G.* aff. *G. pachyderma* in the sense of Cifelli and Smith (1970) may be in the reproductive or the last stage and end its life at the 'immature forms': In consequence of encrustation, they converge to *G. pachyderma* in gross shape.

The wall structure of *Globigerina pachyderma* and *Globoquadrina dutertrei* is schematically shown in Fig. 22.

Based on examination of the wall structure of *Globigerina pachyderma* and *Globigerina incompta* under the scanning electron microscope, Kennett and Srinivasan (1980) recognized no fundamental difference in surface wall structure between both species and included the latter under the synonym of the former.

However, as already stated, in the reticulate microcrystalline wall structure (representing an ontogenetic stage before encrustation), contrasting differences are exhibited between the two species. As shown in the figure of their *G. pachyderma* (right coiled) (Kennett and Srinivasan, *op. cit.*, Pl. 4, fig. 5) and that of the form referred to *G. incompta* in the present study (Pl. 32, fig. 4) the pore area is funnel-shaped and each pore exists in a concave pore area one by one; the ridge is sometimes not so prominent but forms a distinct barrier between the pore areas at high magnification. The pore area of *Globoquadrina dutertrei* is also funnel-shaped as shown in Pl. 31, figs. 2, 3 and is identical to that of *Globigerina incompta*.

Further, Kennett and Srinivasan (*op. cit.*, Pl. 26, figs. 4, 5; Pl. 28, fig. 4) showed that the pore area of *Globigerina pachyderma* is often funnel-shape. Those features are also seen in the form referred to *G. pachyderma* in the present study (Pl. 27, fig. 4). On these specimens signs of encrustation are recognized to some extent. In the earlier stage before encrustation, however, pores are distributed irregularly on a flat wall surface between the ridges so that "a pore per pore area" structure does not develop (Pl. 26, figs. 3, 6).

Thus *Globigerina pachyderma* and *Globigerina incompta* are clearly distinguished on the specimens with reticulate microcrystalline structure (before encrustation), and the wall structure of *G. incompta* is identical with that of *Globoquadrina dutertrei*.

3. *Morphometrics*

Shell enlargement in association with chamber addition is investigated under a microscope by the same method as the growth analysis. Specimens of *G. pachyderma*, *G. bulloides* and *G. quinqueloba* were picked up from samples at St. 1, and those of *G. dutertrei* s.s., *G. incompta* and *G.* aff. *G. pachyderma* were from St. 2. As is the case with *G. pachyderma*, the enlargement of the maximum diameter mainly depends on the size of a proloculus. Therefore, the comparison of shell enlargement should be made among species by using specimens with the same proloculus diameter. In this study, specimens having a proloculus diameter of 12.5 μm were employed except for *G. incompta* and *G.* aff. *G. pachyderma* whose proloculus diameters are much larger (15.0 μm to 22.5 μm).

G. dutertrei s.s. also clearly displays a rapid enlargement of the test diameter when the proloculus diameter is large (Fig. 13). Shell enlargement of *G. incompta* and *G.* aff. *G. pachyderma* are almost within the range of *G. dutertrei* s.s. whose proloculus extends from 12.5 μm to 22.5 μm in diameter. Among specimens with a proloculus diameter of 12.5 μm, *G. dutertrei* s.s. is more rapid in shell enlargement than *G. pachyderma*, and has a close similarity to *G. bulloides* (Fig. 13). Shell enlargements of *G. pachyderma* are similar to those of *G. quinqueloba*.

In short, there are great similarities in the shell enlargement among *G. dutertrei* s.s., *G. incompta* and *G.* aff. *G. pachyderma*, and their maximum dimension grows more rapidly than that of *G. pachyderma* whose tendency is very similar to *G. quinqueloba*.

Such similarities in the shell enlargement, wall structure, and morphology in their early stages imply a close phylogenetic relation between *G. pachyderma* and *G. quinqueloba*.

4. *Ecologic distribution and conclusion of taxonomy*

It is well known that knowledges on the ecological distribution of each taxon add support to natural classification. Therefore, a detailed examination of the distribution pattern of each species will also aid to clarify the taxonomic problems with *Globigerina pachyderma-Globoquadrina* plexus.

Taking account of the variation range and ontogenetic changes in gross shape, *G. pachyderma* at both St. 1 and 2 can be discriminated from *G. dutertrei* s.l. on the population basis. As already discussed, *G. dutertrei* s.l. exists at St. 2 in the warm-core eddy and is entirely absent at St. 1 which bears no evidence of a strong intrusion of warm water. On the other hand, *G. pachyderma* exists at St. 1 in the Oyashio (cold-water mass), and its appearance at intermediate depths at St. 2 is made by the cold water intrusion from the Oyashio area. Stations 1 and 2 are no more than about 120 km apart, although the sampling time is different. The mutually exclusive distribution probably indicates that *G. dutertrei* s.l.

and *G. pachyderma* belong to two different taxa.

Cifelli (1973) stated that *G. incompta* and *G. pachyderma* are never caught together by surface tows in the north Atlantic. This also probably implies that *G. incompta* and *G. pachyderma* inhabit different water masses.

G. dutertrei s.s. -*G. incompta*-*G.* aff. *G. pachyderma*, accompanied by intermediate forms in ontogeny, appear in the water column within a short-towed lateral distance of about 1 km at St. 2.

To clarify the distinctions among *G. dutertrei* s.s., *G. incompta*, and *G.* aff. *G. pachyderma*, Cifelli and Smith (*op. cit.*) put their main criteria on apertural size and a wall texture, the both show a reciprocal trend in those taxa. The relationship between water temperature and intraspecific morphologic variation (surface texture and apertural size) in such species as *G. bulloides* may suggest a general tendency that, in the colder section within its distribution, apertural size decreases and a shell highly thickens, frequently decorated with well developed euhedral crystals. Such a relationship indicates that *G. dutertrei* s.s., *G. incompta*, and *G.* aff. *G. pachyderma* are all in the range of morphologic variation in a single species.

Encrusted specimens dominate the populations of *G. dutertrei* s.s. and *G. incompta* in the lower part of the epipelagic layer and the second maximum concentration layer. *G.* aff. *G. pachyderma* increases its abundance and relative frequency at those layers (Fig. 7). On the other hand, the adults of *G. pachyderma*, showing a tendency toward encrustation, also gather about those layers. Subsequently, the encrusted specimens of *G. dutertrei* s.s., *G. incompta* and the whole *G.* aff. *G. pachyderma* can be interpreted as forms in the terminal

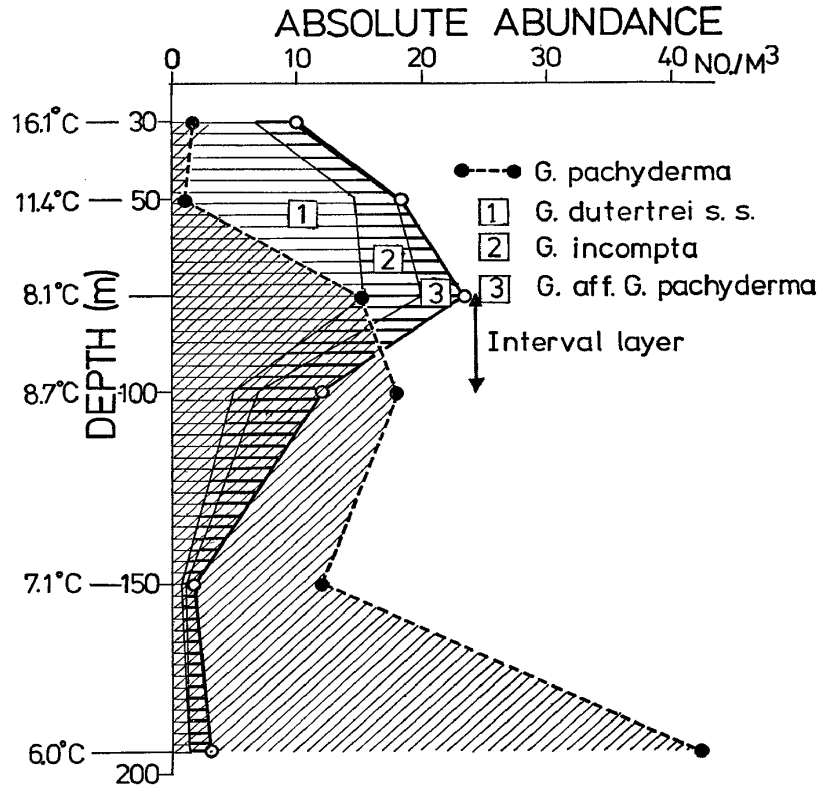

Fig. 23. Concentration of *Globigerina pachyderma* and *Globoquadrina dutertrei* in the water column at KT-77-8 Station 2.

stage of a single species.

In addition, the concentration pattern of those taxa does not show any definite depth stratification except for *G.* aff. *G. pachyderma* whose pattern is not conformable with others' (Fig. 23). Bé (1960a) mentioned from the bathymetric study on planktonic foraminifera that there is no clear evidence of the existence of any stenobathic species or any stratification of species at different depth layers. Therefore, if *G.* aff. *G. pachyderma* were a distinct taxon, the distribution pattern shown in Fig. 23 would be compatible with a general tendency. Such discrepancies also deny the possibility that *G.* aff. *G. pachyderma* represents a distinct species or subspecies.

Bé (1969) also mentioned that various specific populations of the genus *Globorotalia* and *Globoquadrina* have a greater range of depth habitat, while the population of the genus *Globigerina* concentrates in the upper layer of the epipelagic zone. The distribution pattern of *G. dutertrei* and *G. pachyderma* in this study well matches to this general trend.

At St. 1, *G. pachyderma* dominates the upper 50 m layer in the same manner as the other globigerine species. On the other hand, *G. dutertrei* at St. 2 is concentrated in the subsurface layer and is scarce in the upper 30 m layer. Those general concentration pattern of both species in water column also displays that *G. dutertrei* belongs to the genus *Globoquadrina* or the family Globorotaliidae, and *G. pachyderma* to the genus *Globigerina*.

In a summary, the results of examination of 1) the gross morphologic characters of each ontogenetic stage, 2) wall structure, 3) morphometrics, and 4) ecologic distribution pattern on each taxon all indicate that *G. pachyderma* belongs to the genus *Globigerina* and *G. dutertrei* to the genus *Globoquadrina*.

In samples collected at St. 1, 98.4 percent of *G. pachyderma* coil sinistrally. At St. 2, 99.6 percent of *G. pachyderma* coil sinistrally, and 99.3 percent of *G. dutertrei* coil dextrally. Examination in this study was conducted in a limited area within the distribution of both *G. dutertrei* and *G. pachyderma*. Therefore, it can probably be concluded that: 1) The so-called right-coiled variety of *G. pachyderma* is in a reproductive phase or a form in the immature stage of *G. dutertrei*. 2) This form dominates the deeper and colder part of the concentration layer of *G. dutertrei* in the mixed water with a prominent thermocline. 3) Subsequently, where the warm current loses its indigenous characters such as high temperature and salinity through a mixing with cold water or thinning out at its extremities, the so-called right-coiled variety of *G. pachyderma* probably increases its percentage to the whole population of *G. dutertrei*. 4) *G. pachyderma* bears mostly left-coiled specimens and lives in higher latitudes than the subpolar region, where no marked effect of the warm currents prevails.

MAJOR FACTORS CONTROLLING THE DISTRIBUTION PATTERN OF *G. PACHYDERMA* ON THE SEA BOTTOM

This study concludes that, 1) the so-called right-coiled variety of *Globigerina pachyderma* is one of the facies of *Globoquadrina dutertrei*, 2) the populations of *G. pachyderma* and *G. dutertrei* are distributed in different water masses; in detail, *G. dutertrei* dominates the warm current, while *G. pachyderma* the cold water and the mixing water of warm and cold waters – they distribute mutually exclusively depending on the character of water masses, 3) a water temperature around 8°C is crucial upon the existence of both taxa, 4) such distributions well

matches to the world-wide distribution pattern described by previous authors (Bé and Tolderlund, 1971; Bé and Hamlin, 1967; Bradshaw, 1959), and 5) as juveniles, which are probably more sensitive to the environments, gather in the upper layer, their distribution may be more strongly confined by the water condition of the upper layer.

The seasonal distribution of planktonic foraminifera is studied by Tolderlund and Bé (1971). They mentioned that in the subarctic region in their sense, the left-coiled *G. pachyderma* is exaggeratedly abundant in spring (May and June), and the right-coiled ones dominate in autumn. The population of the left-coiled form in the subarctic area wholly predominates in spring.

This study clarifies that, 1) in the subtropical convergent area, the shell of *G. pachyderma* in the upper water layer is largely brought forth through reproduction, and its turnover time is probably shortened during blooming in spring, and 2) the shell of planktonic foraminifera should be deposited quickly on the sea bottom without remarkable lateral transportation by currents.

It may be then concluded that, 1) in the subtropical convergent area, the shell output of *G. pachyderma* to the sea bottom is concentrated in spring, 2) the ratio of *G. pachyderma* to *G. dutertrei* in bottom sediments is mainly controlled by the limit of the distribution of *G. pachyderma* which is confined to the subpolar-polar area, 3) a water temperature around 8°C in spring is crucial upon the distribution of *G. pachyderma* and *G. dutertrei*.

Therefore, the boundary between the distribution of those two taxa on the sea bottom agrees with the isothermal line around 8°C at the sea surface in spring as shown by Ericson (1959) as a result of studies on the so-called left-and right-coiled populations of *G. pachyderma*. Kawai (1972) showed that such an iso-

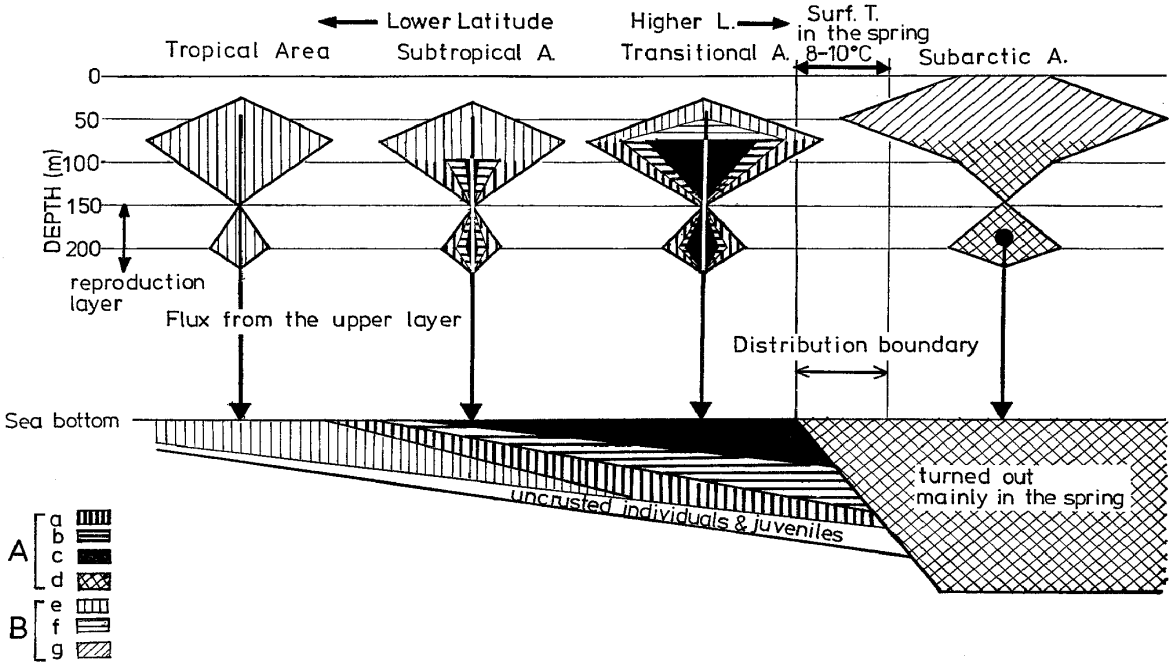

Fig. 24. Scheme of latitudinal changes of intra- and inter-specific composition of *Globigerina pachyderma* and *Globoquadrina dutertrei*. A, encrusted specimens; a. *Globoquadrina dutertrei* s.s.; b, *Globigerina incompta*; c, *Globigerina* aff. *G. pachyderma*; d, *Globigerina pachyderma*; B, uncrusted specimens; e, *Globoquadrina dutertrei* s.s.; f, *Globigerina incompta*; g, *Globigerina pachyderma*.

thermal line is apparently accordant to the southern limit of the Oyashio current or the northern extension limit of the Kuroshio current in spring at the Northwestern Pacific.

The latitudinal distribution pattern of *Globigerina pachyderma* and *Globoquadrina dutertrei* in both sediments and water column is schematically shown in Fig. 24.

SUMMARY AND REMARKS

The results from this study are as follows.

(1) In the designation of the faunal province by Bé and Tolderlund (1971) and Bradshaw (1959), St. 1 is situated in the Oyashio area which yields subarctic-arctic species, and St. 2 in the warm-core eddy in the perturbed area where not only subarctic species but also transitional species inhabit. At St. 1, *Globigerina pachyderma* is the most dominant species, on the other hand, at St. 2, *Globoquadrina dutertrei* (*G. dutertrei* s.s., *Globigerina incompta* and *Globigerina* aff. *Globigerina pachyderma* as described by Cifelli and Smith (1970) from the north Atlantic) also dominates in association with other minor temperate-warm water species. As in the case of Bé and Tolderlund (*op. cit.*), only two or three species predominate at both stations, irrespective of the number of species contained.

(2) Species at St. 1 show ontogenetic segregation in water column, but only *G. dutertrei* shows clear ontogenetic segregation at St. 2 and has a large number of juveniles in the upper layer. This may indicate that *G. dutertrei* has specific adaptability to the warm-core eddy mixed with the cold water which results in the same distribution of the species that Bradshaw (*op. cit.*) illustrated.

(3) Most of the populations of planktonic foraminifera gather in the upper 150 m layer. In detail, the distribution pattern of each species displays two maxima; one exists at a depth around 50 m in the epipelagic layer and the other at a depth of 200 m. Those concentration profiles largely correspond to that of Chl. *-a* values or the standing stock of phytoplankton.

(4) At St. 2, the subarctic species such as *G. pachyderma*, *G. quinqueloba* and *G. bulloides* are scarce in the upper layer and gather more abundantly in the lower maximum concentration layer. This fact may show the subsidence of northern cold water species together with the Oyashio water down to the intermediate layer of the perturbed area through a mixing. This is probably an example of the 'subtropical submergence' (Sverdrup et al., 1942) of cold water species. A mixing, not only lateral but also vertical, of cold and warm water masses in the perturbed area, where St. 2 is situated, can be estimated from the appearance of the encrusted specimens of *G. pachyderma* in the upper layer.

(5) In consequence, the distribution pattern of species corresponds well with that of water masses. This fact shows that planktonic foraminifera is efficient in recognition of the shape and location of water masses, particularly of upper 200 m, even for a complicated water in the perturbed area.

(6) Examination of the proloculus diameter of each species from different water depths shows that planktonic foraminifera includes microspheric and megalospheric forms that may correspond to sexual and asexual generations, respectively. They alternate their generations in different layers or seasons each other.

From the viewpoint of proloculus diameter, it is estimated that *G. pachyderma* has exceptionally adapted to the cold water, and that around 8°C is

a critical water temperature upon the existence of *G. dutertrei*.

(7) The ontogenetic segregation and daily vertical movement of planktonic foraminifera, particularly *G. pachyderma*, in water column was examined at St. 1 through the use of specimens from both tows and sediment traps (collectors). Juveniles gather in the upper 30 m layer or euphotic layer, and adults are in preparation for reproduction in the lower part of the upper epipelagic layer and lower maximum concentration layer. Populations descend about an interval of 50 m at night as a probable resultant from the up- and downward movements, and ascend in the morning. Some of the adults in the epipelagic layer descend after sunset to the lower maximum concentration layer to reproduce.

An addition of a small ultimate chamber and encrustation of the test of *G. pachyderma* and other species (*G. bulloides*, *G. dutertrei* and *G. quinqueloba*) are probably of pre-reproductive phase. The addition of the small ultimate chamber is done before the encrustation.

The reproduction takes place synchronously once a day early in the morning at depths of 150 m to 250 m, and then the brought-forth shells descend due to their own settling velocity of each species. The settling velocities of empty shells, calculated on an analysis of the peaks of concentration in the water column and density in sediment traps are: 900 m/day for *G. pachyderma*, 600 m/day for *G. quinqueloba*, and 200 m/day for *G. uvula*. The calculated settling velocity of *G. pachyderma* well matches to the value logically calculated after the method of Berger and Piper (1972).

All the above-mentioned facts show that the populations in the upper and deeper layers are affiliated with each other through ontogenetic and daily migration. The reasoning is agreeable with the accounts by Tolderlund and Bé (1971). The assemblages in the upper layer match in specific association to ones in the deeper layer.

(8) Populations in flux produce a bottom population with a bias toward adults. Therefore, it is not reasonable to simply assort relative age groups of fossil populations in the light of knowledge of living populations collected by surface tows.

(9) The turnover time of each species at St. 1 shows that the fertility of water, particularly in blooming seasons, may remarkably increases reproductivity of planktonic foraminifera. In the Oyashio area, the output of tests of planktonic foraminifera in the upper layer is mainly conducted through reproduction during the blooming in spring.

(10) Encrustation of *G. pachyderma* is done in the deep layer from 50 to 150 m. The amount of calcite for the encrustation is equal to or more than that for specimens before encrustation. The tests of *G. pachyderma* are mainly brought forth in the Oyashio area in spring. This strategy should also be elucidated on an oxygen isotype analysis for paleotemperature by using the tests of planktonic foraminifera.

(11) The number of chambers of planktonic foraminifera in the last stage is largely depends on the diameter of a proloculus. Therefore, it is unreliable to judge ontogenetic stages simply based on the number of chambers. In order to describe ontogenetic stages completely, the value of proloculus diameter is needed.

(12) Encrustation of the test of *G. pachyderma* is made in a reproductive phase, and flux of those tests to the bottom sediments is conducted mainly through reproduction. On the other hand, examination of fractured specimens by scanning electron micrographs shows that there exists no interruption caused by differences in crystal growth. Those facts explain the lack of transitional forms among the populations of *G. pachyderma* from bottom sediments.

(13) Examination of wall structure in different ontogenetic stages shows a great similarity between *G. pachyderma* and other globigerine species such as *G. bulloides* and *G. quinqueloba*. On the other hand, *G. dutertrei* s.s. -*G. incompta*-*G.* aff. *G. pachyderma* complex has entirely the same wall structure, which is characteristics of the genus *Globoquadrina*.

The ontogenetic development of gross shapes shows that *G. dutertrei* s.s. -*G. incompta*-*G.* aff. *G. pachyderma* have basic characters of the family Globorotaliidae. On the other hand, *G. pachyderma* has the same characters that globigerine species have, and resembles closely *G. quinqueloba* in their early stages.

Morphometrics on those species shows that the mode of shell enlargement along with chamber addition is closely similar among *G. dutertrei* s.s. -*G. incompta*-*G.* aff. *G. pachyderma* complex, and that of *G. pachyderma* is more retarded and similar to that of *G. quinqueloba*. All the above imply a close phylogenetic relationship between *G. pachyderma* and *G. quinqueloba*. Retraction of spines in *G. pachyderma* can be interpreted by adaptation to the cold water of high viscosity and density.

(14) Observations of the distribution pattern of populations of *G. dutertrei* and of other species in different stages in the water column show that *G. dutertrei* belongs to the genus *Globoquadrina* and *G. pachyderma* to the genus *Globigerina*, respectively.

G. aff. *G. pachyderma* and the encrusted *G. incompta* are of reproductive phase of the last stage of *G. dutertrei* s.s. in 'immature forms'.

They inhabit different water masses and *G. dutertrei* is absent in the subarctic area where is free from a marked effect of warm water masses.

(15) Most of the populations of *G. pachyderma* are left-coiled, while most of *G. dutertrei* right-coiled. Stations 1 and 2 are located in a limited area of the distribution of both *G. dutertrei* and *G. pachyderma*. Therefore, the name of *G. pachyderma* should be confined to the populations composed mostly of left-coiled specimens that are distributed in the cold water in high latitudes where no marked effect of the warm currents prevails. The so-called right-coiled variety of *G. pachyderma* is synonymous with *G. dutertrei*, some of whose individuals converge in morphology to those of *G. pachyderma* in the cooler section within its distribution.

(16) *G. dutertrei* is a warm water species, and *G. pachyderma* is a cold water species. The lateral and vertical concentration patterns of *G. pachyderma* and *G. dutertrei*, and examination on the proloculus diameters show that a water temperature of around 8°C is crucial upon their existence.

In the subarctic area, populations of *G. pachyderma* probably bloom in spring. On the other hand, the turnover time of planktonic foraminifera probably shortens during the fertile time. The shell output of *G. pachyderma* is mostly done through reproduction.

Therefore, the shells of *G. pachyderma* in bottom sediments are composed mostly of specimens after reproduction turned out mainly in spring. Tolderlund and Bé (1971) showed that the population of the left-coiled *G. pachyderma* remarkably dominates the subarctic area in spring. Juveniles of planktonic foraminifera, which are more sensible to environments, gather in the upper layer.

It is particularly noteworthy that as initially mentioned by Ericson (1959) the isothermal line of a surface temperature around 8°C in spring largely matches to the boundary between the distributions of the so-called left- and right-coiled specimens of *G. pachyderma* in bottom sediments. This boundary also nearly corresponds to the limit of the cold surface water (subpolar water) in spring.

(17) In the cold region, the existence

of *G. dutertrei* indicates the influence of warm currents.

(18) In natural classification of planktonic foraminifera, it is necessary to deliberate on ontogenetic variations in water column.

(19) Planktonic foraminifera take place reproduction at various ontogenetic stages, so that neither the shell diameter nor chamber numbers can be necessarily indicators of the degree of maturity.

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Table 1. Number of specimens of planktonic foraminifera collected by plankton nets (live specimens) at KT–78–7 Station 1

Species \ Sample	01	02	03	04	05	06	07	08	09	10	11	12	13
Globigerina bulloides	39	79	92	74	112	92	95	95	20	19	18	7	9
G. pachyderma	222	182	206	217	211	198	210	162	110	45	96	75	65
G. quinqueloba	51	50	77	28	53	15	15	13	4	3	4	1	
Juveniles (*G. pachyderma-G. bulloides-G. quinqueloba*)	80	41											
Globigerinita glutinata			1		1		4	14	3	9	3		4
G. uvula	8	6	7	1	7	8	2					1	
Globorotalia scitula									4	2		2	6
Hastigerinella riedeli					5								
Total no.	400	358	383	320	389	313	326	284	141	78	121	86	84
Aliquot	1/32	1/64	1/128	1/256	1/128	1/128	1/8	1/32	1/32	1/16	3/16	1/4	11/32

Table 2. Number of specimens of planktonic foraminifera collected by plankton nets (empty specimens) at KT–78–7 Station 1

Species \ Sample	01	02	03	04	05	06	07	08	09	10	11	12	13
Globigerina bulloides								2	8	43	67	43	54
G. pachyderma								17	104	315	39	51	53
G. quinqueloba								1	13	6	5	25	31
Globigerinita glutinata												2	1
G. uvula								2			1	3	2
Globorotalia scitula										1		1	
Total no.								22	125	365	112	125	141
Aliquot	1/32	1/64	1/128	1/256	1/128	1/128	1/8	1/32	1/32	1/16	3/16	1/4	11/32

Table 3. Number of specimens of planktonic foraminifera collected by plankton nets (live specimens) at KT–77–8 Station 2

Species \ Sample	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20
Globigerina bulloides		6	13	4	29	14	5	51	13	2	23	25	4	40	20	10	37	12	1	110
G. pachyderma	23	80	55	23	164	112	127	647	603	174	223	401	182	538	188	102	615	88	29	712
G. quinqueloba	1	3	20	25	16	11	15	60	28	42	172	115	17	6	17	3	2	6	4	16
G. aff. *G. pachyderma*	2	2	7	5	37	31	6	27	2	2	29	36	5	2	6	6	3			
G. incompta	2		103	74	51	12	6			11	58	24	6		4	1		1	4	
Globoquadrina dutertrei s. s.		2	220	274	166	30	11	19	22	17	12	27	17	3	1	1	4	5	1	
Globigerinita glutinata			1	2	3	2			3	2	2		1						1	
G. uvula								11	11		19	16	2		10	1				
Globigerinoides ruber			6								1	5								
G. tenellus			1																	
Globorotalia inflata			5	5	5	10	1		8	2				1			1			
G. scitula						2	1		2	5	11	2	9		2	5	2		3	2
Hastigerinella riedeli											1									
Unidentified foraminifera		5	8	10				37		9	23	17	4	6				19	9	13
Total no.	28	98	439	422	471	224	172	852	692	266	574	668	247	596	248	129	664	131	52	853
Aliquot	1/4	1/2	1/4	1/8	1/16	1/32	1/16	1/16	1/4	1/4	1/4	1/4	1/16	1/2	1/16	1/4	1/16	1/2	1/2	1/16

Table 4. Number of specimens of planktonic foraminifera collected by plankton nets (empty specimens) at KT–77–8 Station 2

Species \ Sample	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20
Globigerina bulloides							3	7	3				3		2	1	1	8	10	4
G. pachyderma							52	85	481				54	82	1	23	7	86	34	55
G. quinqueloba							27	28	118				16	12	4		3	36	17	37
G. aff. *G. pachyderma*							1	4	8								1	9	14	7
G. incompta								11	4					1					4	6
Globoquadrina dutertrei s. s.								2	5				1	13		1		11	4	
Globigerinita glutinata								2					1	1						2
G. uvula							2	7	20				1	2	2	1		9	1	5
Globigerinoides ruber								1	2											
Globorotalia inflata							1							16				2	1	2
G. scitula								1										2	1	
G. truncatulinoides							1											1	1	
Hastigerinella riedeli							1	1	2											
Orbulina universa									1											
Total no.							88	149	644				76	127	9	26	12	163	89	118
Aliquot	1/4	1/2	1/4	1/8	1/16	1/32	1/16	1/16	1/4	1/4	1/4	1/4	1/16	1/2	1/16	1/4	1/16	1/2	1/2	1/16

Table 5. Number of specimens of planktonic foraminifera in the sediment traps (collector) (live specimens) during the nighttime (21:00, May 27–9:00, May 28, 1978)

Species \ Depth (m)	50	100	150	200	250	300	400	500
Globigerina bulloides	9	33	4	30	12	1	4	
G. pachyderma	161	293	19	111	36	17	8	8
G. quinqueloba	42	62	6	21	6	3	6	
Juveniles (*G. pachyderma*-*G. bulloides*-*G. quinqueloba*)	202	84	18	79	62	23	19	9
Globigerinita glutinata	5	4	1	1	6	2		
G. uvula	376	214	12	50	12	21	5	11
Globorotalia scitula								1
Hastigerinella riedeli		1				1		
Unidentified foraminifera		1						
Total no.	795	692	60	292	134	68	42	29
Examined area (cm^2)	119.2	119.2	119.2	119.2	119.2	119.2	119.2	101.9

Table 6. Number of specimens of planktonic foraminifera in the sediment traps (collector) (empty specimens) during the nighttime (21:00, May 27–9:00, May 28, 1978)

Species \ Depth (m)	50	100	150	200	250	300	400	500
Globigerina bulloides	1		5	17	1		4	
G. pachyderma	2	1	7	12	17	4	6	
G. quinqueloba	8	23	13	42	21	16	27	31
Juveniles (*G. pachyderma-G. bulloides-G. quinqueloba*)						20	28	22
Globigerinita glutinata							1	3
G. uvula	77	34	42	147	67	192	242	86
Unidentified foraminifera	4			1				1
Total no.	92	58	67	219	106	232	308	143
Examined area (cm^2)	119.2	119.2	119.2		119.2	119.2	119.2	101.9

Table 7. Number of specimens of planktonic foraminifera in the sediment traps (collector) (live specimens) during the daytime (9:30–19:00, May 27, 1978)

Species \ Depth (m)	100	150	200	250	300	400	500
Globigerina bulloides	19	40	3	5	1	1	
G. pachyderma	87	35	4	11	36	3	21
G. quinqueloba	24	20	1	8	1		
Juveniles (*G. pachyderma-G. bulloides-G. quinqueloba*)	54	30	25	12	8	20	10
Globigerinita glutinata	3						
G. uvula	23	5	4	7	9		1
Globorotalia scitula					1		1
Hastigerinella riedeli							1
Total no.	210	130	37	43	56	24	34
Examined area (cm^2)	101.9	101.9	101.9		101.9	101.9	101.9

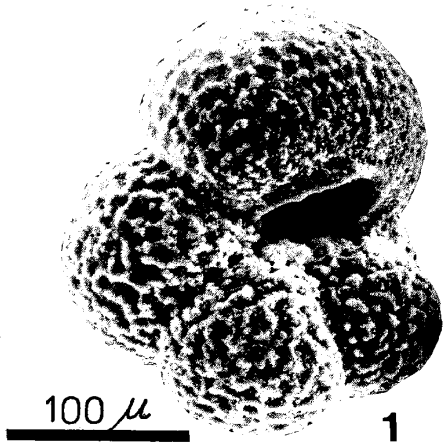
Table 8. Number of specimens of planktonic foraminifera in the sediment traps (collector)(empty specimens) during the daytime (9:30–19:00, May 27, 1978)

Species \ Depth (m)	100	150	200	250	300	400	500
Globigerina bulloides	4	3	2		2		
G. pachyderma	1	4	4	3	9	12	18
G. quinqueloba	9	7	8	20	9	9	17
Globigerinita uvula	29	20	21	43	71	7	20
Unidentified foraminifera	1						1
Total no.	44	34	35	66	91	28	56
Examined area (cm^2)	101.9	101.9	101.9		101.9	101.9	101.9

Plate 26

Figs. 1–3. *Globigerina pachyderma* (Ehrenberg) from a depth of 0 m (surface water) at St. 1.
1-Umbilical view. Note distinct peripheral indentation and globigerine-like gross shape.
2-Enlarged view of apertural area. Aperture is high-arched, and a distinct lip is developed on apertural base. The ultimate chamber has many nodes on its wall surface.
3-Enlarged view of the surface of the penultimate chamber. Nodes are connected to one another to construct ridges. Pores are circular in their outline of different size, and are randomly distributed in inter-ridge area, leaving a distance from ridges.

Figs. 4–6. *Globigerina pachyderma* from a depth of 50 m at St. 1.
4-Umbilical view. Wall structure is somewhat developed as compared with the specimens from surface water but peripheral lobulation is still distinct.
5-Enlarged view of apertural area. Apertural lip is inflated and constructs a rim.
6-Enlarged view of the surface of penultimate chamber. Ridge has added its width and height, and inter-ridge area becomes more restricted. Pore area is entirely flat and pores are randomly distributed at some distance from ridges.



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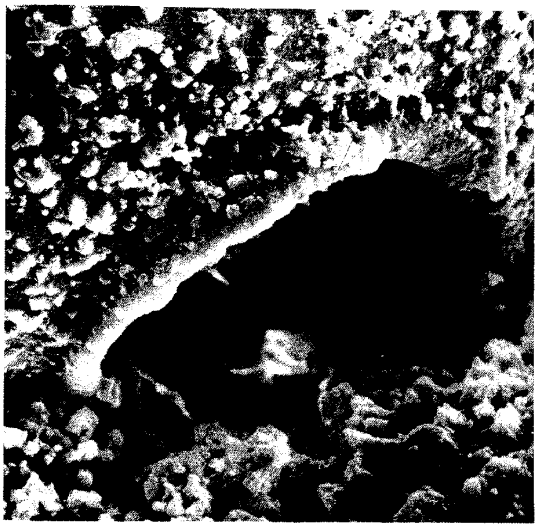

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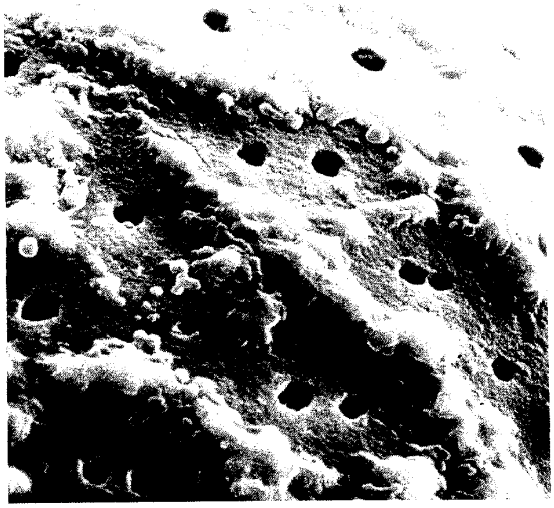

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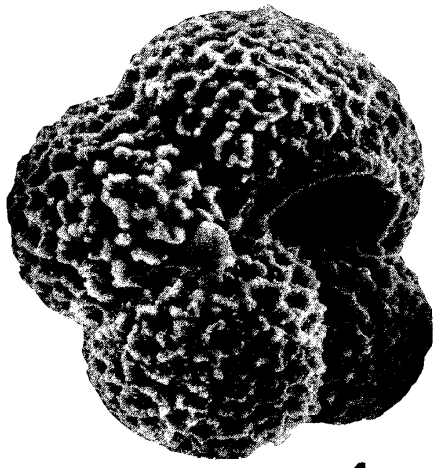

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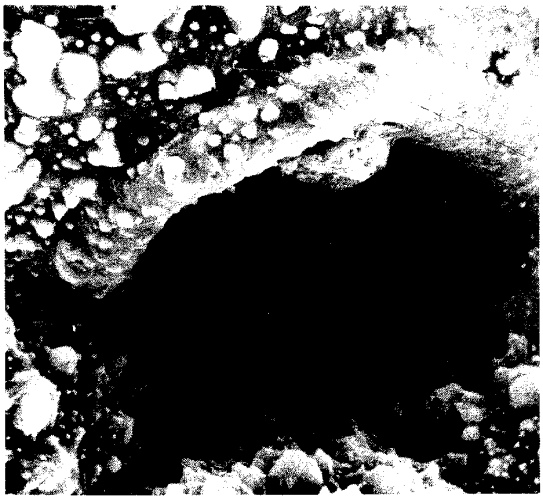

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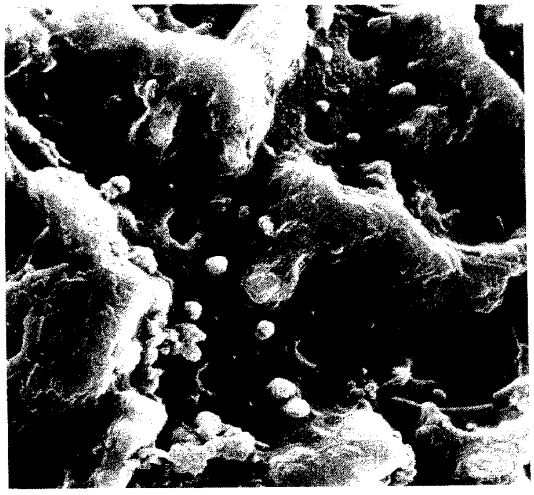

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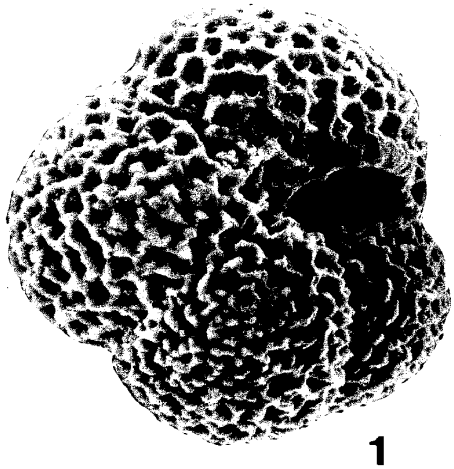
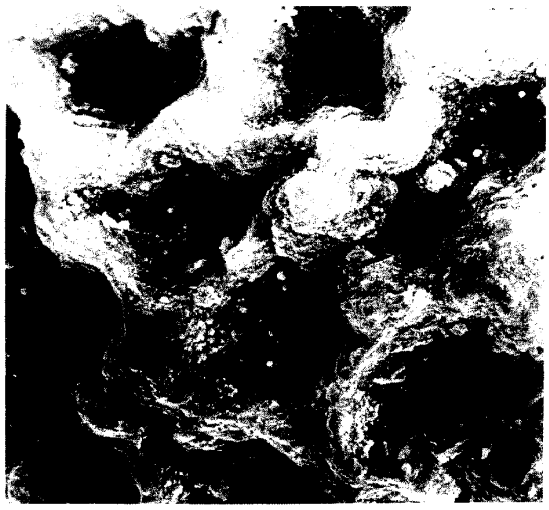


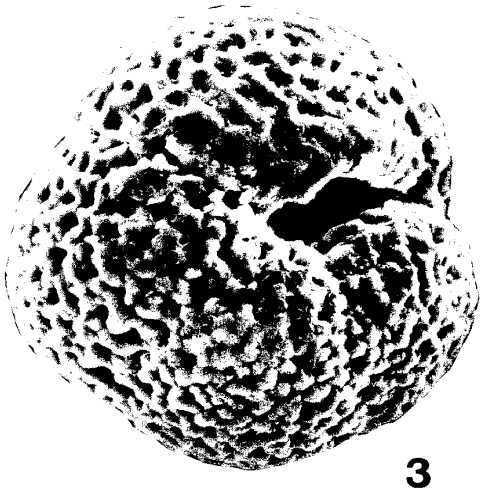
1

50 μ



10 μ

2

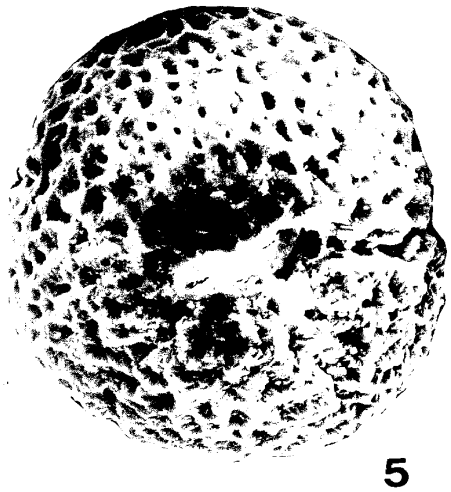


3

50 μ

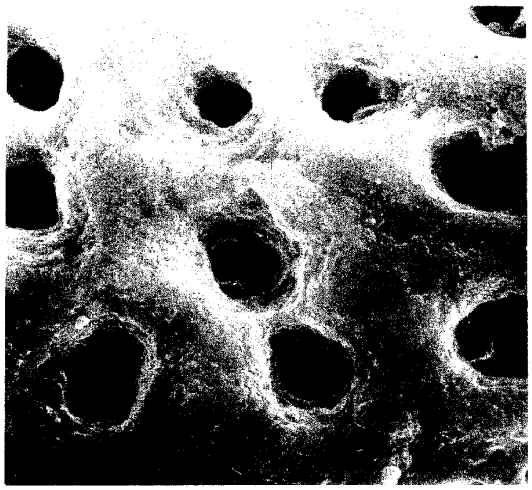
10 μ

4



5

50 μ



10 μ

6

Plate 27

Figs. 1, 2. *Globigerina pachyderma* (Ehrenberg) from a depth of 75 m at St. 1.

1–Umbilical view. Due to encrustation of wall surface, peripheral lobulation is not so distinct as compared with specimens at the preceding stage (Pl. 26, fig. 4), and apertural opening becomes restricted.

2–Enlarged view of the ultimate chamber. The ridges become connected with each other more intimately. The ridges have added their width and height, and the pore areas are significantly constricted but are still kept flat.

Figs. 3, 4. *Globigerina pachyderma* from a depth of 100 m at St. 1.

3-Umbilical view. Test encrustation is more advanced, and the peripheral outline is less significantly lobulate. Aperture is constricted and septal furrow is slightly depressed.

4–Enlarged view of the ultimate chamber. As the result of encrustation of test, pores are confined to the narrow trench between ridges, but pore area, if any, is still kept flat.

Figs. 5, 6. *Globigerina pachyderma* from a depth of 150 m at St. 1.

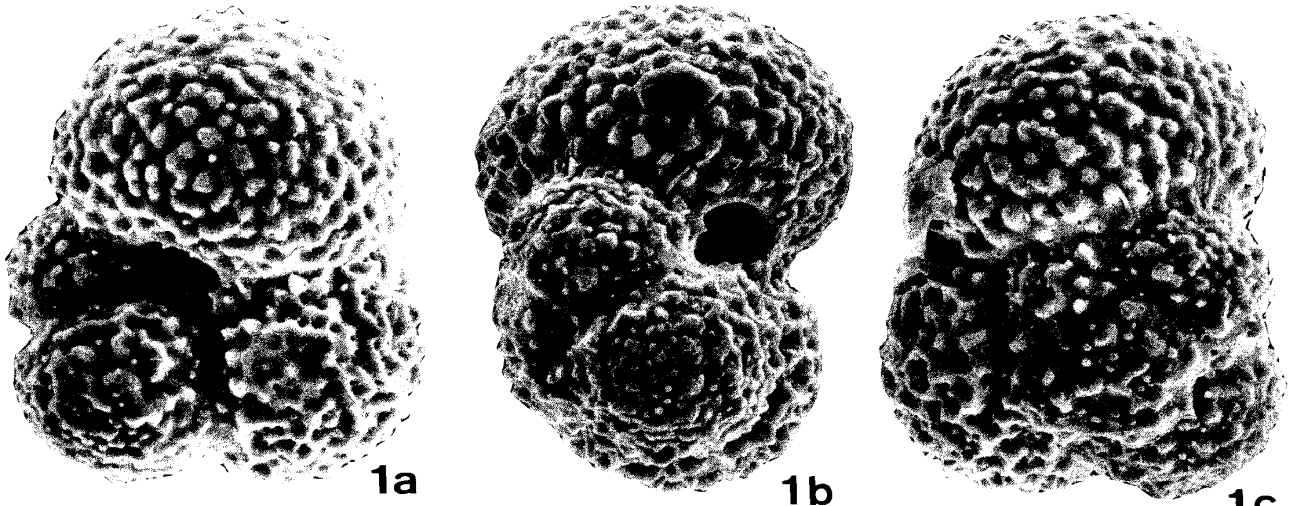
5-Umbilical view. Encrustation of test is advanced and a gross shape is of the so-called *Globigerina pachyderma*. Septal furrow is entirely buried under the encrusted test, and the peripheral outline is oval to subglobular in shape. Aperture exists as a slit from umbilical to extraumbilical area showing the character of the genus *Globorotalia*.

6–Enlarged view of the ultimate chamber. Wall surface is completely covered by cryptocrystalline calcite, and areas around pores are entirely lost. Pore exists as an independent hole on the test surface, being irregular in size and distance.

Plate 28

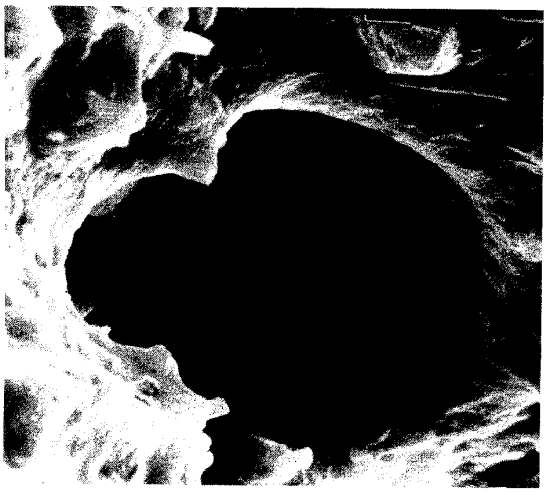
Figs. 1–3. *Globigerina bulloides* d'Orbigny from a depth of 0 m (surface water) at St. 1.
1a–Umbilical view. 1b–Side view. 1c–Dorsal view. This form of *G. bulloides* is identical to *G. bulloides* var. *trilocularis* Boltovskoy.
2–Enlarged view of apertural area. Spines are kept particularly around apertural area. A faint lip decorates apertural margin.
3–Pores, irregular in size and distance, are distributed and sometimes attached to spine bases or tubercles.

Figs. 4, 5. *Globigerina bulloides* from a depth of 100 m at St. 1.
4–Encrusted is the test particularly of early chambers in the last whorl. Peripheral indentation is lost and aperture exists as a slit as in the case of the typical form of *G. pachyderma*. Spines are still kept in apertural opening.
5–Enlarged view of the ultimate chamber. Spine bases are connected with one another to construct ridges, and have added their width and height, and pores are distributed in the narrow trench between ridges as in the case of *G. pachyderma*, except for areas around undulate pores.



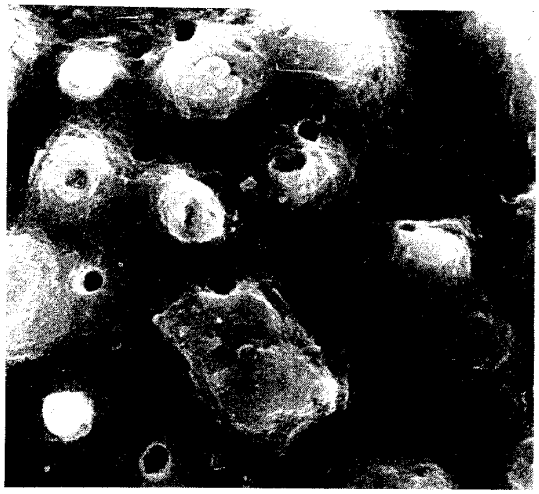
1a 1b 1c

50 μ



2

10 μ

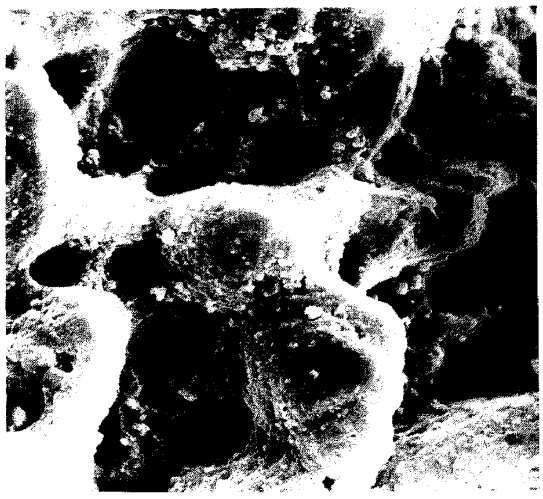


3

10 μ

4

100 μ



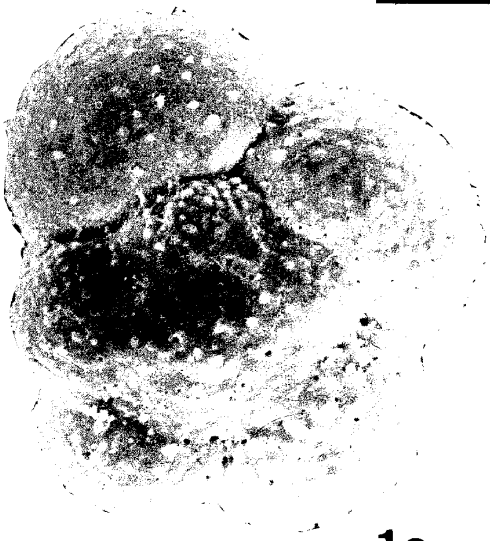
5

10 μ

1a

50 μ

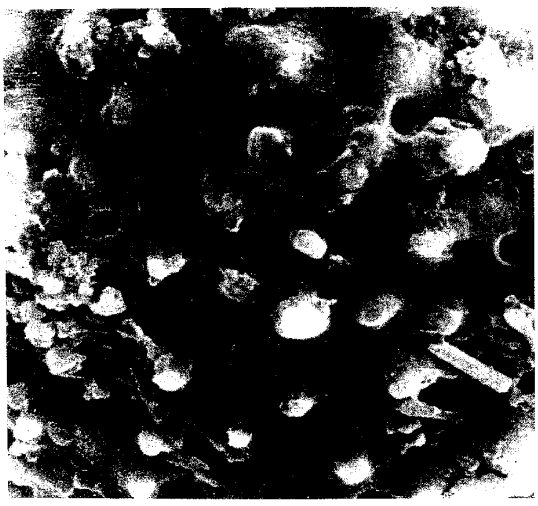
1b



1c

2

10 μ



10 μ

3

Plate 29

Figs. 1–3. *Globigerina quinqueloba* Natland with 13 chambers from a depth of 30 m at St. 1.
1a–Umbilical view. 1b–Side view. 1c–Dorsal view. Test wall is finely perforate and has many spines on its surface.
2–Enlarged view of apertural area. A faint lip is developed on apertural margin.
3–Enlarged view of the penultimate chamber. Pores, different in size and shape, are irregularly distributed between spine bases or tubercles, showing a close affinity with *G. pachyderma* of Plate 26, fig. 2.

Plate 30

Figs. 1–3. *Globoquadrina dutertrei* (d'Orbigny) s.s. with 7 chambers from a depth of 30 m at St. 2.

1–Umbilical view. This specimen has a flat evolute side and a convex umbilical side. A crescent to triangular lip is attached to the chamber surface with a distinct joint and extends to cover umbilical area. The ultimate chamber has a shoulder at the junction with the lip. Test wall is smooth and sutures on the umbilical side are slightly curved, although those on the dorsal side radiate. Chambers are depressed. In gross shape, it shows the characters of the genus *Globorotalia*.

2–Enlarged view of umbilical area. Chamber is attached to the preceding one leaving behind a slight distance to open umbilicus wide.

4–Enlarged view of the ultimate chamber. Wall is smooth and circular pores exist in a slight depression.

Figs. 4–6. Umbilical view of *Globoquadrina dutertrei* s.s.

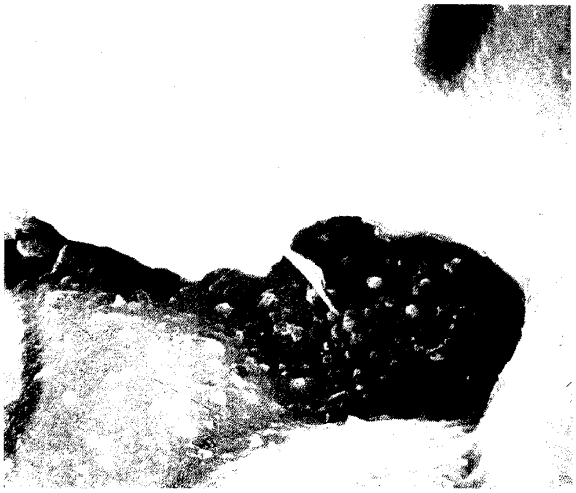
4–Specimen with 9 chambers from a depth of 30 m at St. 2. Wall surface shows slight relief, and is finely perforate.

5–Specimen with 15 chambers. Wall surface is coarsened through accentuation of relief around pores particularly in the initial chamber of the last whorl.

6–Specimen with 15 chambers. Umbilicus is clearly open.

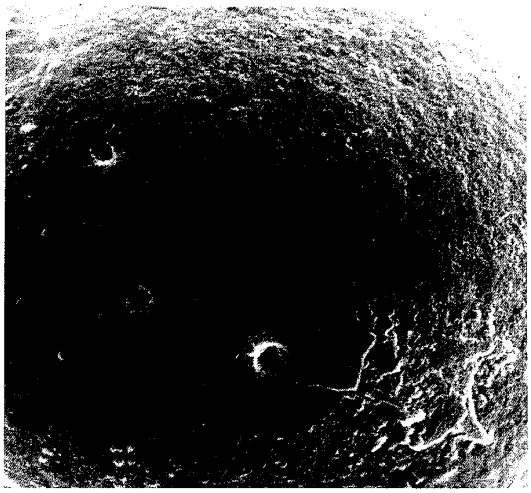
40 μ

1



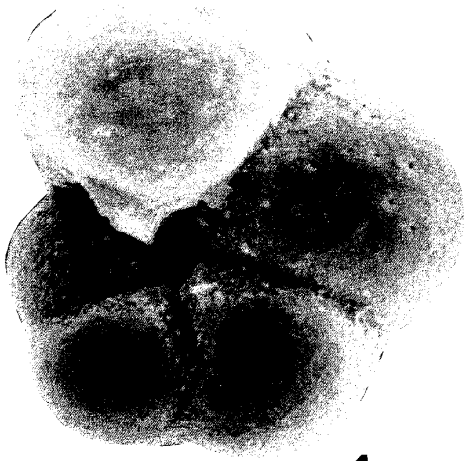
10 μ

2



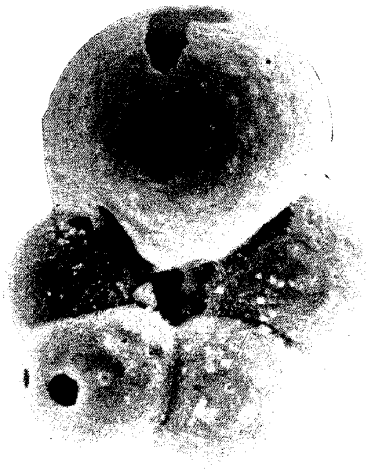
10 μ

3



40 μ

4



50 μ

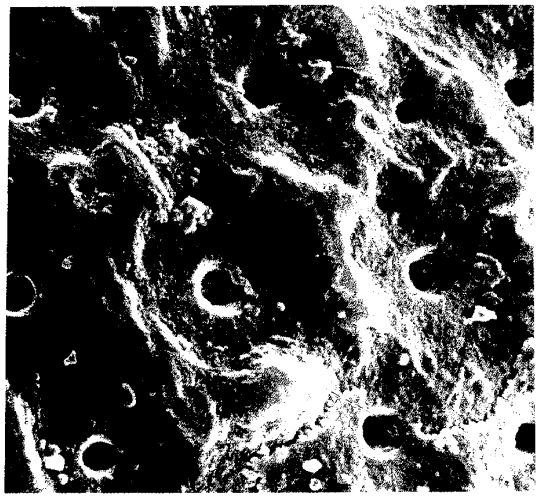
5

100 μ

6

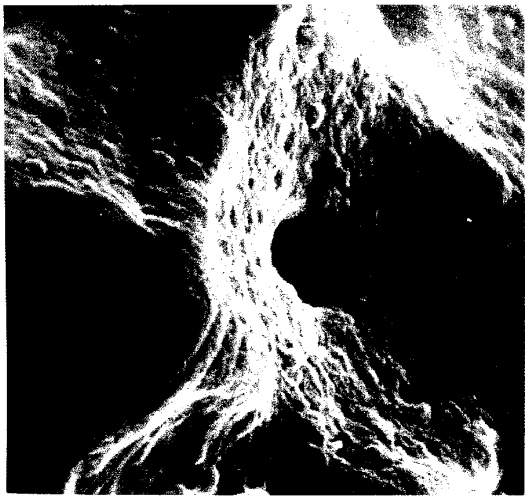
1

100 μ



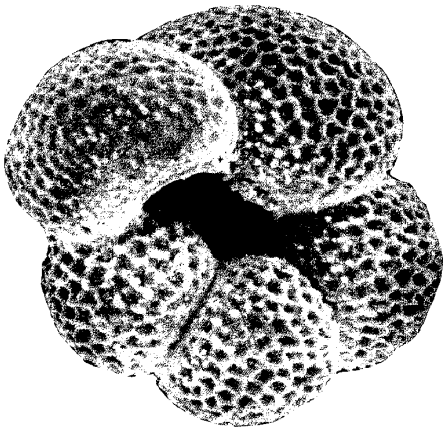
2

10 μ

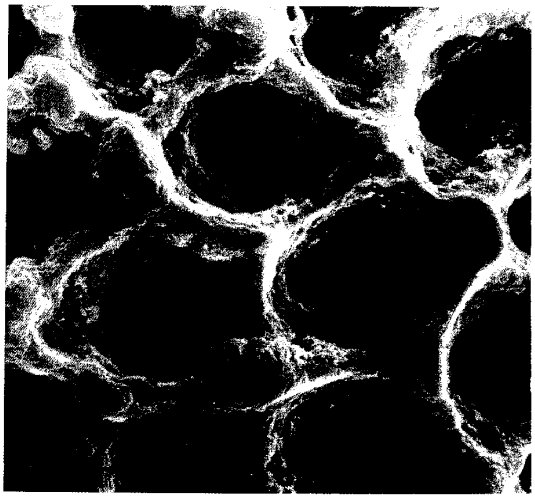


3

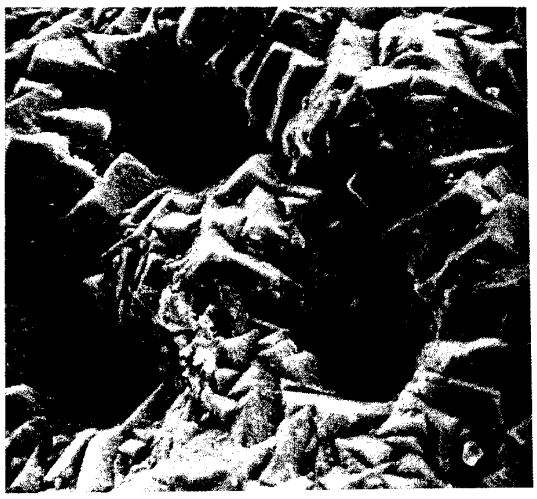
5 μ



100 μ 4



20 μ 5



10 μ 6

Plate 31

Figs. 1–3. *Globoquadrina dutertrei* (d'Orbigny) s.s. with 14 chambers from a depth of 30 m at St. 2.

1–Umbilical view of *G. dutertrei* s.s.

2–Enlarged view of the ultimate chamber. Pores in the center of pore area, which are slight but distinct depressions, are of a size, and regularly distributed on wall surface. Each of them is completely encircled by ridges which have been developed from the surface relief at the preceding stage.

3–Enlarged view of the pore area, showing distinctly concaved pore area.

Figs. 4–6. *Globoquadrina dutertrei* s.s. with 15 chambers from a depth of 30 m at St. 2.

4–Umbilical view. This form at this stage shows a clear feature of *Globoquadrina dutertrei* s.s. A globular ultimate chamber is attached facing its aperture to the axis of whorl. The peripheral outline is circular and lobulate.

5–Enlarged view of the penultimate chamber. Pore area is significantly concave. Pores are of a size and clearly encircled by well developed polygonal ridges, which are particularly prominent at the junction, and are regularly distributed.

6–Enlarged view of the penultimate chamber of *Globoquadrina dutertrei* s.s. from a depth of 150 m at St. 2. Euhedral crystals are developed on the surface of wall and encircle pores.

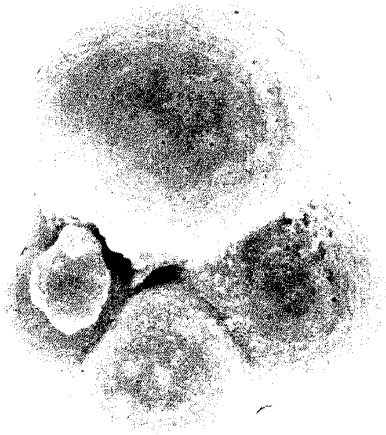
Plate 32

Figs. 1, 2. A juvenile of *Globigerina incompta* Cifelli from a depth of 30 m at St. 2.
1–Umbilical view. A crescent lip is attached to the chamber surface with a linear junction and extends to cover umbilical area. Aperture exists from umbilicus to extraumbilicus. The ultimate chamber has a shoulder at the junction with lip. Test wall is smooth and sutures on the umbilical side slightly curved. Surface is finely perforated. In gross shape, it shows the character of the genus *Globorotalia*.
2–Enlarged view of the ultimate chamber. Wall is smooth and circular pores exist in a slight depression.

Figs. 3, 4. *Globigerina incompta* with 10 chambers from a depth of 30m at St. 2.
3–Umbilical view. Wall surface is coarsened through accentuation of relief around pores.
4–Enlarged view of the ultimate chamber. Pores uniform in size are regularly distributed in the center of a concave pore area, which is surrounded by polygonal papillae. This figure shows a close affinity with *Globoquadrina dutertrei* s.s. (Plate 31, fig. 2).

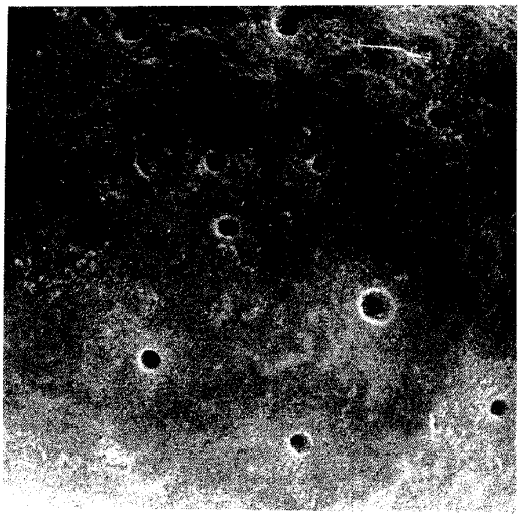
Fig. 5. Umbilical view of *Globigerina incompta* with 10 chambers from a depth of 30 m at St. 2. Wall surface is coarsened through the development of papillae at the preceding stage.

Fig. 6. Umbilical view of the *Globigerina incompta* with 11 chambers from a depth of 30 m at St. 2.



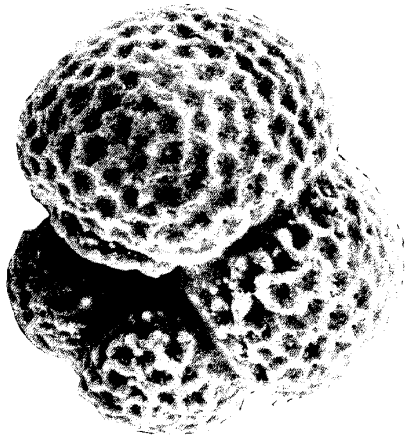
1

50 μ

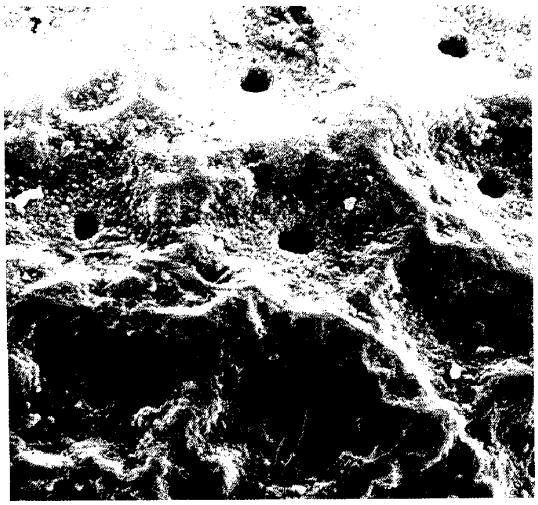


2

10 μ

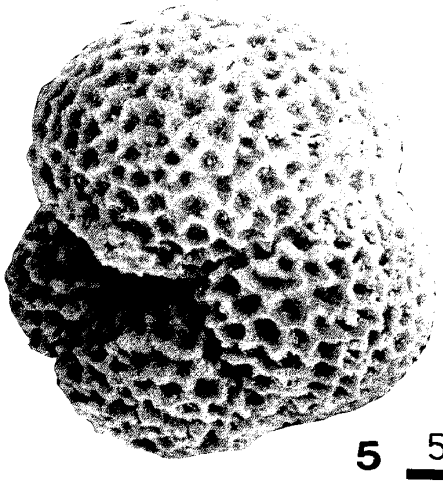


50 μ 3

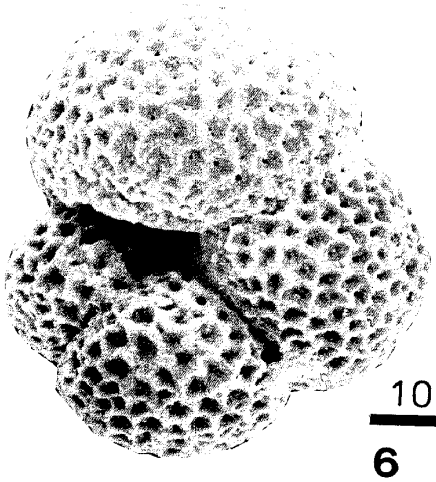


10 μ

4

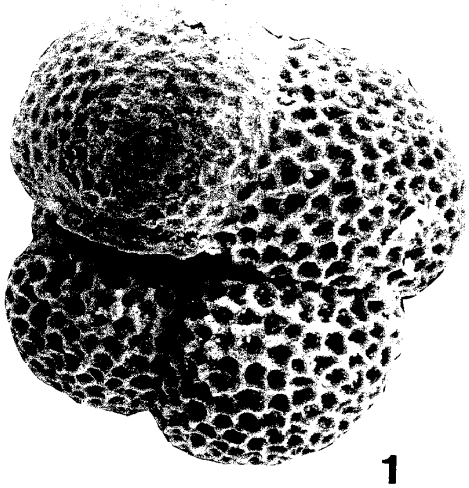


5 50 μ



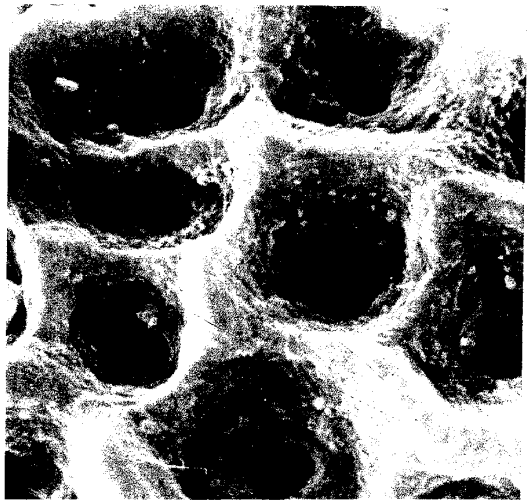
100 μ

6



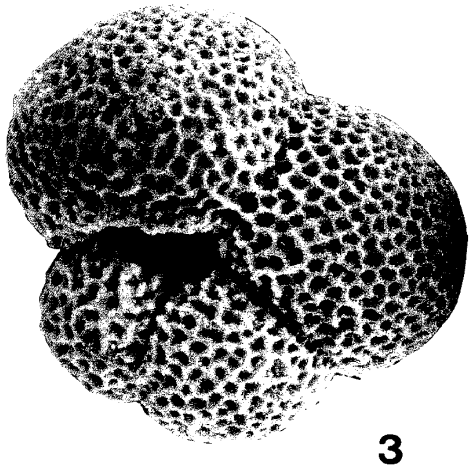
1

100 μ



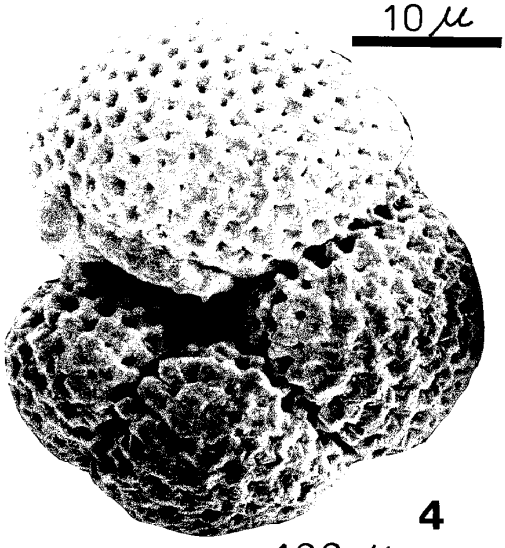
2

10 μ



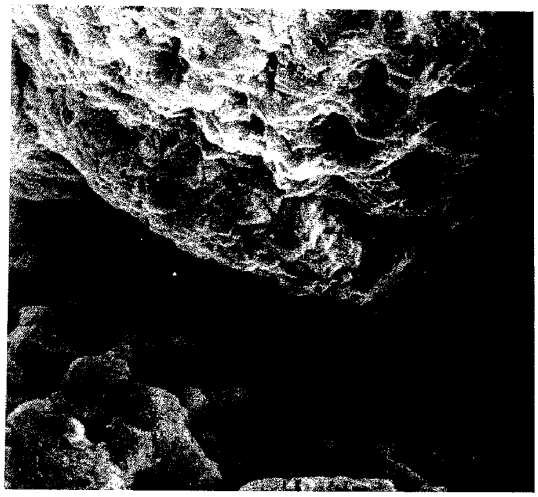
3

100 μ



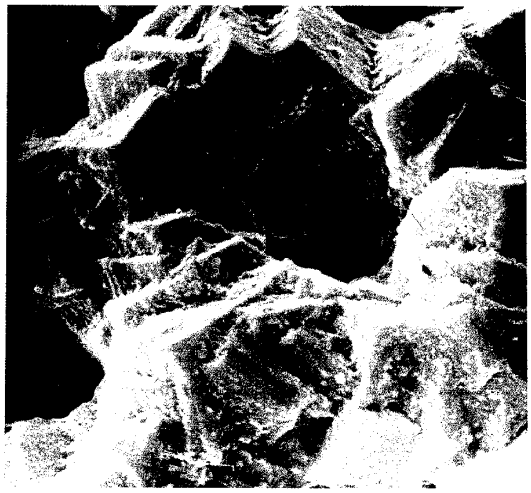
4

100 μ



40 μ

5



10 μ

6

Plate 33

Figs. 1, 2. *Globigerina incompta* Cifelli with 12 chambers from a depth of 75 m at St. 2.
1–Umbilical view. A crescent lip extends from umbilicus to extraumbilicus.
2–Enlarged view of the antipenultimate chamber. Completely circular pores of uniform size are regularly distributed in the center of pore pits surrounded by polygonal ridges as those of *G. dutertrei* s.s. (Plate 31, fig. 5).

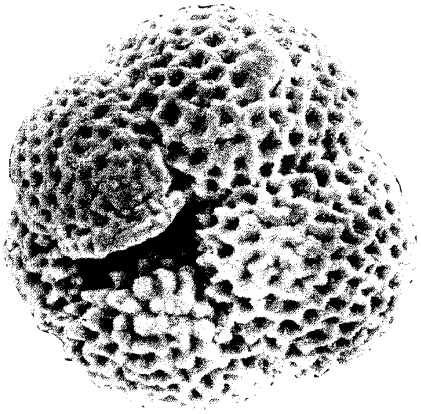
Fig. 3. Umbilical view of *Globigerina incompta* with 12 chambers.

Figs. 4–6. *Globigerina incompta* from a depth of 150 m at St. 2.
4–Umbilical view. Wall surface is covered with crystals particularly in early chambers of the last whorl. A gross shape does not remarkably change from that in the early stages. As the result of encrustation, septal furrow is buried and peripheral indentation becomes indistinct.
5–Enlarged view of apertural area. Chambers are attached to the former ones, leaving behind a slight distance so that umbilicus opens in polygonal shape. A crescent lip is attached to the former chamber with a linear junction and extends to cover umbilical area as does *G. dutertrei* s.s. The lips of the former chambers can be seen as tooth plates.
6–Enlarged view of the antipenultimate chamber. Euhedral crystals with well-developed growth facets surround pores.

Plate 34

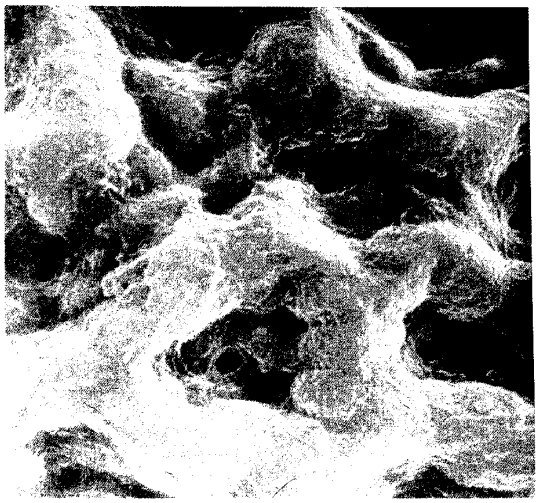
Figs. 1–3. *Globigerina incompta* Cifelli (kummerform) from a depth of 75 m at St. 2.
1–Umbilical view. As the result of shell thickening, peripheral indentation becomes significantly weak and closely resembles the encrusted forms of *Globigerina pachyderma* in gross shape.
2–Enlarged view of apertural area. A crescent lip is developed from umbilicus to extraumbilicus. Umbilicus shows a polygonal feature. Pustules are seen in apertural opening.
3–Enlarged view of the ultimate chamber. Each pore is regularly distributed in funnel-shaped pore areas surrounded by papillae.

Figs. 4–6. *Globigerina* aff. *Globigerina pachyderma* (Ehrenberg) from a depth of 150 m at St. 2.
4–Umbilical view. As the result of encrustation, peripheral indentation is almost lost, and septal furrow is buried. Apertural opening is small, which is a character of this species.
5–Enlarged view of apertural area. A crescent lip is developed to cover umbilicus. The lip is also covered by euhedral calcite crystals as well as by chamber surface.
6–Enlarged view of the ultimate chamber. Each pore exists in a funnel-shaped pore area. Calcite crystals with growth facet surround each pore as in the case of *G. incompta* and *G. dutertrei* s.s. in the advanced stages.

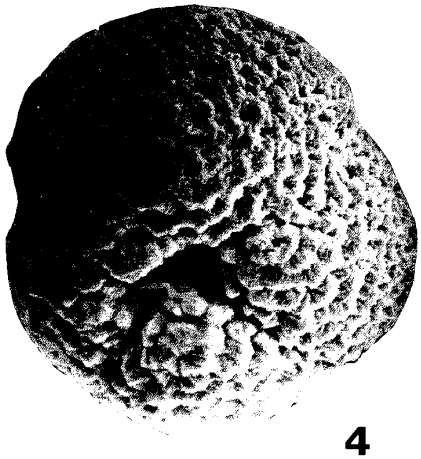


100 μ 1

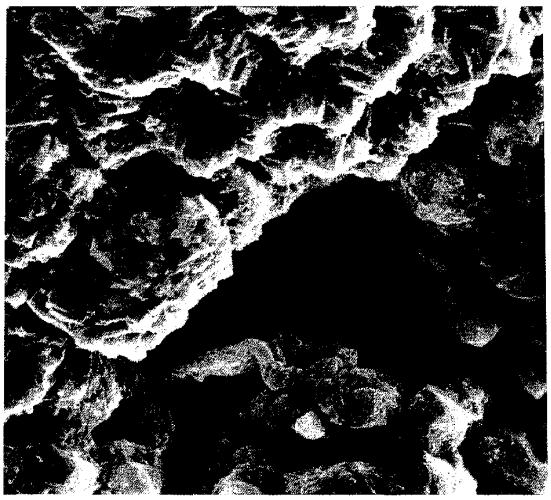
20 μ 2



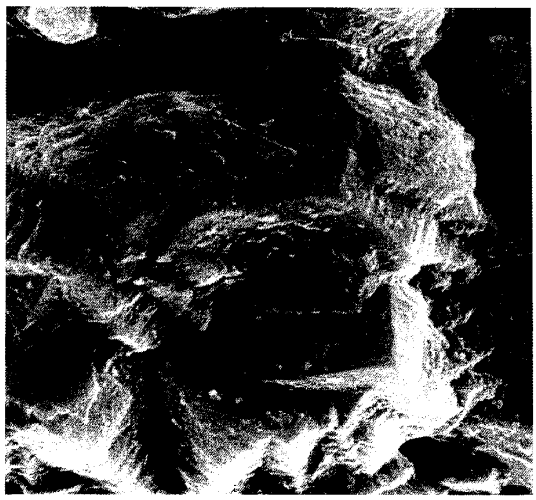
10 μ 3



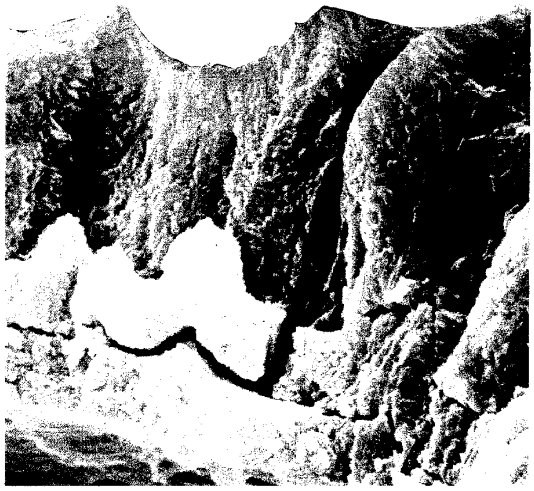
100 μ 4



20 μ 5

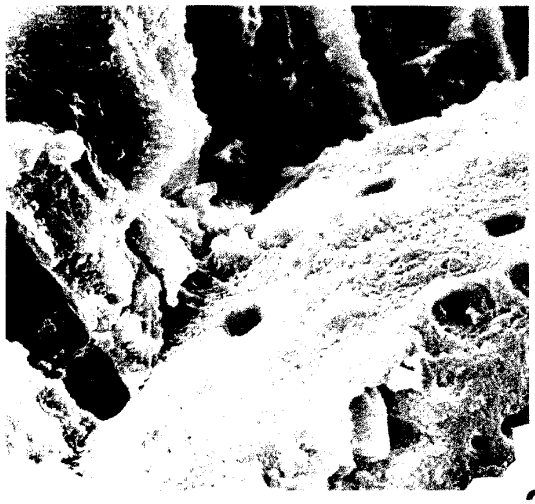


5 μ 6



10 μ

1



10 μ

2

10 μ

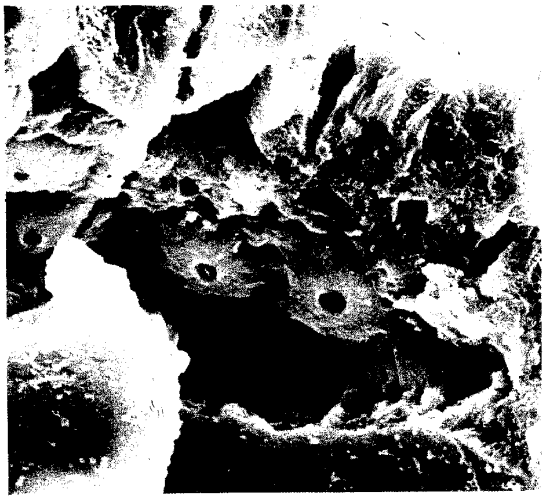
3

10 μ

4

10 μ

5



20 μ

6

Plate 35

Figs. 1, 2. *Globigerina pachyderma* (Ehrenberg)

1–Cross section of test wall shows that pore area is entirely flat, and pores exist as a cylindrical hole in the test wall. Encrustation progresses in relation to crystal growth without interruption.

2–Wall surface with the outer layers peeled off. Pore area is entirely flat, and pores are distributed detaching from tubercles.

Figs. 3, 4. *Globoquadrina dutertrei* s.s. (d'Orbigny)

3-Cross section of test wall. Pore area is concave, and intervals between lamellae are larger on the ridge than in areas near the pore. Encrustation layer does not show any interruption of crystal growth.

4–Inner surface of the ultimate chamber after peeling the inner lamellar (mould) off. This shows funnel-shaped pore areas and entirely circular pores, regularly distributed, of uniform size.

Figs. 5, 6. *Globigerina* aff. *Globigerina pachyderma* (Ehrenberg)

5–Cross section of a juvenile of *G.* aff. *G. pachyderma*. The test wall before encrustation (arrow) also has a funnel-shaped pore area as do *G. dutertrei* s.s. and *G. incompta*.

6–Wall surface with the inner layers peeled off. Mould shows that pore areas are funnel-shaped, and that entirely circular pores of uniform size are regularly distributed as in the case of *G. dutertrei* s.s. and *G. incompta*.