Wurstkammer specimens of the planktic foraminifer *Neogloboquadrina* pachyderma (sinistral): A new morphotype from the Arctic Ocean and the Weddell Sea

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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 pachydernia* (sinistral) (Ehrenberg) is described and its occurences 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 occurence of living specimens of N. pachyderma in the Weddell Sea ice (Spindler & Dieckmann, 1986, Spindler et al., 1990, Dieckmann 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

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Figure 1. Core location of Core PS2185 in the central Arctic Ocean (Lomonosov-Ridge).

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 μ m mesh-size sieve and later dry-sieved. The coarse fraction was dry-sieved into the subfractions 63-125, 125-250 and 250-500 μ m. The wurstkammer and kummerform specimens were counted in the 250-500 μ m 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

40°E 70°W 50° 409 30° 20% 109 ŝ 104 20% 30° 60° 60 S.Orkney S d Hise **PS1388** Astrid Ridae Weddell Sea 70° 70 Antarctic Shelf 80°S 80°S 70°W 60° 50 30" 20 107 0., 10 20 30 40°E 40 < 2000 m > 2000 m > 3000 m > 4000 m > 5000 m

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

Figure 2. Core location of Core PS1388 in the eastern Weddell Sea.



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.) δ^{18} O 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 μ m) 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).



Figure 4a,b. Percentages of wurstkammer and kummerform specimens of *Neogloboquadrina pachyderma* (sin.) of total *N. pachyderma* (sin.) in the fraction 250-500 µm in Core PS1388, eastern Weddell Sea (oxygen isotope Stages 6 to 1).

Figure 5a,b. Concentration of wurstkammer and kummerform specimens of *Neogloboquadrina pachyderma* (sin.) in the fraction 250-500 µm/g dry sediment in Core PS2185, central Arctic Ocean (oxygen isotope Stages 4 to 1).

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



Figure 6a,b. Concentration of wurstkammer and kummerform specimens of *Neogloboquadrina pachyderma* (sin.) in the fraction 250-500 µm/g dry sediment in Core PS1388, eastern Weddell Sea (oxygen isotope Stages 6 to 1).



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-

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Figure 8a,b. Wurstkammer/kummerform ratio of specimens *N. pachyderma* (sin.) in the fraction 250-500 µm in Core PS2185, central Arctic Ocean (oxygen isotope Stages 4 to 1) and in Core PS1388, eastern Weddell Sea (oxygen isotope Stages 6 to 1).

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 μ m 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 μ m 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 and kummerform 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 interpretated 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 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).

Kummerform 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 *et al.* (1987) discovered that specimens of the planktic 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 foraminifera.

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.

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Plate 1. SEM-photographs of *Neogloboquadrina pachuderma* (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. 1: Regular-formed specimen (122 ka B.P.). Fig. 11: 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 (18 ka B.P.).