Seasonality in microhabitats of rose bengal stained deep-sea benthic foraminifera from the New Jersey continental margin

MICHAEL A. KAMINSKI¹, AMAL M. AL HASSAWI², and WOLFGANG KUHNT³
1. Research School of Geological & Geophysical Sciences, UCL, Gower Street, London WC1E 6BT, UK
2. Department of Anatomy & Developmental Biology, UCL, Gower Street, London WC1E 6BT, UK
3. Institut und Museum für Geologie und Paläontologie, CAU, Olshausenstr. 40, D-24118 Kiel, Germany

ABSTRACT
Analysis of Rose Bengal stained calcareous benthic foraminifera in a box core taken at a water depth of 3098 m on the New Jersey continental margin in late February (before the spring phytoplankton bloom) reveals important differences in the vertical distribution of taxa when compared with the post-bloom data of Corliss (1985) from a nearby station. Winter populations display a large subsurface peak in the foraminiferal population and consist of „deep infaunal“ forms such as Globobulimina and Melonis, whereas the late summer populations sampled by Corliss consist largely of „epifaunal“ taxa such as Hoeglundina and Cibicidoides. The near lack of live „epifaunal“ forms in winter may be attributed to low seasonal food supply and the cumulative effects of predation at the sediment surface. In the absence of the „epifaunal morpho-group“, infaunal taxa such as Melonis rise to occupy the shallow subsurface habitat (0-4 cm depth). Alternatively, low winter populations of epifaunal forms may be part of a natural seasonal phase in their life cycle, as observed in some shallow-water foraminifera.

INTRODUCTION
Benthic foraminifera display enormous ecological adaptability, and constitute more than half of the total meiofaunal biomass in the deep sea (Shirayama, 1984). However, precious little is known about the population dynamics of deep-sea taxa. In a series of papers, Corliss and co-workers have determined that individual foraminiferal morphogroups occupy microhabitats that are vertically partitioned with respect to the sediment/water interface and pointed out the relationship between vertical stratification and the shape of the foraminiferal test (Corliss, 1985; Corliss & Emerson, 1988; Rathburn & Corliss, 1994). In a subsequent study, a positive correlation was observed between the proportion of infaunal morphogroups and the flux of organic matter to the sea floor (Corliss & Chen, 1988). However, the flux of organic matter to the ocean floor (especially phytodetritus) is seasonal, and the benthic foraminiferal populations have been documented to react quickly to seasonal fluctuations in food supply (Gooday, 1988). If benthic populations in the deep sea are limited by the amount of available food as numerous studies suggest, it is therefore reasonable to propose that both populations and habitat preferences of benthic foraminifera may change in response to the seasonal cycles of food flux.

The foraminiferal data originally presented by Corliss (1985) was collected in September 1980, and provides a snapshot of the population structure sampled after the marine phytoplankton bloom. In this study, we document the distribution of Rose Bengal stained calcareous benthic foraminifera from the upper 15 cm of sediments in a boxcore from the New Jersey continental margin. The boxcore was collected in late February, 1990, which is before the spring phytoplankton bloom. Therefore, if the vertical distribution of benthic foraminiferal morphotypes within sediment displays seasonality, we ought to observe differences between samples collected before and after the spring bloom. To achieve this goal, we compare our data set with that of Corliss (1985).

MATERIAL AND METHODS
Boxcore 89038-020 examined in this study was collected on board the CSS Hudson at 37°31.23'N, 72°00.97'W from a water depth of 3098 m on the New Jersey continental margin off Atlantic City (figure 1). This depth is within 100 m of the boxcore (38°12.9'N, 71°30.4'W; 3000 m depth) that Corliss sampled in 1980 for his classic study of benthic foraminiferal microhabitats (Corliss, 1985). The lithology of Boxcore 89038-020 consisted of 6 cm of brown homogeneous soft clay underlain by 4-5 cm of light brown clay. A distinct color change associated with a major change in redox conditions is observed at 10 cm depth. Below 10 cm the sediment consists of olive gray stiff clay with mottling by bioturbating organisms. The sediment in the core was subdivided on board ship, and slices (one cm thick) from one of the subcores were taken from the sediment/water interface to a depth of 20 cm. Each 75-cm³ subsample was preserved in a buffered formalin solution. In the laboratory, samples were gently washed over a 63 μm sieve, and preserved in a 50% methanol solution. Samples were treated with Rose Bengal (a protein-specific stain) to highlight organisms that were alive at the time of collection. All stained foraminifera were picked from the >150 μm fraction to ensure that our data and results are directly comparable to those of Corliss (1985). We counted only the calcareous benthic foraminifera with bright red-stained protoplasm. Agglutinated foraminifera were ignored for the purpose of this comparison. We noticed that many stained foraminifera contained protoplasm that did not fully occupy the test. In many cases the final chamber or chambers were empty. These specimens were counted as live, but the data were recorded separately. Some deep-sea benthic foraminifera have been observed to double their protoplasm mass within three days of being fed (Altenbach, 1992), indicating that benthic foraminifera can survive extended periods with little food. The foraminiferal census data are presented in Table 1.

RESULTS
At our station the dominant species group was represented by Globobulimina spp. and Chilostomella oolina (Schwager) which accounted for a broad subsurface peak in the foraminiferal fauna between 5 and 10 cm below the sediment/water interface. However, these forms did occur in lower numbers to the base of the studied depth interval at 15 cm. Both Globobulimina and Chilostomella were identified by Corliss (1985) as deep infaunal deposit feeders, preferring a habitat deeper than 5 cm on the New Jersey margin. The second most abundant species in the winter population is Melonis barleeanum (Williamson) which was found mainly within the upper four centimeters, but may extend to a depth of 10 cm. However, the specimens occurring below 3 cm mainly contained partial protoplasm.
and may have been in a stressed or dormant state owing to the seasonal lack of food. In Corliss' late summer data, *M. barleeanum* occupied an intermediate depth habitat of between 1 and 5 cm. Surprisingly, stained specimens of epifaunal taxa such as Hoeglundina elegans, Cibicidoides wuellerstorfii, and Cibicidoides spp. were absent from the uppermost centimeter of the sediment column, although their dead tests were common at this site. Single stained individuals of Hoeglundina elegans, Oridorsalis spp., Cibicidoides wuellerstorfii, C. kullenbergi, and C. bradyi were present in the subsurface, and most specimens contained protoplasm that only partially occupied the test. This is in marked contrast to the summer populations which were dominated by Hoeglundina elegans, Oridorsalis, and Cibicidoides wuellerstorfii.

### DISCUSSION & CONCLUSIONS

Comparison of our winter samples with Corliss (1985) reveals large differences in both the population structure and the microhabitat preference of lower bathyal benthic foraminifera (figure 2). The late summer foraminiferal populations sampled by Corliss were dominated by epifaunal forms. Some of the smaller epifaunal foraminifera may be opportunistic taxa whose life cycle is linked to the seasonal supply of phytoplankton detritus. Following the spring phytoplankton bloom in the North Atlantic, a number of species of calcareous benthic foraminifera apparently reproduce and rapidly invade the fluffy layer of detritus that arrives at the sea floor (Gooday, 1993). However, by winter this ephemeral food source has been exhausted, and the epifaunal benthic foraminiferal population apparently collapses. There may be several reasons (or a combination of reasons) why the numbers of epifaunal benthics are lower in winter at our station. One cause for the drastically lowered populations may be predation. In the absence of abundant food, there would low population growth, and predation pressure would tend to further reduce the number of foraminifera. A number of grazing metazoans, such as holothurians, gastropods and polychetes, are known to ingest benthic foraminifera (Lipps, 1983). Another explanation for low numbers of winter epifaunal taxa is the possibility of a natural seasonality in the life cycle of deep-sea benthic foraminifera, as observed in some shallow-water foraminiferal species. Our data suggest that, in the absence of epifaunal taxa, the shallow infaunal species *M. barleeanum* rises through the sediment column to occupy the surface layer. This species has also been observed to occupy the sediment surface in the Norwegian Sea during winter, whereas at other times in the year it was found at a depth of 3-4 cm (Lutze, 1987).

The deep infaunal taxa appear to be less sensitive to seasonal fluctuations in food supply than taxa that have a preferred epifaunal or shallow infaunal mode of life. After the spring bloom, the organic carbon from the phytodetritus is removed from the sediment surface by surface grazing metazoans and deposited in their burrows (Aller & Aller, 1986). This resource may serve as a food for

### Table 1. Benthic foraminiferal census data in Core 89038-20. Depth is in cm. Numbers indicate specimens with full protoplasm – specimens with partial protoplasm.

<table>
<thead>
<tr>
<th>Species</th>
<th>Depth in cm</th>
<th>Full-Partial Protoplasm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cibicidoides kullenbergi</td>
<td>F-P</td>
<td>F-P</td>
</tr>
<tr>
<td>Cibicidoides bradyi</td>
<td>2-4</td>
<td>1-7</td>
</tr>
<tr>
<td>Chilostomella ovina</td>
<td>2-6</td>
<td>3-4</td>
</tr>
<tr>
<td>Globobulimina australis</td>
<td>0-3</td>
<td>0-11</td>
</tr>
<tr>
<td>Globobulimina sp. A</td>
<td>0-1</td>
<td>0-1</td>
</tr>
<tr>
<td>Globobulimina affinis</td>
<td>0-6</td>
<td>2-0</td>
</tr>
<tr>
<td>Hoeglundina elegans</td>
<td>0-2</td>
<td>2-0</td>
</tr>
<tr>
<td>Melonis barleeanum</td>
<td>1-0</td>
<td></td>
</tr>
<tr>
<td>Oridorsalis sp.</td>
<td>0-1</td>
<td></td>
</tr>
<tr>
<td>Pullenia subcarinata</td>
<td>0-1</td>
<td></td>
</tr>
<tr>
<td>Pullenia olivacea</td>
<td>0-1</td>
<td></td>
</tr>
<tr>
<td>Pringo sp.</td>
<td>0-1</td>
<td></td>
</tr>
<tr>
<td>Quinqueloculina sp.</td>
<td>0-1</td>
<td></td>
</tr>
<tr>
<td>Quinqueloculina striata</td>
<td>0-1</td>
<td></td>
</tr>
</tbody>
</table>
bacteria and ultimately for infaunal detritivores such as benthic foraminifera during the winter season. Increasing preservation of organic matter and high numbers of bacteria are often found in association with the subsurface redox boundary. This level was observed at 10 cm depth in Core 89038-20 and is associated with a strong subsurface peak in Globobulimina, a form known to ingest bacteria and associated sediment particles (Goldstein & Corliss, 1994). A less pronounced subsurface peak in benthic foraminiferal numbers is also evident in Corliss' summer data. This may indicate that the redox boundary is seasonally stable and provides a constant source of food for the deep infaunal detritivores.

We believe our observation of strong seasonality among cosmopolitan deep-water benthic foraminifera has important repercussions for interpretations of benthic foraminiferal biogeography (because most studies of live populations are based on samples collected during the summer months) as well as for studies of Cenozoic palaeoecography based on the isotopic composition of foraminiferal calcite (which use taxa that are representative of water-column conditions present during only a fraction of the year). The deep sea environment must be sampled at a much higher temporal resolution before we can fully understand the life cycle of these deep sea organisms. Once the relation of seasonal microhabitats and life-cycles of deep-water benthic foraminifera are more firmly established, benthic populations may prove to be a sensitive monitor of the seasonal carbon flux to the seafloor.

ACKNOWLEDGEMENTS

W. Kuhnt thanks the Captain & crew of the CSS Hudson and Dr. K. Moran for the opportunity to participate on cruise no. 89038. Amal Al Hassawi acknowledges support of a postgraduate studentship from the Kuwait Public Authority for Higher Education & Training at UCL. We thank A. Altenbach, B.H. Corliss, A.E.I. Holbourn, A.R. Lord, and J. Wollenburg for reading an early draft of this manuscript.

REFERENCES


Psamminopelta gradsteini n.sp., a new species of Paleogene deep-water agglutinated foraminifera from the northern North Atlantic and Polish Outer Carpathians

MICHAEL A. KAMINSKI¹ and STANISŁAW GEROCH²

1. Research School of Geological & Geophysical Sciences, UCL, Gower Street, London WC1E 6BT, UK
2. Institute of Geological Sciences, Jagiellonian University, ul. Oleantry 2a, 30-063 Krakow, Poland.
(deceased).¹

ABSTRACT
We describe the new species Psamminopelta gradsteini Kaminski and Geroch, n. sp. from green shales of Eocene age from the Labrador Sea, Norwegian Sea, and the Silesian Unit of the Polish Outer Carpathians. The species is characterised by its small, gracile test and numerous evolute whors. The more or less synchronous appearance of Psamminopelta gradsteini n.sp. in middle to late Eocene green shales in three geographically separated areas means that the species is probably cosmopolitan, and is a useful stratigraphical index species in the abyssal area of the Atlantic and Tethys oceans.

INTRODUCTION
The deep water agglutinated foraminifera (DWAF) are widely distributed in oceanic sediments deposited beneath the Carbonate Compensation Depth throughout the world ocean. Although some faunal endemism may admittedly exist in semi-isolated oceanic basins such as the North Sea (e.g. Gradstein & Kaminski, 1989), as a general rule most DWAF species are cosmopolitan in distribution. This particularly applies to the faunas of the abyssal plains.

On various occasions over the years, the authors of this study have carried out direct comparisons of DWAF assemblages from classic localities in the Atlantic and Carpathian regions for the purpose of establishing a standardised taxonomic framework for biostratigraphical studies. Our earlier comparative studies have shown, for example, that a number of species described from the Paleogene of Trinidad by Cushman and co-workers in the 1930's and 1940's are identical with those first described from the Carpathian flysch by Grzybowski and co-workers at the turn of the 19th/20th centuries (Kaminski et al. 1988; Kaminski & Geroch, 1993). In another instance, a species newly found in Trinidad by the first author also turned up in samples from the Polish Carpathians (Kaminski & Geroch, 1987). It would appear that the faunal links between the Atlantic Ocean and the Carpathian flysch basins were indeed strong, at least until the Oligocene when Alpine tectonic movements severed the connections between the two areas.

The purpose of this note is to assign formal taxonomic status to yet another new species of cosmopolitan DWAF that has been found in the Eocene of the northern North Atlantic and Carpathi-

¹ Prof. Stan Geroch visited the GEOMAR bungalow in the spring of 1991 to carry out comparative studies of microfossils with the first author. At this time, the matter of the new Psamminopelta was discussed, and Prof. Geroch contributed photographs of specimens of the species from the Carpathian flysch. We again discussed this species in 1992 - 1993 while we were carrying out our revision of the Paleogene species from the Grzybowski Collection (Kaminski & Geroch, 1993). Although the idea carrying out more taxonomic work was discussed and a preliminary description of the species was written at that time, Prof. Geroch's death in 1995 precluded him from taking part in the actual writing of this paper. However, photographs of the Carpathian specimens used in this paper were made by him. Because of his initial contribution to this paper he is included here as the co-author.

an deep sea basins. The species has been reported previously under various names, notably in four (possibly five) different studies of Paleogene DWAF from DSDP and ODP localities in the Labrador Sea and Norwegian Sea. The species may have also been observed by Grzybowski (1901) from the Paleocene of the Carpathians, but as specimen is not preserved in the collections we cannot be certain of the synonymy. We therefore propose the new name \textit{Psamminopelta gradsteini} n.sp. and provide a formal description of the species.

\textbf{SYSTEMATIC TAXONOMY}

Family \textit{RZEHAKINIDAE} Cushman, 1933

\textit{Psamminopelta} differs from \textit{Rzehakinia} in having flat sides and in the absence of any wall thickening over the flat sides of the test. Loeblich \& Tappan (1987) reported the stratigraphic distribution of the genus as Cretaceous. Reports of this genus in the Norwegian Sea extend its known stratigraphic range to the Miocene.

\textit{Psamminopelta gradsteini} Kaminski \& Geroch, n. sp.

\textit{Textfigure 1; Plate 1, figs. 1-9.}

\textit{aff. Ammodiscus polygyrus} (abnormal).—Grzybowski, 1901, pl. 8, fig. 27.


\textit{Spirosignoilimella compressa} Matsunaga.—Miller \textit{et al}., 1982, p. 20, pl. 2, fig. 5; —Kaminski \textit{et al}., 1989. pl. 5, fig. 6.


\textbf{Diagnosis:} A gracile species of \textit{Psamminopelta} with a thin wall and a concave initial part.

\textbf{Type Specimen:} Currently housed in the first author’s collection at University College London. Holotype and paratypes will be deposited in the micropalaeontology collections of the Natural History Museum, London.

\textbf{Type Level:} Upper Eocene.

\textbf{Type Locality:} ODP Site 647, Southern Labrador Sea. Holotype is from Sample 647A-45R-1, 14-17cm.

\textbf{Diagnostic Features:} Test small, wholly planispiral, flat or weakly biconcave, evolute, with two chambers per whorl. Proloculus is minute. Chambers increase in diameter slowly, and do not overlap preceeding whorls. Specimens consist of as many as eight sets of whorls, and have a poorly developed spiral suture. Periphery is rounded. Aperture is an eccentric slit at the end of a produced neck.

\textbf{Size:} Specimens from ODP Site 647 are up to 0.6 mm in length, 0.28 mm in width.

\textbf{Derivation of Name:} In honour of Dr. Felix M. Gradstein (Saga Petroleum), who was co-author of three of the ODP papers that originally reported this species under various names. Also in recognition of his long-standing work on the systematics and biostratigraphy of DWAF from the northern North Atlantic region.

\textbf{Figure 1.} Internal structure of \textit{Psamminopelta gradsteini} n.sp., drawn from transmitted light photographs. Specimens from the upper Eocene of Biecz, Poland, magnification ca. x160.

\textbf{Observed Occurrences:} This species may have been seen by J. Grzybowski in the Paleogene of the Gorlice region of the Carpathians. The specimen illustrated by Grzybowski (1901) as "\textit{Ammodiscus polygyrus} (abnormal)" in his plate 8, fig. 27 is certainly reminiscent of our species. However, this specimen is not preserved in the collection, and has no formal status. Miller \textit{et al}. (1982) reported this form as \textit{Spirosignoilimella compressa} from the upper middle Eocene to upper Eocene of DSDP Site 112 in the Labrador Sea. Verdenius \& van Hinte (1983) illustrated specimens as \textit{Spirolocammina lamposa} from DSDP Hole 338 which probably fit the description of \textit{Psamminopelta gradsteini} n.sp. Osterman \& Spiegler (in press) illustrated a specimen as \textit{S. compressa} from the Miocene at Site 909, west of Spitsbergen.

We observed \textit{Psamminopelta gradsteini} n.sp. in
the upper middle Eocene to lower Oligocene at Sites 112 and 647 in the southern Labrador Sea (Kaminski et al., 1989), in the upper Eocene to Oligocene at ODP Site 643 in the Norwegian-Greenland Sea (Kaminski et al., 1990), and in middle to upper Eocene (A. latus Zone) green claystones of the Silesian Unit of the Polish Carpathians, in Biec, Poland.

**Known Stratigraphic Range:** upper middle Eocene to lower Miocene. The first occurrence of this species is a useful biostratigraphic datum in the upper middle Eocene in the deep Labrador Sea and Norwegian Sea.

**Bathymetry:** lower bathyal to abyssal.

**Remarks:** One of us (MAK) originally believed this form to represent one of the alternate generations of *S. compressa*, and therefore included it together with the latter species in data from ODP Site 647 (Kaminski et al., 1989). However, after closer examination of material from both the Labrador and Norwegian-Greenland Sea, we have been unable to find any individuals of this species with spirosigmoidal initial coiling. Moreover, at both localities, the first occurrence of this form occurs lower in the stratigraphic section than that of the typical *S. compressa* Matsunaga. There is also a paleobathymetrical separation between *S. compressa* and *P. gradsteini* n.sp. in the North Sea region. *Psamminopelta gradsteini* n.sp. is rare in the North Sea, and is only observed in the deepest parts of the basin and at the abyssal ODP sites, whereas *S. compressa* is widely distributed. *Psamminopelta gradsteini* n.sp. occurs in low numbers in the middle to upper Eocene (Ammodiscus latus Zone) of the Silesian basin of the Polish Carpathians, but in this area *S. compressa* has not been observed. Based on the above observations, we now believe it is necessary to separate this species from *S. compressa*.

Although some specimens may be slightly asymmetrical, others are almost perfectly symmetrical. The species therefore cannot be placed in the genus *Spirolocammina* Earland, 1934. *Spirolocamminia* is a strongly sigmoidal modern genus described from the Antarctic seas).

*Psamminopelta gradsteini* n.sp. is most similar in morphology to Paleocene specimens of *Rzehakina minima* from the Central North Sea. The major differences can be found in the nature of the initial portion of the test. *Rzehakina minima* has a larger proloculus than *Psamminopelta gradsteini* n.sp. Topotype specimens of *R. minima* from Lizard Springs are broader and thicker, and have perfectly flat lateral sides, whereas *Psamminopelta gradsteini* n.sp. is biconcave. Many specimens of *Psamminopelta gradsteini* n.sp. have broken centers, indicating that the proloculus and first whorls must have been extremely thin-walled. Schröder-Adams & McNeil (1994) described the new species *Psamminopelta arca* from the Oligocene Kugmallit sequence in the Beaufort-Mackenzie Basin. This species differs in its thicker test and more rounded outline.

**Acknowledgements**

We thank Jaroslaw Migacz for help with the figures and Dennis Grieg (Chevron, USA) for assistance with the SEM work. Jeno Nagy reviewed the paper. This is contribution no. 57 of the Deep-Water Agglutinated Foraminiferal Project.

**References**


Plate 1. *Pseudomopela gradsteini* n.sp.

Fig. 1a,b. Oligocene, ODP Site 643, Norwegian Sea, Sample 643A-44R-5, 79-84 cm, x145.
Fig. 2a,b. Oligocene, ODP Site 643, Norwegian Sea, Sample 643A-44R-5, 79-84 cm, x145.
Fig. 3. Upper Eocene, ODP Site 647, Labrador Sea, Sample 647A-36R-4, 49-52 cm, x175.
Fig. 4-6. Upper Middle Eocene, ODP Site 647, Labrador Sea, Sample 647A-45R-1, 14-17 cm, 4,5, Paratypes, 6, Holotype, x132.
Fig. 7-8. Upper Middle Eocene, ODP Site 647, Labrador Sea, Sample 647A-45R-2, 20-24 cm, x142.
Fig. 9. Upper Eocene, Silesian Unit of the Polish Carpathians near Biecz, Poland. x140.
Wurstkammer specimens of the planktic foraminifer Neogloboquadrina pachyderma (sinistral): A new morphotype from the Arctic Ocean and the Weddell Sea

HARALD HOMMERS
GEOMAR - Research Center for Marine Geosciences, Wischhofstraße 1-3, D-24148 Kiel, Germany

ABSTRACT
From two cores of the central Arctic Ocean and the Southern Ocean (Weddell Sea) a new morphotype of the planktic foraminifer Neogloboquadrina pachyderma (sinistral) (Ehrenberg) with "sausage" shaped final chambers (i.e. "Wurstkammer") is described. A comparison of these morphotypes in the two polar regions shows significant differences in shape and frequency during the last 70,000 years in the central Arctic Ocean and during the last 140,000 years in the Weddell Sea. In the central Arctic Ocean the frequency of wurstkammer specimens can be correlated to that of the so-called kummerform specimens during the last 70,000 years; this correlation cannot be seen in a core from the Weddell Sea. The wurstkammer and kummerform specimens are interpreted as being end-members of a morphological progressional line. The abnormal chamber growth is probably an adaption to various environmental stress conditions found in the two polar regions during the last 70,000 in the Arctic and 140,000 years in the Antarctic, but the reasons for this abnormality are not yet fully understood.

INTRODUCTION
In this study, a new morphotype of the planktic foraminifer Neogloboquadrina pachyderma (sinistral) (Ehrenberg) is described and its occurrences in the central Arctic (Fig. 1) and the South Atlantic Ocean (Weddell Sea, Fig. 2) is compared. The last chambers of these specimens are „sausage“ shaped („Wurstkammer“ = sausage chamber), especially in Core PS2185, or are more inflated (in Core PS1388).

Earlier studies concentrated mainly on the integration of the planktic foraminifer species N. pachyderma (sin.) within the total planktic foraminifer taxa. Since the 1970’s several workers have studied the paleoceanographic and ecological parameters of this polar species, such as the evaluation of coiling directions and of frequency distributions (Kennett, 1968, Keller, 1978).

In the 1980’s, research on the recent distribution of planktic foraminifers in the water column was strengthened by plankton tow and sediment trap experiments, especially in the Pacific Ocean (Arikawa, 1983, Reynolds & Thunell, 1986).

During the 1990’s, detailed studies of the vertical and horizontal distribution of N. pachyderma in the water column of the Arctic Ocean (Carstens & Wefer, 1992) and the South Atlantic (Donner & Wefer, 1994, Berberich, 1996) have been carried out. Several tropical and subtropical planktic foraminifer species (i.e. Globigerinoides sacculifer, Globigerinella siphonifera and Orbulina universa) have been successfully cultured under varying laboratory conditions (e.g. temperature, salinity, food) (Hemleben et al., 1987, Hemleben et al., 1989, Bijma et al., 1990, Bijma et al., 1992). Studies of N. pachyderma in the Weddell Sea have focused on its distribution and abundance in the water column with and without sea ice cover, and on the occurrence of living specimens of N. pachyderma in the Weddell Sea ice (Spindler & Diekmann, 1986, Spindler et al., 1990, Diekmann et al., 1991, Berberich, 1996). Culture experiments to demonstrate the special adaption of N. pachyderma to high salinities in Antarctic sea ice have been carried out by Spindler (1996).

MATERIAL & METHODS
Samples of two sediment cores were examined: Core PS2185 in the central Arctic Ocean (Lomonosov Ridge, core location 87°32.0’N 144°22.9’E, 1051 m water depth, Fig. 1) and Core PS1388 in the eastern Weddell Sea (core location

69°02.0'S; 5°55.0'W, 2526 m water depth, Fig. 2). Core PS2185 was recovered during the Arktis-VIII/3 expedition of RV „Polarstern“ (Fütterer, 1992) and Core PS1388 during the Antarktis-IV/3 expedition (Fütterer, 1987).

All samples were wet-sieved over a 63 μm mesh-size sieve and later dry-sieved. The coarse fraction was dry-sieved into the subfractions 63-125, 125-250 and 250-500 μm. The wurstkammer and kummerform specimens were counted in the 250-500 μm fraction and calculated for the total sample (specimens per gram dry sediment). Simultaneously the wurstkammer specimens were picked for SEM-analysis. Ongoing work shows that only few specimens of N. pachyderma (sin.) with wurstkammer-shaped chambers occur in the subfraction 125-250 μm.

A wurstkammer is defined as one of the last chambers of N. pachyderma (sin.) which is, in contrast to a kummerform chamber, normally two to three times more elongated than the previous chamber. They are normally „sausage“ shaped with a width/length ratio of 0.25 - 0.50. These wurstkammers usually grow at an angle of 90° to the trochospiral growth direction and overlap earlier chambers. This study covers the last 70,000 years including isotope Stages 4 to 1 in Core PS2185 (Arctic Ocean, Fig. 3) and the last 140,000 years spanning isotope Stages 6 to 1 in Core PS1388 (Weddell Sea).
Wurstkammer specimens of *Neogloboquadrina pachyderma* (sinistral)

![Diagram of isotopic stages](image)

Figure 3a,b. Percentages of wurstkammer and kummerform specimens of *Neogloboquadrina pachyderma* (sin.) of total *N. pachyderma* (sin.) specimens in the fraction 250-500 µm in Core PS2185, central Arctic Ocean (oxygen isotope Stages 4 to 1).

Sea, Fig. 4). Of special interest are the morphological and faunal changes in the wurstkammer specimens during the glacial/interglacial transitions 6/5 (Termination II) and 2/1 (Termination I). These time spans are recorded in Core PS1388 through stable oxygen isotope data, but between 52-24 ka B.P. no samples are available (Figs. 4, 6, 7b, 8b). Samples in Core PS2185 cover the last 70,000 years dated through AMS-ages and stable oxygen isotope data (Nørgaard-Pedersen, 1996). The stratigraphical basement of Core PS1388 (Weddell Sea) used in this study, is the *N. pachyderma* (sin.) δ18O curve, carried out by Grobe *et al.* (1990) and Grobe & Mackensen (1992). The stratigraphic fix points are in accordance with Martinson *et al.* (1987).

RESULTS
Morphological results of the wurstkammer specimens (interpretation of SEM-photographs)
The scanning electron microscope photographs (Plates 1 and 2) show abnormal shell growth (i.e. „Wurstkammer” specimens) in comparison to normal shell growth. Here the „Wurstkammer” morphotypes are defined as *N. pachyderma* (sin.) specimens with abnormally elongated last chambers. In these specimens the final chambers are not normally arranged in a trochospire. The wurstkammers appear to grow at an angle of 90° to the normal growth direction, thus overlapping the spiral and umbilical parts of the test in the form of a „sausage”. Usually only one chamber is formed as a wurstkammer, but occasionally two or more wurstkammers can be seen in one specimen. In this case the last wurstkammer is larger in size and more elongated than the others (Plate 1: Fig. IV).

In the two polar regions morphologically different types of wurstkammer specimens can be found:

a) In samples from the central Arctic Ocean (Core PS2185) relatively long wurstkammers dominate (Plate 1: Fig. Ia, Ib, III, IV). These chambers can be up to three times larger than the penultimate chamber. The very wide aperture of the wurstkammer specimens in comparison to normal specimens of *N. pachyderma* (sin.) is another important characteristic feature (Plate 1: Fig. Ib, III).

b) Many wurstkammer specimens in the Weddell Sea (Core PS1388) differ in shape from those of the Arctic Ocean: The wurstkammers formed here are more inflated as they have a lower length/width ratio than the wurstkammers from Core PS2185 (Plate 2: Fig. IIIa, IVb).

In addition to the *N. pachyderma* wurstkammer specimens with large terminal chambers, samples also contain specimens with rudimentary last chambers, so called kummerform-specimens (Berger, 1969; Olsson, 1973) (Plate 2: Fig. II). Berger (1969) first described these specimens: he defined kummerforms as specimens with a smaller or equal-sized final chamber as the penultimate one. In exceptional cases kummerkammers and wurstkammers occur in the same specimen: Here the last chamber is formed as a kummerkammer whereas the penultimate and antepenultimate chambers are formed as wurstkammers (Plate 1: Fig. IV).

Quantitative analysis of wurstkammer/kummerform *N. pachyderma* (sin.) specimens in the subfraction 250-500 µm
In the sediment samples of Core PS2185 the maximum frequency of wurstkammer specimens is found at the beginning of oxygen isotope Stage 3 (up to 22% of the total *N. pachyderma* specimens in the subfraction 250-500 µm) and at Termination I (up to about 12%, Fig. 3a). The lowest frequencies of wurstkammer specimens appear in Termination II (about 0%), in Stage 2 (about 2%) and in the Holocene (up to 3%) (Fig. 3a). Highest numbers of kummerform specimens occur at the same time as the wurstkammer specimens, i.e. at the beginning of Stage 3 (27% frequency) and at Termination I (21%). Frequency minima occur at stage boundary 4/3, in the middle part of Stage 3 and in the upper Holocene (Fig. 3b).
In Core PS1388 wurstkammer specimens can be observed mainly within Stage 5 (about 9%) and in the Holocene. Frequency minima appear at Termination II, Termination I and in the lower Holocene, a weak minimum occurs in Stage 4 (Fig. 4a).

Most of the kummerform specimens appear in Substage 5.5 (about 26%), in Stage 4 (about 9%) and in the Holocene (11%) (Fig. 4b). Frequency minima occur at Termination II, within Stage 5, at Termination I and in the Holocene (Fig. 4b).

Concentrations of wurstkammer/kummerform specimens in the subfraction 250-500 μm
In Core PS2185 no wurstkammer specimens are found in the upper part of Stage 4 and at stage boundary 4/3. The numbers increase throughout Stage 3 with highest test concentrations found in the middle part of Stage 3 (up to 11 specimens/g dry sediment) (Fig. 5a). At the end of Stage 3 the number of wurstkammer specimens decreases rapidly down to only 1 wurstkammer specimen/g in Stage 2. During the Holocene the concentration increases slightly up to 2.5 specimens/g (Fig. 5a). The corresponding plot of the kummerform concentrations shows a similar trend (Fig. 5b): Lowest concentrations of kummerform specimens are found in the upper part of Stage 4 and at stage boundary 4/3 (0 specimens/g). Highest concentrations occur in Stage 3 (up to 18 specimens/g, Fig. 5b). Concentrations here are on average twice as high as the wurstkammer specimens.

In contrast, concentrations of wurstkammer
Wurstkammer specimens of *Neogloboquadrina pachyderma* (sinistral) specimens are very high in Core PS1388 (more than 600 wurstkammer specimens/g dry sediment near Substage 5.5 about 115 ka B.P.) (Fig. 6a). Concentrations decrease rapidly after this short maximum, although a minor maximum occurs at stage boundary 5/4 (about 150 wurstkammer specimens/g). Throughout Stage 4 a second decrease takes place. In Stages 3 and 2 concentrations are low (about 15 wurstkammer specimens/g). At Termination I and in the Holocene all wurstkammer specimens disappear (Fig. 6a). Kummerform specimens generally show lower concentrations than the wurstkammer specimens although they follow a similar trend to the wurstkammer speci-
mens. Maximum concentrations were observed in Stage 5 with 170 kummerform individuals/g (Fig. 6b).

The concentration of the total specimens of *N. pachyderma* (sin.) in the fraction 250-500 µm is up to 250 specimens/g dry sediment in Stage 3 in Core PS2185, a lower peak is observed in the Holocene with about 50 specimens/g (Fig. 7a). Lowest concentrations can be seen at stage boundary 4/3 (0 specimens/g) and in Stage 2 (about 20 specimens/g).

In Core PS1388 highest concentrations are seen in two maxima within Stage 5 with 2750 specimens/g at 115 ka B.P. and 2100 specimens/g at 105 ka B.P.; minima occur at Terminations II and I (0 specimens/g) (Fig. 7b).

The highest concentration of total specimens of *N. pachyderma* (sin.) is up to 30 times higher in the Weddell Sea than in the Arctic Ocean (Fig. 7a, 7b). The concentration curve of total specimens of *N. pachyderma* (sin.) in the Arctic Ocean and the Weddell Sea (Fig. 7a, b) correlates well with the concentration of kummerform specimens in the fraction 250-500 µm in the same cores (Fig. 5b, 6b), whereas the correlation to the wurstkammer curves is not so evident (Fig. 5a, 6a).

The wurstkammer/kummerform ratio in the Arctic Ocean in the fraction 250-500 µm is low (up to 1.4 in Stage 5 and 1.7 in Stage 3) (Fig. 8a) compared with the wurstkammer/kummerform ratio in the Weddell Sea (up to 4.2 in Stage 5 and 2.2 in the Holocene) (Fig. 8b). In the Arctic Ocean lowest wurstkammer/kummerform ratios can be found in the upper part of Stage 4, at stage boundary 4/3 and in Stage 2 (0.05), highest values are seen in Stage 3 (up to 1.8, Fig. 8a). In the Weddell Sea maxima of the wurstkammer/kummerform ratio occur in Stage 5 at 112 ka B.P. (4.1), near stage boundary 5/4 (3.2) and in the upper Holocene (3.2).

**DISCUSSION & CONCLUSION**

The comparison of the quantitative analyses on the wurstkammer and kummerform specimens in the fraction 250-500 µm in Core PS2185 shows an excellent correlation between these two morphotypes (Fig. 3a, b). In this core, especially in Stage 3 and at Termination I, a high number of wurstkammer and kummerform specimens occur at the same time. The percentage of kummerform individuals is normally two to three times higher than that of the wurstkammer specimens. The ratio between wurstkammer and kummerform specimens is relatively low, indicating only a small difference in the number of wurstkammer and kummerform specimens (Fig. 8a).

These two special morphotypes can be interpreted as end-members of a morphological line and demonstrate the very high morphological variability of *N. pachyderma* (Kennett, 1968; Keller, 1978; Healy-Williams, 1992), clearly evident in the short time intervals between 56-50 and 18-8 ka B.P. (Fig. 3a, b).

In contrast, in Core PS1388 no general correlation between wurstkammer and kummerform
Wurstkammer specimens of Neogloboquadrina pachyderma (sinistral)

types can be found, for example some samples show a high number of wurstkammer specimens together with only a few kummerform specimens (Stage 5, about 90 ka B.P.; Fig. 4a, b).

Wurstkammer growth is probably due to two main reasons (Berberich, 1996):

a) Development of kummerforms in small specimens due to environmental stress, e.g. changes in temperature, salinity and food supply (Berger, 1971; Bé & Van Donk, 1971; Hecht & Savin, 1972).

b) Development of kummerforms in large specimens due to reproduction stress. Hemleben foraminifer G. sacculifer form kummerform chambers instead of normally shaped last chambers shortly before reproduction.

If kummerform and wurstkammer specimens are considered as end-members of a morphological progression, then the reasons above i.e. environmental/reproduction stress need to be further analysed. If the formation of a wurstkammer is compared with the building of the sack-like chamber in specimens of G. sacculifer, then reproduction stress would be the most important reason for forming a wurstkammer. This is supported by the large number of wurstkammer specimens found in the fraction 250-500 μm in contrast to the fraction 125-250 μm where there are only a few such specimens. Therefore, the wurstkammers were formed mainly in the adult stage, when reproduction occurs. Secondary calcification of N. pachyderma tests formed shortly before reproduction (Kennett, 1968; Bé & Hemleben, 1977; Meggers, 1996) appears to be less well developed on wurstkammer individuals from either core (Plate 1: Fig. IIa, b, III; Plate 2: Fig. IIIa, b).

On the other hand the formation of wurstkammer specimens due to environmental stress is supported by:

1. their extensive appearance during time intervals of the last 140,000 years that are characterized by strong climate change, i.e. in very early Stage 3 and at Termination I (Nørgaard-Pedersen, 1996) the change of meltwater to normal salinity conditions could cause the appearance of large numbers of wurstkammer and kummerform specimens in the Arctic Ocean (Fig. 3a, b).

2. the abnormal shell growth of the wurstkammer individuals: the abnormality of the wurstkammer chambers is not only restricted to size and shape, as in the sack-like chambers of G. sacculifer, but there is also an abnormality in growth direction (often a second growth direction perpendicular to the main one). These specimens may terminate normal growth in one direction due to strong environmental stresses, and then build enlarged chambers with growth in a new direction. The different morphological shapes of the wurstkammer chambers in each of the two polar cores point to different strong environmental factors influencing N. pachyderma populations in the Arctic Ocean and the Weddell Sea.

Earlier works (Bé & Hutson, 1977; Boltovskoy, 1982) were unable to find causes for abnormal shell growth in planktic foraminifers.

To obtain more details about the formation of wurstkammer specimens additional studies of N. pachyderma shells in sediment surface samples, in samples from sediment traps and in plankton net tows need to be carried out. Especially the North Atlantic and the South Atlantic are interesting regions for further studies because of their different oceanic conditions and geological history to compare the biology and the fossil record of the bipolar populations of N. pachyderma. Culture experiments are also necessary to test the various conditions under which wurstkammer growth takes place.

ACKNOWLEDGEMENTS

Many thanks to H. Bauch, who supported this work on the wurstkammer specimens and with whom I had many helpful discussions. The manuscript was critically read and improved by M. Spindler. Thanks also go to A. v. Doetinchem for help at the scanning electron microscope, J. Heinze for SEM-photographs, U. Wollschlager for sample preparation, R. Spielhagen and N. Nørgaard-Pedersen for samples and stratigraphical data of Core PS2185 and H. Grobe, A. Mackensen and G. Kuhn for sample material from Core PS1388. C. Hass reviewed an earlier version of this paper. S. Kinsey and P. Goldschmidt corrected the English. This work is supported by the Deutsche Forschungsgemeinschaft (Schwerpunktlehrprogram „Antarktisforschung“).

REFERENCES

Arikawa, R. 1983. Distribution and taxonomy of Globigerina pachyderma (Ehrenberg) off the Sanriku Coast, Northeast Honshu, Science Reports of the Tohoku University, Sendai, Second Series (Geology), 53, 103-157.


Nørgaard-Pedersen, N., (in press). Late Quaternary Arctic Ocean sediment records: Surface ocean conditions and provenance of ice-rafted debris. GEOMAR Report.


Plate 1. SEM-photographs of *Neogloboquadrina pachyderma* (sin.) wurstkammer specimens in Core PS2185 (central Arctic Ocean). Fig. Ia, b: Wurstkammer specimens in different views (49 ka B.P.). Fig. IIa, b: Wurstkammer specimens in different views (78 ka B.P.). Fig. III: Wurstkammer specimen (122 ka B.P.). Fig. IV: Wurstkammer specimen (78 ka B.P.).
Plate 2. SEM-photographs of Neogloboquadrina pachyderma (sin.) wurstkammer specimens in Core PS1388 (Weddell Sea). Fig. I: Regular-formed specimen (122 ka B.P.). Fig. II: Kummerform specimen (15 ka B.P.). Fig. IIIa, b: Wurstkammer specimens in different views (18 ka B.P.). Fig. IVa, b: Wurstkammer specimens in different views (132 ka B.P.).