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A resolution for the coiling direction paradox in *Neogloboquadrina pachyderma*

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[1] We present new data on genotypic differences and biogeographic distribution of coiling types in the living planktonic foraminiferal morphospecies *Neogloboquadrina pachyderma*. The genetic evidence demonstrates that coiling direction in *N. pachyderma* is a genetic trait, heritable through time, and is not a morphological feature reflecting ecophenotypic variation. The two opposite coiling morphotypes appear to have diverged during the late Miocene, and they have distinctly different ecologies. In combination with fossil evidence, biogeography, and ecology the degree of genetic distinction between the two coiling types of *N. pachyderma* strongly implies that they should be considered different species. We propose the adoption of the widely recognized name *N. incompta* for the right coiling morphospecies. The genetic evidence also demonstrates a low level (<3%) of aberrant coiling associated with both morphotypes. The abundance of these aberrant specimens has no relationship with the environment. These findings have important consequences for the use of *N. pachyderma* and *N. incompta* as paleoceanographic signal carriers in polar and subpolar waters.

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1. Introduction

[2] Planktonic foraminifera with trochospirally arranged chambers can produce shells with two different coiling directions. Some species show a strong preference for either right-handed or left-handed coiling, while other species exhibit mixed coiling proportions. Some species display a pattern of distinct shifts in the ratio of the coiling types in space and/or through time. The relationship between environmental parameters and coiling ratio in such species has been quantitatively described and coiling ratios are used extensively by paleoceanographers to reconstruct past marine environments. However, the underlying mechanisms controlling coiling direction are not understood. Many workers have traditionally assumed it to be a morphological feature reflecting ecophenotypic variation, paving the way for the widespread use of coiling ratios as paleoenvironmental indicators [Ericson, 1959; Ericson *et al.*, 1954; Bandy, 1960; Boltovskoy, 1973]. In a study exploring the causal mechanisms controlling coiling direction in planktonic foraminifera, Brummer and Kroon [1988] concluded that the systematic changes in coiling direction observed throughout the fossil record most likely reflected genetically

determined binary traits and were not driven by environmental factors. This was also the conclusion drawn by Norris and Nishi [2001], who argue that coiling patterns in tropical planktonic foraminifera are heritable through time and are not environmentally controlled. Recent genetic studies have corroborated this conclusion, as coiling direction is clearly associated with genetic distinction and not the environment [Darling *et al.*, 2000, 2003, 2004; de Vargas *et al.*, 2001]. The previously reported links between coiling and environmental factors in these species result from the different ecological preferences of the genetically distinct coiling types.

[3] The neogloboquadrinid clade exhibits a strong preferential coiling direction, approaching 100%. The tropical and warmer water morphospecies *Neogloboquadrina dutertrei* and *Pulleniatina obliquiloculata* are currently dominantly right coiling although they have exhibited ~100% left coiling in the past [Saito, 1976]. The cooler water counterpart of this family is *N. pachyderma*. Despite some morphological resemblance between warmer-water specimens of this species and *N. dutertrei*, there is ample evidence that the lineages leading to these modern species separated 10.4 Myr ago [Spencer-Cervato *et al.*, 1994] and that the extant forms differ in their ecology and biogeography [Hilbrecht, 1997]. The pachyderma-dutertrei (P-D) morphological intergrades mentioned throughout the literature resemble *N. pachyderma* in their ecological adaptations and are thought to be morphological variants of *N. pachyderma* [Hilbrecht, 1997]. This has yet to be determined genetically. *Neogloboquadrina pachyderma* has two distinct coiling forms with virtually mutually exclusive distribution that appears to be controlled by water temperature [Ericson, 1959; Bandy, 1960; Bé and Hamlin, 1967; Kennett, 1968; Arikawa, 1983; Reynolds and Thunell, 1986]. The significance of the distinct distribution of the two coiling types has

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been disputed for many years. There have been suggestions throughout the literature that left coiling *N. pachyderma* may be taxonomically distinct from its right coiling counterpart [Vella, 1974; Vincent and Berger, 1981]. This has now been confirmed by molecular evidence, showing that coiling direction in *N. pachyderma* is associated with substantial genetic divergence [Darling et al., 2000, 2003, 2004].

[4] Although the biased coiling preference in the neogloboquadrinid clade approaches 100%, it is not absolute. In the present day, the left coiling genotypes of *N. pachyderma* dominate the polar high latitudes [Darling et al., 2004] and the right coiling genotypes of *N. pachyderma* frequent the more temperate zones [Darling et al., 2000, 2003]. However, a small percentage of tests with a right coiling morphology (1–3%) persist in the plankton and sedimentary record even in the most extreme polar conditions [Pflaumann et al., 1996; Bauch et al., 2003]. Until recently, it was unknown whether their presence indicated sporadic incursions of subpolar waters into the Arctic, rare expatriation from the subpolar water mass or whether they were aberrant right coiling forms of the left coiling genotype. Following extensive genetic investigation of the high-latitude regions of both hemispheres, it is now clear that these rare right coiling specimens represent aberrant forms of the left coiling genotype [Bauch et al., 2003; Darling et al., 2004].

[5] This discovery causes a serious nomenclature paradox and complicates the use of this species as a paleoceanographic indicator. In combination with fossil evidence and their biogeographical and ecological differences, the degree of genetic distinction between the two coiling types of *N. pachyderma* strongly implies that we should consider them as different species [Darling et al., 2000, 2004]. For many years micropaleontologists have wrestled with the morphological plasticity of *N. pachyderma* and applied new names to a plethora of morphological variants. Much of the taxonomic confusion comes from the comparison between the ontogenetic stages of *N. pachyderma* in the water column and the final gametogenic form found in the sediments. Paleoceanographers have had the additional hardship of continual reference to coiling direction with all the ambiguities that it can produce in the literature. The recent genetic evidence now adds considerably to the confusion when referring to a left coiling genotype that coils right [Bauch et al., 2003].

[6] Here we present new data on the genetic relationships and global biogeographical distributions of the different types of right coiling *N. pachyderma*. We also present new data on aberrant coiling in the left coiling *N. pachyderma* genetic types described by Darling et al [2004]. We show that the provincial ranges of the left and right coiling *N. pachyderma* genetic types are distinct and their different ecologies are mirrored by substantial genetic difference. Genotyping shows that coiling direction is not an absolute discriminator between *N. pachyderma* genotypes and that aberrant coiling is a consistent pattern in both left and right coiling genotypes of *N. pachyderma*. We propose the reclassification of the right coiling *N. pachyderma* genotypes as a distinct species to simplify nomenclature and

reference. We explain the rationale behind the adoption of a different species name and demonstrate to what degree the coiling ratio can be used to indicate presence or absence of each of the two species.

2. Methods

2.1. Sampling Localities

[7] Right coiling *N. pachyderma* specimens were collected between 1997 and 2002 during seven cruises and one coastal collection. Details of sampling stations and collection method are listed in Table 1.

2.2. Molecular Methods

2.2.1. Isolation and Sequencing of Small Subunit Genes

[8] DNA extraction, polymerase chain reaction amplification of a ~1000 base pair region of the terminal 3' end of the foraminiferal small subunit (SSU) ribosomal (r) RNA gene and sequencing of an ~500 base pair fragment for genotype confirmation were as described previously [Darling et al., 2003]. The gene fragments for the right coiling *N. pachyderma* genotypes were sequenced directly as no ambiguities were detected in any of the sequences. A limited degree of ambiguity was detected in the gene repeats for left coiling *N. pachyderma* genotypes and it was sometimes necessary to clone and sequence as described by Darling et al. [2004]. In all cases, intra-individual variation was minimal compared to between genotype variation.

2.2.2. Phylogenetic Analysis

[9] Partial SSU rDNA sequences were aligned manually within the Genetic Data Environment (GDE) package [Smith et al., 1994]. Five hundred and six unambiguously aligned nucleotide sites were utilized in phylogenetic analyses incorporating representatives of all spinose planktonic groups sequenced to date, 6 nonspinose planktonic morphospecies and 15 benthic foraminiferal taxa. Six hundred and eighty-five unambiguously aligned sites were utilized in analyses incorporating only the Neogloboquadrinid taxa. Phylogenetic trees were constructed using the neighbor-joining (NJ) [Saitou and Nei, 1987] distance method within Paup* package version 4.0d64 [Swofford, 2003]. Genetic distances were corrected for multiple hits using the general time reversible (GTR) model [Lanave et al., 1984] with a gamma correction [Gu et al., 1995] employed to account for between-site rate variation. Parameters were estimated using likelihood by iteration from an initial NJ tree. Bootstrap resampling (2000 replicates) was employed to assign support to branches in the trees [Felsenstein, 1985].

2.3. Sediment Samples

[10] To assess the variability of coiling ratios in *N. pachyderma* in modern surface sediments, we have examined the Atlantic database of planktonic foraminifer counts assembled by the MARGO project [Kucera et al., 2005]. This database is based on species counts in the >150 μm fraction. In polar and subpolar waters, planktonic foraminifera are dominated by relatively small species. Therefore we have also examined a South Atlantic database of species counts based on the >125 μm fraction [Niebler

Table 1. Sampling Localities for Right Coiling *N. pachyderma*

Location	Cruise	Date	Collection Method	Genotyped Specimens
Denmark Strait, 59°57'N/11°34'W to 62°22'N/40°33'W	R/V <i>Professor Logachev</i> , Dutch/Danish Cruise	August/September 1997	surface pumped, 4.5 m depth, 78 µm mesh screens, vertical tows 250 m depth, 78 µm mesh	n = 24
Norwegian Sea, 63°41'N/4°2'E to 68°13'N/4°0'E	FS <i>Polarstern</i> , Cruise ARKXV/1 (AWI, Germany)	June 1999	surface pumped, 6 m depth, 63 µm mesh screen	n = 17
UK to Iceland, 50°50'N/05°51'W to 62°20'N/22°27'W	RRS <i>Discovery</i> , Cruise 262 (NERC, UK)	April 2002	surface pumped, 6 m depth, 78 µm mesh	n = 55
South Atlantic, Falkland Islands to the Antarctic Peninsula, 52°19'S/58°16'W to 58°34'S/64°81'W and 55°55'S/45°02'W to 52°21'S/56°75'W	RRS <i>James Clark Ross</i> , Cruises JR19 and JR48 (British Antarctic Survey)	March 1997 and April 2000	surface pumped, 6 m depth, 63–125 µm mesh screens, vertical tows, 100 m depth, 63 µ mesh	n = 34
Benguela System off Walvis Bay, Namibia, (0–30 nautical miles from the coast at 23°S)	R/V <i>Welwitschia</i> NATMIRC (Namibia) Research Institute of the Ministry of Fisheries and Marine Resources	November 2001	vertical tows, 50 m depth, 63 µm mesh	n = 15
Santa Barbara Channel, northern Gulf of California, northern coastline of the Santa Barbara Channel at ~34°40'N and between 120°40'E and 120°10'E	inshore boat (University of California, Santa Barbara, USA)	July and September 1999	shallow plankton tows depth to 50 m (approximate level of thermocline) 63 µm mesh	n = 8
Vancouver Island to the Aleutian Islands, North Pacific, 49°41'N/128°43'W to 52°48'N/141°47'W	<i>Sir Wilfrid Laurier</i> Canadian Coast Guard Ship Canadian Arctic cruise	July 2002	surface pumped 6 m depth, 83 µm mesh screens vertical tows 100 m depth, 63 µ mesh	n = 20

and Gersonde, 1998]. Annual sea surface temperatures (SST) at 10 m depth for the locations of all sediment samples were extracted from the World Ocean Atlas 1998 database, using the WOA98 sample extraction and interpolation tool developed in the MARGO project (see <http://www.palmod.uni-bremen.de/~csn/woasample.html>). To highlight the general pattern of the relationship between coiling ratio and sea surface temperature, we have divided sediment samples in each hemisphere into one degree centigrade intervals and determined total counts of both coiling types of *N. pachyderma* in these zones.

3. Results

3.1. Genetic Relationships

[11] The evolutionary relationships among the planktonic foraminiferal morphospecies are shown in a neighbor-joining tree (Figure 1). The phylogeny includes genotypes of all spinose morphospecies sequenced to date, the nonspinose neogloboquadrinid clade, *Globorotalia inflata* and the microperforates *Globigerinita uvula* and *Globigerinita glutinata*. The planktonic foraminifera are shown within a background of benthic morphospecies sequenced by Pawlowski *et al.* [1997] and rooted on the benthic foraminifer *Allogromia*, an early evolving group in the history of the foraminiferal clade [Pawlowski *et al.*, 2003]. The phylogeny specifically highlights the marked genetic distinction between the three different morphospecies *N. pachyderma*, *G. glutinata* and *Turborotalita quinqueloba* which look very similar in the

water column. The phylogenetic tree clearly demonstrates that all the genotypes ascribed to each of these morphospecies cluster together in monophyletic groups and the morphospecies fall separately within expected regions of the tree. The genotypic variants of *N. pachyderma* cluster with the other members of the *Neogloboquadrina* group and fall within the planktonic nonspinose and benthic region of the tree. The microperforate *G. glutinata* falls separately, but also clusters within the benthic groups. The genotypes of *T. quinqueloba* however all cluster together and fall within the spinose cluster and are the most genetically divergent of all the SSU genetic types of planktonic foraminifera sequenced to date. There is thus no possibility of confusion between the genotypes of these morphospecies.

[12] The coiling ratio grouping (group I and II) of Brummer and Kroon [1988] are also shown (Figure 1), highlighting the relationship between coiling direction mode and the genetic/morphological groups. Group I is associated with the spinose and microperforate morphospecies. This group has an average coiling ratio scattered around 50% with the exception of two morphospecies. *Globigerina bulloides* has been shown to have a higher percentage left coiling ratio of 65% (n = 14,561) [Brummer and Kroon, 1988] and 63% (n = 441) [Darling *et al.*, 2003] respectively. *Globigerinoides sacculifer* also has a higher percentage left coiling ratio of 60% (n = 10,650) [Brummer and Kroon, 1988]. Group II is associated with the nonspinose macroperforate species which in the present day have nearly 100% biased coiling [Srinivasan and Kennett, 1976; Brummer and Kroon, 1988].

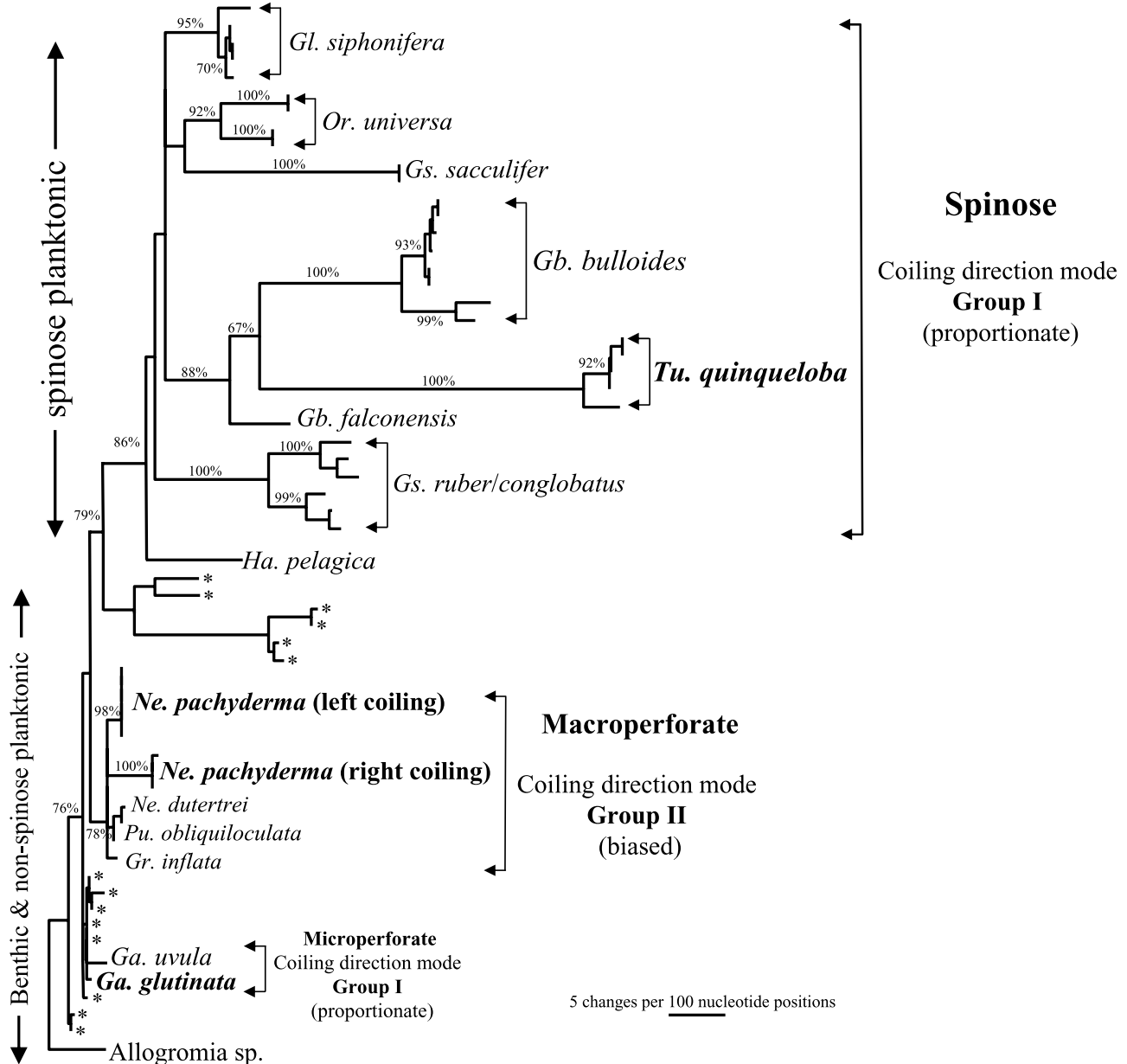


Figure 1. Neighbor-joining SSU rDNA phylogenetic tree (506 nucleotide sites) showing the evolutionary relationship between the different morphospecies of planktonic foraminifers. The phylogeny is rooted on the benthic foraminifer *Allogromia*. Other benthic species are denoted by an asterisk. Bootstrap values (2000 replicates) are expressed as a percentage and indicate support for branches within the tree. Bootstrap values are only shown for branches that are supported in over 70% of bootstrap replicates. The phylogeny clearly shows the substantial genetic distance between the morphospecies *N. pachyderma*, *G. glutinata*, and *T. quinqueloba* and demonstrates that genotypes of these morphospecies cannot be confused. The two coiling mode groups, defined by *Brummer and Kroon* [1988], are highlighted. Abbreviations are *Gl*, *Globigerinella*; *Or*, *Orbulina*; *Gs*, *Globigerinoides*; *Gb*, *Globigerina*; *Tu*, *Turborotalita*; *Ha*, *Hastigerina*; *Ne*, *Neogloboquadrina*; *Pu*, *Pulleniatina*; *Gr*, *Globorotalia*; and *Ga*, *Globigerinita*.

[13] The evolutionary relationships within the *Neogloboquadrina* clade are shown in Figure 2. The phylogeny is based on 685 nucleotide sites and is rooted on *G. inflata* which shared a common ancestor with the *Neogloboquadrina* lineage in the late Oligocene [Kennett and Srinivasan, 1983]. The tree includes all genetic types of *N. pachyderma* sequenced to date

[Darling et al., 2003, 2004]. The predominantly right coiling genotypes of *N. pachyderma* fall on an exceptionally long branch in the tree making it impossible to resolve their evolutionary relatedness to the other members of the neogloboquadrinid clade. This highlights the divergent nature of the left and right coiling genotypes of *N. pachyderma*.

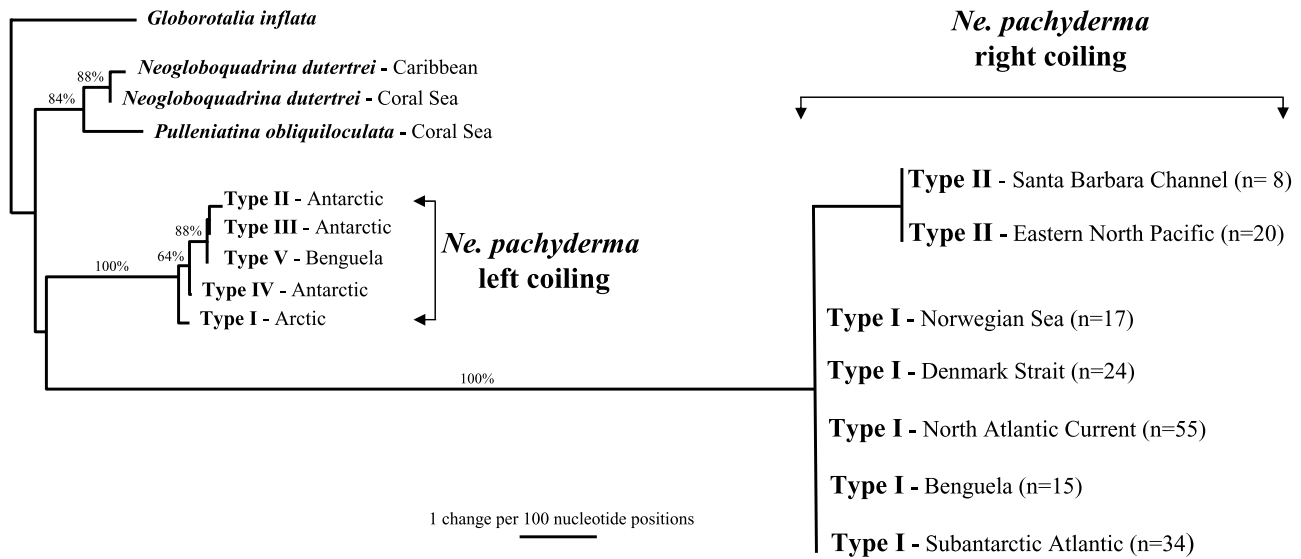


Figure 2. Neighbor-joining SSU rDNA phylogenetic tree (685 nucleotide sites) highlighting the evolutionary relationships among the Neogloboquadrinidae. The phylogeny is rooted on *G. inflata*. The tree highlights the highly divergent nature of the left and right coiling genotypes of *N. pachyderma*. Bootstrap values are expressed as a percentage and indicate support for branches within the tree. Bootstrap values are only shown for branches that are strongly supported in over 70% of bootstrap replicates. *Ne* is *Neogloboquadrina*. NGenBank accession numbers are *Ne. pachyderma* (sin) Types I–V, AY305329, AY305330, AY305331, AF250120, and AY305332 and *Ne. pachyderma* (dex) Types I–II, AF250117 (Denmark Strait) and AF250118 (Subantarctic) and AY241711.

3.2. Biogeography of Left Coiling *N. pachyderma* Genotypes in the Atlantic Ocean and the Antarctic

[14] Five distinct left coiling *N. pachyderma* genotypes were identified by Darling *et al.* [2004] in the Atlantic Arctic and Antarctic subpolar/polar waters and the Benguela upwelling system. Figure 3 shows their distribution and additionally includes the occurrence of aberrant right coiling specimens that are genetically identical to the respective left coiling genotypes. Aberrant right coiling specimens of the left coiling genotype were found within all left coiling genotype populations throughout their geographical range (Figure 3).

3.3. Biogeography of Right Coiling *N. pachyderma* Genotypes in the Atlantic Arctic, Antarctic, Benguela Upwelling System, and North Pacific

[15] In the Atlantic, right coiling *N. pachyderma* currently shows a substantially lower genetic diversity than left coiling *N. pachyderma*. Extensive sampling of the higher-latitude transitional and subpolar Atlantic provinces of both hemispheres have identified only one right coiling genotype (Type I; $n = 145$; Figure 4) as apposed to five left coiling genotypes to date (Types I–V; Figure 3) [Darling *et al.*, 2004]. The right coiling Type I genotype was found in waters from between 3.4°–9.9°C (Antarctic; $n = 34$), 9.3°–11.7°C (Norwegian Sea; $n = 17$), 2.5°–12.7°C (Denmark Strait; $n = 24$), and 8.0°–10.1°C (North Atlantic Current; $n = 55$). Right coiling *N. pachyderma* Type I was also found in the Benguela system at temperatures between 12.0°–14.0°C ($n = 15$; Figure 4). A second genetically distinct right coiling genotype has been identified in the North Pacific ($n = 28$; Figure 4) in water temperatures between

12°–14.5°C (eastern North Pacific; $n = 20$) and 14°–17.5°C (Santa Barbara Channel; $n = 8$). To date, aberrant coiling has been detected in all the populations of the right coiling Type I genotype but not in the right coiling Type II genotype. This absence is most likely due to low sample numbers in the North Pacific. As sampling was confined to the subpolar provinces within both oceans, with the exception of the Benguela Current, no data are available yet from the transitional zones where the upper temperature ranges of right coiling *N. pachyderma* are found. The data presented here thus only characterize the lower temperature range of right coiling *N. pachyderma*.

3.4. *N. pachyderma* Coiling Ratios

3.4.1. Plankton Percentage Coiling Counts in Left Coiling *N. pachyderma*

[16] It is important to note that abundance of coiling types among the genotyped specimens is not representative of the natural population, as our collections were biased during picking to include as many specimens of the rarer coiling variant as possible. Since morphology alone cannot currently be used to discriminate between genotypes, representative coiling ratio counts are restricted to regions where genotyping can confirm assemblage monospecificity.

[17] Assemblages of the Arctic polar left coiling *N. pachyderma* Type I contained a small percentage of tests with an aberrant right coiling morphology ($n = 15$) [Bauch *et al.*, 2003; Darling *et al.*, 2004] (Figure 3). Multinet counts (8 stations at five depth intervals between 0 and 500 m) of *N. pachyderma* from the Greenland Sea ($n = 58,895$; Table 2) indicate a right coiling ratio of 2.1% in the Arctic polar water mass [Stangeew, 2001].

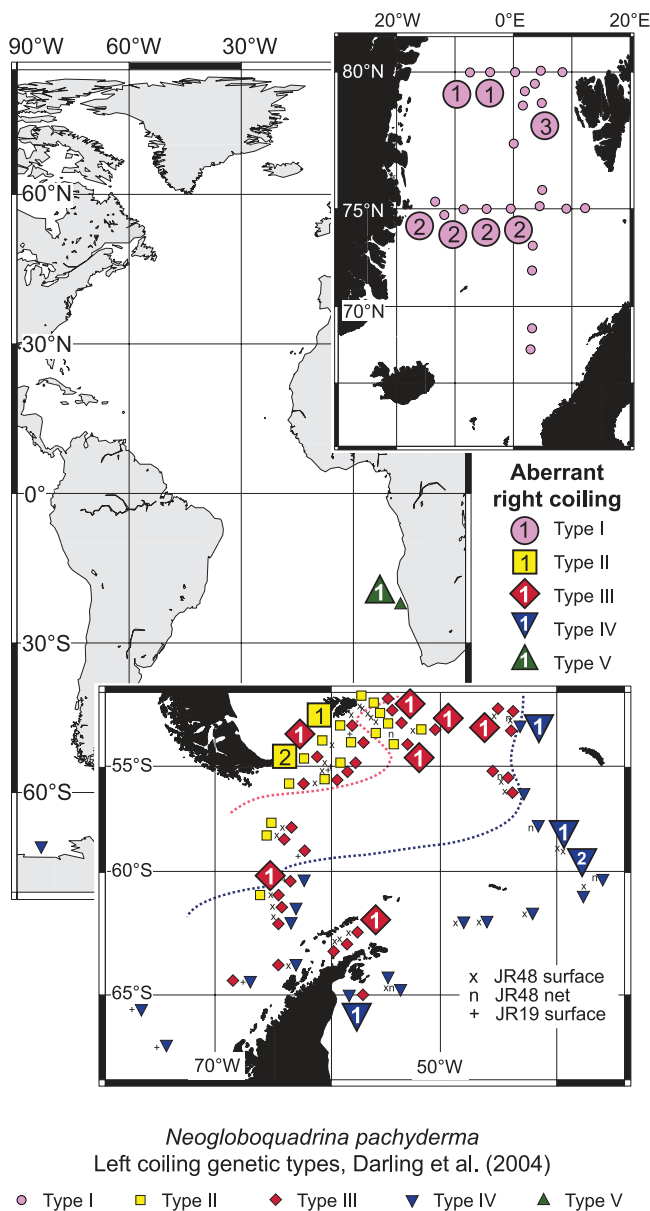


Figure 3. Distribution of the five distinct left coiling *N. pachyderma* genotypes in the Atlantic and Antarctic waters [Darling et al., 2004] showing the number of aberrant right coiling specimens found within the populations of the left coiling genetic types.

[18] In the South Atlantic and Southern Ocean, all assemblages of the four distinct genotypes of left coiling *N. pachyderma* (Types II–V; Figure 3) [Darling et al., 2004] contained a small percentage with an aberrant right coiling morphology: Type II ($n = 3$), Type III ($n = 8$), Type IV ($n = 5$) and Type V ($n = 1$). Type II and Type III were found north of the polar front and frequent the same subpolar water masses as the right coiling *N. pachyderma* Type I. Owing to the mixing of different genotypes, it was not possible to carry out assemblage counts to determine coiling ratios of genotypes in these water masses. However, it was possible to determine the percentage of aberrant right

coiling in the polar water mass south of the polar front. The living *N. pachyderma* assemblage in the Weddell Sea is almost exclusively left coiling *N. pachyderma* genotype IV (Figure 3). *N. pachyderma* specimens in bulk plankton samples taken from this region have a right coiling percentage of 3.1% ($n = 740$; Table 2).

3.4.2. Plankton Coiling Counts in Right Coiling *N. pachyderma*

[19] Assemblages of the right coiling *N. pachyderma* genotype were also found to include a small percentage with an aberrant left coiling morphology (Figure 4). In the Atlantic, 8 left coiling specimens of the right coiling *N. pachyderma* Type I genotype ($n = 145$) were identified. As mentioned above, coiling ratios cannot be obtained from the genotyped specimen values as our collections were biased during picking to include as many specimens of the rarer coiling variant as possible. However, as only a single right coiling genetic type frequents the Atlantic, coiling ratios can be calculated from assemblage data for this genotype if analyses are confined to transitional regions devoid of left coiling genotypes. *N. pachyderma* specimens ($n = 5813$) collected by plankton tow from transitional water masses in the North Atlantic by Brummer and Kroon [1988], have a left coiling ratio of 1.5% (Table 2).

[20] Sampling of the right coiling *N. pachyderma* Type II specimens ($n = 20$) in the eastern North Pacific transect was restricted to the subpolar water mass where both left and right coiling genotypes were found in a mixed assemblage. We were therefore unable to calculate coiling ratios for the right coiling Type II genotype from bulk plankton samples. However, the right coiling *N. pachyderma* specimens found in the Santa Barbara Channel [Darling et al., 2003; this study] were also all Type II ($n = 8$) which strongly suggests that the right coiling *N. pachyderma* collected in sediment trap samples from the San Pedro Basin off the coast of southern California by Sautter and Thunell [1991] would have been right coiling *N. pachyderma* Type II. They collected 4658 specimens of right coiling *N. pachyderma* of which less than 1% were left coiling (Table 2).

3.4.3. Sediment Core Top Coiling Ratios

[21] The coiling ratio of *N. pachyderma* in the living assemblage is reflected in core top samples [Kucera et al., 2005; Niebler and Gersonde, 1998] (Figure 5). The percentage right coiling of *N. pachyderma* in planktonic foraminiferal assemblages from North and South Atlantic core tops plotted against annual average SST shows that the change from left to right coiling in the North Atlantic (4° – 10° C) takes place over a slightly narrower range of temperatures than in the South Atlantic (4° – 12° C). Since the right coiling *N. pachyderma* Type I populations in both the North and South Atlantic are the same genetic type [Darling et al., 2000; this study, Figure 3], the differences in the sediment coiling ratio values must be due to different adaptations of the genetically distinct left coiling *N. pachyderma* genotypes in each hemisphere. North Atlantic left coiling *N. pachyderma* Type I does not live at temperatures above 10° C while the southern left coiling *N. pachyderma* genotypes II and III occupy the same subpolar/transitional water as the right coiling genotype I (Figure 3) at temperatures between 10° and 12° C.

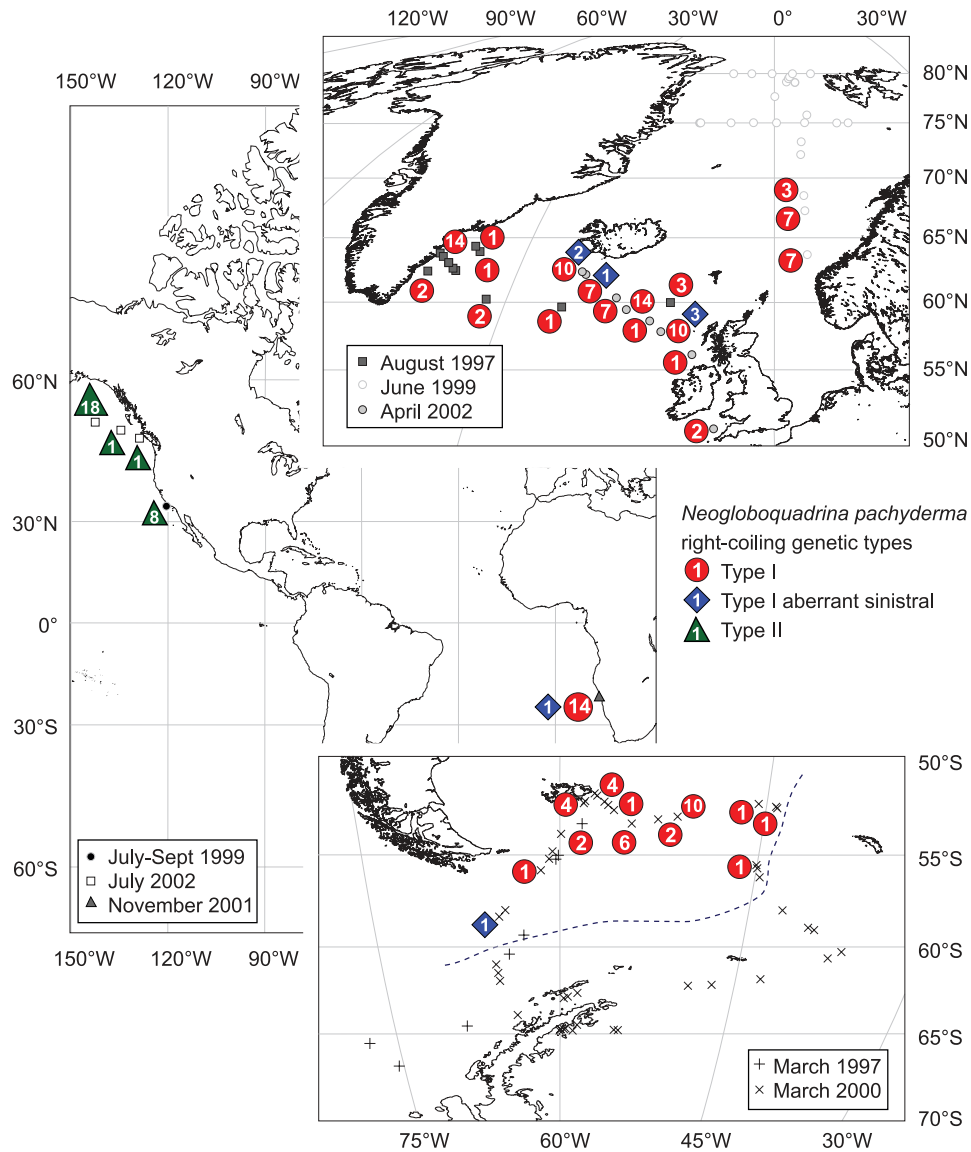


Figure 4. Sampling localities and distribution of right coiling *N. pachyderma* genotypes (n = 173). Only two right coiling genotypes have been identified to date as opposed to the five left coiling genotypes [Darling et al., 2003, 2004]. The right coiling Type I genotype was found throughout the Atlantic (n = 145), and a second genetically distinct right coiling genotype was found in the North Pacific (n = 28).

Table 2. *N. pachyderma* Right Coiling Ratios From Plankton and Sediment Trap Counts

Region	Foraminiferal Province	Collection Method	Total Left Coiling	Total Right Coiling	Right Coiling, %
Arctic	polar	multinets 0–500 m	58,895	1,237	2.1
Greenland Sea	[Stangeew, 2001]				
Antarctic	polar	pump and net 0–100 m	718	22	3.1
Weddell Sea	(this study)				
North Atlantic	transitional	plankton net	87	5,813	98.5
Mid-North Atlantic longitudinal transect	[Brummer and Kroon, 1988]				
North Pacific	transitional	sediment trap	47	4,611	99.0
San Pedro Basin	[Sautter and Thunell, 1991]				
S. Californian Bight					

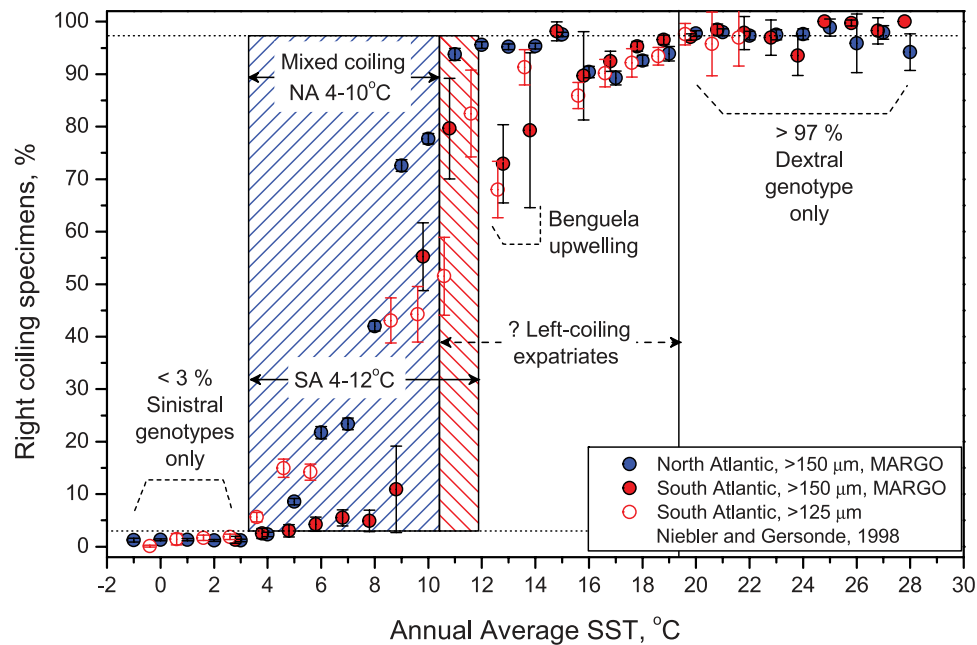


Figure 5. Percentage of *N. pachyderma* right coiling in planktonic foraminiferal assemblages from North and South Atlantic core tops [Kucera et al., 2005; Niebler and Gersonde, 1998] plotted against sea surface temperature. Vertical bars show 95% confidence intervals for the percentage values. The plot demonstrates the similarities and differences between hemispheres in the change from left to right coiling. Right coiling percentages in the sediments are very similar in both polar provinces (1.25% and 1.31%) and the warm zones (97.6% and 97.4%).

[22] The presence of a relict left coiling *N. pachyderma* Type V in the Benguela system (Figure 3) is manifested in a predictable dip in right coiling percentage in the South Atlantic assemblage. However, between 15° and 19°C SST there is a complementary dip in percent right coiling in both hemispheres. This does not coincide with any known left coiling population at these latitudes and possibly reflects the deposition of left coiling tests expatriated from subpolar waters into the ocean gyres.

[23] Right coiling percentages in the sediments are very similar in both Atlantic polar provinces (1.25% and 1.31%). This percentage value represents a single genotypic left coiling population in the Arctic (Type I) but in the Antarctic it represents a mixed genotypic left coiling population (Types II, III or IV). These values can however be taken to define the absence of any right coiling *N. pachyderma* genetic types in the sediment. Both values are significantly lower ($p < 0.05$) than the coiling ratio counts from the plankton of 2.1% (Arctic polar) and 3.1% (Antarctic polar) (Table 2). The slightly higher coiling ratio values in the plankton may possibly reflect the difficulty in discriminating small *N. pachyderma* from small juvenile *T. quinqueloba*. The transitional and subtropical regions of both hemispheres also show similar values of right coiling percentages (97.6% and 97.4%). In this case the sediment-derived percentages are slightly lower than estimates from the plankton (98.5% and 99.0%) which may suggest low-level expatriation of left coiling *N. pachyderma* from upwelling regions.

[24] Analysis of assemblage counts from the >125 μm fraction in the South Atlantic [Niebler and Gersonde, 1998]

confirm the general pattern of coiling ratio relationship to temperature (Figure 5), indicating that the ranges of the coiling provinces are robust and not affected by assemblage size bias. Crucially, the percentage of aberrant coiling in both the polar (<3°C) and subtropical (>19°C) regions is statistically indistinguishable in the counts based on the two different size fractions.

3.5. Taxonomic Status of *N. pachyderma*

[25] There now is considerable evidence from the biogeography, ecology and degree of genetic distinction that the right and left coiling forms of *N. pachyderma* are different biological species [Darling et al., 2000, 2004; this study]. In order to clarify the taxonomic status of this morphospecies, we have located and examined original materials on which the description of the species was based. We have established that the *Aristerspira pachyderma* specimen illustrated by Ehrenberg [1873] (Figures 6a and 6b, upon which his 1862 species description is based, is representative of the left coiling form of *N. pachyderma*. We have discovered a second Ehrenberg drawing labeled *pachyderma* on the same page as a drawing illustrating the spiral side of the type specimen (Figure 6c). This specimen is also left coiling and shows again the distinct *N. pachyderma* left coiling morphology. Both specimens form part of an assemblage of planktonic foraminifera collected in the North Atlantic, south west of Iceland (62°40'N/29°0'W at 1000 fathoms). An examination of four of Ehrenberg's mica preparations made from the same sediment sample shows that the fauna derives from a mixed coiling province with about 40% left coiling specimens

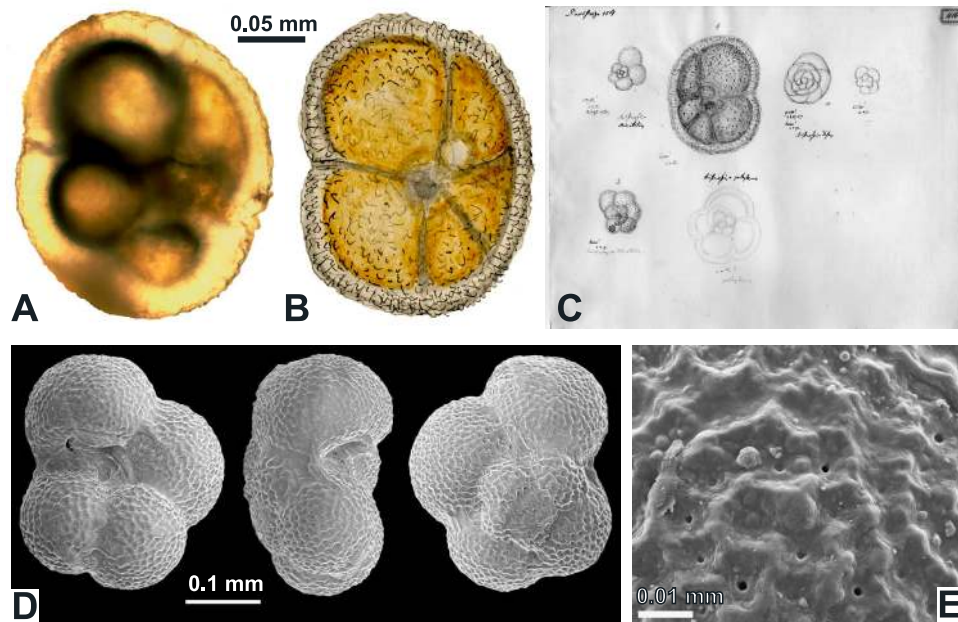


Figure 6. Type specimens of (a–c) *N. pachyderma* and (d and e) *N. incompta*. Figure 6a is a transmitted light photograph (Museum für Naturkunde, Berlin, 313-271506, mica 1, blue ring). Figure 6b is an original drawing (Museum für Naturkunde, Berlin, drawing 1616a) of the *Aristerospira pachyderma* specimen illustrated by Ehrenberg [1873] upon which his 1862 species description was based. Figure 6c is a second unpublished Ehrenberg drawing (Museum für Naturkunde, Berlin, drawing 1616) labeled as *pachyderma* seen below the illustration of the spiral side of the type specimen. Figure 6d shows scanning electron micrographs of the holotype (U.S.N.M. 628588) of *Globigerina incompta* described by Cifelli [1961]. Figure 6e is an enlarged view of the last chamber of a paratype (U.S.N.M. 628591) showing the typical nonspinoso neogloboquadrinid wall structure.

($n = 39$). Thus both the type illustration and Ehrenberg's concept of *N. pachyderma* refer to the left coiling form and the overall morphology of the type specimen and the nature of the assemblage indicate that this species name should be applied to the left coiling genetic type.

[26] The fact that the species name *pachyderma* can be attributed to left coiling forms implies that a different species name must be adopted for the right coiling forms. Having examined numerous earlier described morphospecies, and their type material, we conclude that the most appropriate species name to adopt for the right coiling form is *N. incompta* described by Cifelli [1961]. The holotype (U.S.N.M. 628588) is right coiling (Figure 6d) and was collected from the surface waters of the North Atlantic ($38^{\circ}39'N/69^{\circ}33'W$) within the predominantly right coiling province.

[27] All paratypes of *N. incompta* illustrated by Cifelli [1961] are clearly morphologically nonspinoso right coiling *N. pachyderma*, collected from an assemblage dominated by right coiling forms. The type specimens are described as having highly porous translucent thin walls through which protoplasm can be seen. This indicates that they are immature nongametogenic specimens; otherwise they would have a covering of gametogenic calcite which would thicken the walls and obscure the cytoplasm. Bizarrely, Cifelli [1961] describes the live wet specimens as being “covered in fine elongate spines” which are easily destroyed but which are

almost never seen on dry specimens. There is no doubt that the type specimens are *N. pachyderma* and we must therefore assume that Cifelli [1961] mistakenly described pseudopodia as spines in the living specimens since the neogloboquadrinids are a nonspinoso group. To dispel any doubts about this issue, we have examined the wall structure of paratype U.S.N.M. 628591 under the SEM (Figure 6e). The specimen is clearly nonspinoso, with a typical neogloboquadrinid wall structure of irregular interconnected ridges surrounding small but distinct pores.

4. Discussion and Conclusions

4.1. Genetic Identity and Evolution of *N. pachyderma*

[28] The discovery that planktonic foraminiferal morphospecies often represent several genetic types with distinct ecologies has raised issues about the correctness of identification of genotyped specimens. To conclusively allay such doubts, we have included a phylogeny (Figure 1) highlighting the evolutionary relationships between the planktonic foraminiferal groups which look very similar in the water column and sediments. The genetic tree clearly demonstrates that all the genotypes ascribed to each of the morphospecies *N. pachyderma*, *G. glutinata* and *T. quinqueloba* cluster together in monophyletic groups. The groups are highly distinct from one another and fall separately within expected regions of the tree. There is quite

clearly no possibility of confusion between the genotypes of these morphospecies.

[29] All the genotypic variants of *N. pachyderma* cluster with the other members of the neogloboquadrinid clade and fall within the planktonic nonspinose and benthic region of the phylogeny (Figure 1). The *Neogloboquadrina* tree (Figure 2) highlights the highly divergent nature of the left and right coiling genotypes of *N. pachyderma* and indicates that the two opposite coiling groups must have diverged from one another many millions of years ago [Darling et al., 2004]. This is in agreement with the findings of Bandy [1972], who found preferential coiling ratios in *N. pachyderma* almost at the base of its range in the late Miocene (10.4 Ma [Spencer-Cervato et al., 1994]). Throughout the remainder of the discussion we refer to *N. incompta* for the right coiling morphospecies and *N. pachyderma* for the left coiling morphospecies.

[30] Our findings to date suggest that *N. incompta* has a lower genetic diversity than *N. pachyderma*, as we have found only two distinct genotypes of *N. incompta* globally as apposed to five genotypes of *N. pachyderma* in the Atlantic and Southern Ocean alone [Darling et al., 2004]. The five genotypes of *N. pachyderma* diverged from a subpolar common ancestor during the early Quaternary [Darling et al., 2004]. It is not possible to estimate when the two *N. incompta* genotypes diverged, as the high lineage evolution rate precludes the application of a molecular clock. There is no genetic gradation between *N. incompta*, *N. pachyderma* or *N. dutertrei*. These morphospecies are genetically highly distinct and the evolutionary tree topology suggests a sequence of divergence events entirely consistent with the fossil record.

4.2. Biogeographic Distribution of the *N. pachyderma* Morphospecies and Genotypes

[31] The biogeography, seasonality and ecology of *N. pachyderma* and *N. incompta* are now known in considerable regional detail [Bradshaw, 1959; Parker, 1962; Bé and Hamlin, 1967; Kennett, 1968; Bé and Tolderlund, 1971; Boltovskoy, 1971; Malmgren and Kennett, 1972; Coulbourn et al., 1980; Arikawa, 1983; Reynolds and Thunell, 1986; Spindler and Diekmann, 1986; Sautter and Thunell, 1989; Ufkes and Zachariasse, 1993; Marchant et al., 1998; Zaric et al., 2005]. They are present seasonally in high numbers throughout the higher latitudes. *N. pachyderma* is associated with cold polar and subpolar waters in both hemispheres but relict populations are also found in the upwelling zones of the Benguela system, the Peru-Chile Current and the Oman Margin. *N. incompta* is restricted to the more temperate waters of the global subpolar and transitional zones.

[32] In the Atlantic, the genotypes of *N. pachyderma* have been genetically isolated between the Northern (Type I) and Southern hemispheres (Types II–V) since the early Pleistocene and Types II–V have divergent adaptations in the Southern Ocean [Darling et al., 2004]. This evolutionary history contrasts markedly with that of *N. incompta* Type I, which forms a bipolar monospecific assemblage throughout the Atlantic Ocean in the present day (Figure 4). Such genetic identity indicates that transtropical transit must have occurred in the relatively recent past if not today [Darling et

al., 2000]. The likelihood of genetic exchange between the hemispheres is expected to increase substantially during glacial periods, when tropical Atlantic water temperatures fall accompanied by equatorward extension of the cool water boundary currents [Darling et al., 2000]. Indeed this is confirmed by the low-latitude sedimentary record which demonstrates the frequent occurrence of subpolar species within the equatorial zone during these episodes of cooling [McIntyre et al., 1989]. However, although the subpolar and transitional water masses are separated by considerable distance at present, specimens ascribed to *N. incompta* are found in small numbers in surface sediment samples throughout the tropical Atlantic. Provided these specimens are taxonomically correctly identified, their presence may indicate infrequent, but constant exchange across the tropics in the Holocene. It is unknown whether gene flow is unidirectional or bidirectional.

[33] In the Southern Ocean, the *N. incompta* province extends between the Polar Front and the Subtropical Front [Bé and Tolderlund, 1971; Boltovskoy et al., 1996]. The Antarctic Circumpolar Current dominates the Antarctic water masses and the western drift of the Southern Ocean circulation dictates that *N. incompta* Type I will be found throughout the whole of the subpolar and transitional Southern Ocean water masses. In parallel with its presence in the Benguela System, it will also frequent the cold Humboldt and Peru Currents off western South America.

[34] Bipolarity is not the scenario in the Pacific Ocean, however. The *N. incompta* Type II found in the north Pacific subpolar water mass is genetically distinct from the Atlantic *N. incompta* Type I and is potentially endemic to the North Pacific. The new specimens described here from the North Pacific are identical to those identified by Darling et al. [2003] in the Santa Barbara Channel. Potential North Pacific endemism was also observed by Darling et al. [2003] in the other higher-latitude planktonic foraminifers *G. bulloides* and *T. quinqueloba*. The isolation most likely reflects the hydrographic differences between the northern regions of the Atlantic and Pacific oceans. As yet it is unknown whether the ecological adaptations of *N. incompta* Type II in the North Pacific differ from those of *N. incompta* Type I in the Atlantic and Southern Ocean.

4.3. Evolution of Coiling Modes

[35] In a study exploring the causal mechanisms controlling coiling direction in the modern ocean, Brummer and Kroon [1988] concluded that coiling direction in planktonic foraminifers is most likely genetically determined and not driven by environmental factors. They also showed that there is an apparent relationship between coiling trends and the major planktonic foraminifer groups in the present day. Group I, comprising representatives of the spinose and microperforate clades (Figure 1), exhibited proportionate coiling and Group II, comprising representatives of the nonspinose macroperforate clade (Figure 1), had nearly 100% biased coiling. From analysis of fossil record stratigraphic and biogeographic data, Norris and Nishi [2001] present a strong case for the heritability of coiling in planktonic foraminifers. In a detailed quantitative evolutionary study of coiling trends in the Paleogene in combi-

nation with an assessment of Cretaceous and Neogene coiling trends from the literature, *Norris and Nishi* [2001] conclude that species with biased coiling (~100%) seem to have repeatedly evolved from ancestors with proportionate coiling (~50%). However, once clades have acquired biased coiling they tend to retain it. The application of these data to the present-day coiling modes indicates that the Group I proportionate coiling mode must represent an ancestral state and the Group II biased coiling mode is acquired over time. This means that the spinose group I coiling mode will have arisen in their subbotinid ancestors in the Paleogene and has been retained until the present day [*Norris and Nishi*, 2001]. The spinose group appears exceptional, as all spinose lineages have retained their ancestral proportionate coiling mode for a considerable period of time. However, the proportionate coiling spinose lineages may also exhibit a degree of species specific bias. This was observed in *G. bulloides* whose coiling ratio varies between 50 and 80% left coiling [*Boltovskoy*, 1971; *Brummer and Kroon*, 1988; *Naidu and Malmgren*, 1996; *Darling et al.*, 2003]. There are clearly marked differences in the determinants of coiling direction between Group I and Group II. The whole of the neogloboquadrinid nonspinose group displays the acquired biased coiling mode character with the presumption that they all evolved from a proportionate coiling ancestor. They are therefore now unlikely to lose their biased coiling character.

4.4. Coiling Ratios and Paleoceanographic Interpretations

[36] A number of nonspinose planktonic foraminifers have displayed abrupt or repetitive coiling reversals during geological time providing important biostratigraphic markers and paleoecological tools [*Ericson*, 1959; *Saito*, 1976; *Pfuhl and Shackleton*, 2004]. Genetic studies of biased coiling morphospecies indicate that such coiling direction changes are likely to represent alternation in the presence of different species [*Darling et al.*, 1999, 2000, 2003, 2004; *de Vargas et al.*, 2001]. Taking into account the low-level of reciprocal coiling observed in the *Neogloboquadrina* genotypes [*Bauch et al.*, 2003, this study], coiling direction ratios between 3 and 97% in the fossil record reflect a mixed population of two different species. A transition in the fossil record to opposite coiling does not therefore represent a progressive coiling direction change in a specific lineage, but the increasing dominance of one coiling type in the assemblage. Traditional interpretations of the fossil record have described such coiling direction shifts as an ecophenotypic effect. In reality, it reflects the presence of a mixed assemblage of different species with different environmental preferences. This fact calls for a reevaluation of the significance of coiling reversals through time.

[37] For example, both coiling forms of *Pulleniatina obliquiloculata* apparently became extinct in the Atlantic following the closure of the Panama Isthmus but both coiling forms reappeared in the Atlantic after 1.2 Myr [*Saito*, 1976]. It clearly took time for this tropical specialist to negotiate the rigors of the South African Cape and Benguela System to repopulate the Atlantic from the Indo-Pacific populations 2.4 Myr ago. The lack of correla-

tion in coiling direction patterns between the Indo-Pacific and Atlantic since the Panama Isthmus closure was most likely due to fluctuating environmental conditions at the Cape preventing further passage of the left coiling form. This form appears to have transited the Cape only once since closure, becoming a significant proportion of the *Pulleniatina* Atlantic tropical assemblage in the early Quaternary [*Saito*, 1976]. It eventually became extinct in the Atlantic around 1.7 Myr ago. During the rest of the Quaternary, the Cape and Benguela system must have become sufficiently hostile to prevent subsequent passage of the left coiling form, although it survived in the Indo-Pacific for a further 1 Myr. These differences most likely reflect the differing adaptations of the two opposite coiled species. Whether gene flow currently occurs between the Indo-Pacific and Atlantic right coiling populations remains to be determined. The alternation in coiling direction of *P. obliquiloculata* through time in both oceans therefore reflects not only cyclicity in the global tropical/subtropical hydrographic environments but also the paleoceanographic environment at the Cape gateway [*Darling et al.*, 1999]. There are currently several tropical specialists in the Indo-Pacific that appear unable to enter the Atlantic circulation.

[38] The biased coiling preference of *N. pachyderma* is not absolute as a small percentage of tests with a right coiling morphology (1–3%) are found in planktonic assemblages (Figure 3) and persist in the sedimentary record even in the most extreme polar conditions [*Pflaumann et al.*, 1996; *Bauch et al.*, 2003; *Darling et al.*, 2004]. It is now clear that a similar phenomenon prevails in *N. incompta* where aberrant left coiling forms have been found in genotyped specimens (Figure 4). The percentage of aberrant coiling observed in living assemblages of *N. incompta* is 1% in North Pacific sediment traps and 1.5% in North Atlantic plankton nets (Table 2). Sediment-derived percentages are slightly higher than these estimates (Figure 5). It can therefore only be assumed that assemblages are monospecific when percentage right coiling is greater than 97% in an assemblage. In these assemblages, the presence of left coiling morphotypes does not reflect an incursion of the left coiling *N. pachyderma* cooler water genotypes into a temperate region. In these areas the two coiling types are genetically identical and should thus not be separated for paleoceanographic proxy or geochemical use. Reciprocally, when the right coiling ratio falls below the 97% level, there is an increasing contribution of left coiling genetic types from upwelling or cooler water masses. It is therefore essential to determine coiling ratios before selection of left coiling forms for paleoceanographic use in the temperate water masses. Species can only be meaningfully separated in areas where the right coiling ratio is between 3% and 97%. Outside of this range, there is no relationship between the abundance of the aberrant coiling specimens and sea surface temperature (Figure 5), implying that the coiling ratio signal in the polar and subtropical waters has no paleoceanographic relevance. Congruence in isotopic signature between left and right coiling *N. pachyderma* was demonstrated by *Bauch et al.* [2003] in sediments throughout the last glacial period in cores from the Nordic seas.

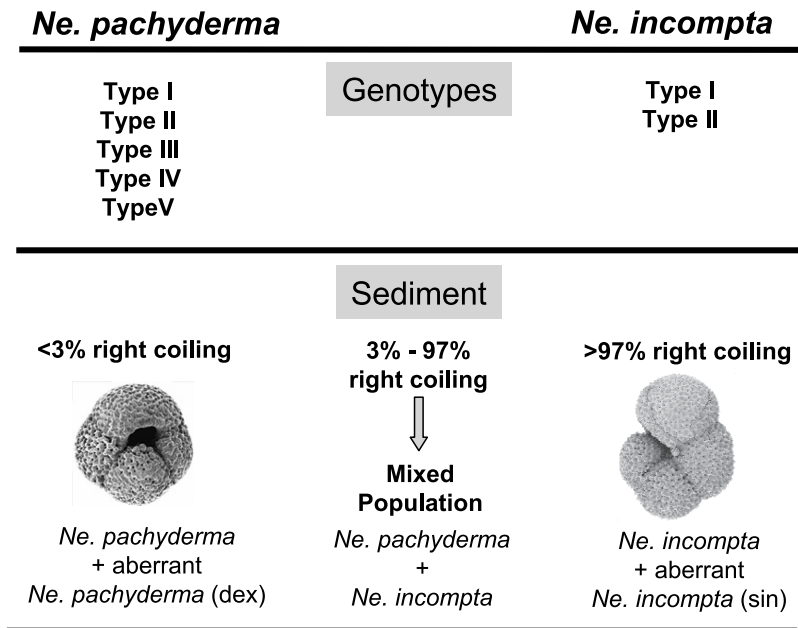


Figure 7. Flow diagram of the simplified nomenclature and classification of high-latitude *Neogloboquadrina* in sediment samples. At <3% right coiling, all left coiling specimens should be referred to as *N. pachyderma*, and all right coiling specimens should be referred to as *N. pachyderma* (dextral). Between 3% and 97% right coiling, all left coiling specimens should be referred to as *N. pachyderma*, and right coiling specimens should be referred to as *N. incompta*. At >97% right coiling, all right coiling specimens should be referred as *N. incompta*, and all left coiling specimens should be referred to as *N. incompta* (sinistral). *Ne* is *Neogloboquadrina*.

[39] It is clearly the case that for transfer functions, there is no benefit in attempting to resolve small changes in percentages of coiling of *N. pachyderma* in the extreme high-latitude regions. It is not possible to determine how many (if any) of these specimens represent expatriates from the other coiling province and how many are the aberrant coiling types of the same species. For example, this problem is highlighted when attempting to estimate sea ice extent during the Last Glacial Maximum. *Kucera et al.* [2005] found that the discrepancies between three different techniques used for SST reconstruction were partly due to differing interpretation of the relationship between SST and the composition of the small “subpolar” faunal fraction. The presence of aberrant coiling in *N. pachyderma* in these assemblages [*Bauch et al.*, 2003] led *Kucera et al.* [2005] to exclude right coiling *N. pachyderma* as an indicator species in these assemblages.

4.5. A Resolution for the *N. pachyderma* Coiling Direction Paradox

[40] We now have considerable evidence from the biogeography, ecology and degree of genetic distinction that the right and left coiling forms of *N. pachyderma* are different species. By adopting the species name *N. incompta* for the right coiling morphotypes and genotypes we can address the

paradoxical problem of there being right coiling morphotypes of left coiling genotypes and left coiling morphotypes of right coiling genotypes. To refer to aberrant coiling specimens, the species name can be simply appended with a coiling direction reference. The application of the new nomenclature is summarized in Figure 7. We note that the species name *N. incompta* is already used by some paleoceanographers to describe specimens representative of the right coiling *N. pachyderma* morphology [e.g., *Schiebel and Hemleben*, 2000] and we here propose that this name be consistently adopted when referring to the dominantly right coiling species.

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References

- Arikawa, R. (1983), Distribution and taxonomy of *Globigerina pachyderma* (Ehrenberg) off the coast, Northeast Honshu, Japan, *Tohoku Univ. Sci. Rep., Ser. 2*, 53, 103–157.
- Bandy, O. L. (1960), The geologic significance of coiling ratios in the foraminifer *Globigerina*

- pachyderma* (Ehrenberg), *J. Paleontol.*, *34*, 671–681.
- Bandy, O. L. (1972), Origin and development of *Globorotalia* (*Turborotalia*) *pachyderma* (Ehrenberg), *Micropaleontology*, *18*, 294–318.
- Bauch, D., K. Darling, J. Simstich, H. A. Bauch, H. Erlenkeuser, and D. Kroon (2003), Palaeoceanographic implications of genetic variation in living North Atlantic *N. pachyderma*, *Nature*, *424*, 299–302.
- Bé, A. W. H., and W. H. Hamlin (1967), Ecology of recent foraminifera, part 3, Distribution in the North Atlantic during the summer of 1962, *Micropaleontology*, *13*, 87–106.
- Bé, A. W. H., and D. S. Tolderlund (1971), Distribution and ecology of planktonic foraminifera, in *The Micropaleontology of Oceans*, edited by B. M. Funnell and W. R. Riedel, pp. 105–150, Cambridge Univ. Press, New York.
- Boltovskoy, E. (1971), Ecology of the planktonic foraminifera living in the surface layer of Drake Passage, *Micropaleontology*, *17*, 53–68.
- Boltovskoy, E. (1973), Note on the determination of absolute surface water temperature by means of the foraminifer *Globigerina bulloides* d'Orbigny, *Palaeontol. Z.*, *47*, 152–155.
- Boltovskoy, E., D. Boltovskoy, N. Correa, and F. Brandini (1996), Planktic foraminifera from the southwestern Atlantic (30°–60°S): Species-specific patterns in the upper 50m, *Mar. Micropaleontol.*, *28*, 53–72.
- Bradshaw, J. S. (1959), Ecology of living planktonic foraminifera in the North and equatorial Pacific Ocean, *Contrib. Cushman Found. Foraminiferal Res.*, *10*, 25–64.
- Brummer, G.-J. A., and D. Kroon (1988), Genetically controlled planktonic foraminiferal coiling ratios as tracers of past ocean dynamics, in *Planktonic Foraminifera as Tracers of Ocean-Climate History*, edited by G.-J. A. Brummer and D. Kroon, pp. 293–298, Free Univ. Press, Amsterdam.
- Cifelli, R. (1961), *Globigerina incompta*, a new species of pelagic foraminifera from the North Atlantic, *Contrib. Cushman Found. Foraminiferal Res.*, *12*, 83–86.
- Coulbourn, W. T., F. L. Parker, and W. H. Berger (1980), Faunal and solution patterns of planktonic foraminifera in surface sediments of the North Pacific, *Mar. Micropaleontol.*, *5*, 329–399.
- Darling, K. F., C. M. Wade, D. Kroon, A. J. Leigh Brown, and J. Bijma (1999), The diversity and distribution of modern planktonic foraminiferal small subunit ribosomal RNA genotypes and their potential as tracers of present and past ocean circulations, *Paleoceanography*, *14*, 3–12.
- Darling, K. F., C. M. Wade, I. A. Steward, D. Kroon, R. Dingle, and A. J. Leigh Brown (2000), Molecular evidence for genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifera, *Nature*, *405*, 43–47.
- Darling, K. F., M. Kucera, C. M. Wade, P. von Langen, and D. Pak (2003), Seasonal distribution of genetic types of planktonic foraminifer morphospecies in the Santa Barbara Channel and its paleoceanographic implications, *Paleoceanography*, *18*(2), 1032, doi:10.1029/2001PA000723.
- Darling, K. F., M. Kucera, C. J. Pudsey, and C. M. Wade (2004), Molecular evidence links cryptic diversification in polar plankton to Quaternary climate dynamics, *Proc. Natl. Acad. Sci. U. S. A.*, *101*, 7657–7662.
- de Vargas, C., S. Renaud, H. Hilbrecht, and J. Pawlowski (2001), Pleistocene adaptive radiation in *Globorotalia truncatulinoides*: Genetic, morphologic, and environmental evidence, *Paleobiology*, *27*, 104–125.
- Ehrenberg, C. G. (1873), Mikrogeologische Studien über das kleinste Leben der Meeres-Tiefgründe aller Zonen und dessen geologischen Einfluss, *K. Akad. Wiss. Berlin Abh.*, *1872*, 131–397.
- Ericson, D. B. (1959), Coiling direction of *Globigerina pachyderma* as a climatic index, *Science*, *130*, 219–220.
- Ericson, D. B., G. Wollin, and J. Wollin (1954), Coiling direction of *Globorotalia truncatulinoides* in deep-sea cores, *Deep Sea Res.*, *2*, 152–158.
- Felsenstein, J. (1985), Confidence limits on phylogenies: An approach using the bootstrap, *Evolution*, *31*, 783–791.
- Gu, X., Y.-X. Fu, and W.-H. Li (1995), Maximum likelihood estimation of the heterogeneity of substitution rate among nucleotide sites, *Mol. Biol. Evol.*, *12*, 546–557.
- Hilbrecht, H. (1997), Morphologic gradation and ecology in *Neogloboquadrina pachyderma* and *N. dutertrei* (planktic foraminifera) from core top sediments, *Mar. Micropaleontol.*, *31*, 31–43.
- Kennett, J. P. (1968), Latitudinal variation in *Globigerina pachyderma* (Ehrenberg) in surface sediments of the southwest Pacific Ocean, *Micropaleontology*, *14*, 305–318.
- Kennett, J. P., and M. S. Srinivasan (1983), *Neogene Planktonic Foraminifera: A Phylogenetic Atlas*, John Wiley, Hoboken, N. J.
- Kucera, M., et al. (2005), Reconstruction of sea-surface temperatures from assemblages of planktonic foraminifera: Multi-technique approach based on geographically constrained calibration data sets and its application to glacial Atlantic and Pacific Oceans, *Quat. Sci. Rev.*, *24*, 951–998.
- Lanave, C., G. Preparata, C. Saccone, and G. Serio (1984), A new method for calculating evolutionary substitution rates, *J. Mol. Evol.*, *20*, 86–93.
- Malmgren, B. A., and J. P. Kennett (1972), Biometric analysis of phenotypic variation: *Globigerina pachyderma* (Ehrenberg) in the South Pacific Ocean, *Micropaleontology*, *18*, 241–248.
- Marchant, M., D. Hebbeln, and G. Wefer (1998), Seasonal flux patterns of planktic foraminifera in the Peru-Chile Current, *Deep Sea Res., Part I*, *45*, 1161–1185.
- McIntyre, A., W. F. Ruddiman, K. Karlin, and A. C. Mix (1989), Surface water response of the equatorial Atlantic Ocean to orbital forcing, *Paleoceanography*, *4*, 19–55.
- Naidu, P. D., and B. A. Malmgren (1996), Relationship between late Quaternary upwelling history and coiling properties of *Neogloboquadrina pachyderma* and *Globigerina bulloides* in the Arabian Sea, *J. Foraminiferal Res.*, *26*, 64–70.
- Niebler, H.-S., and R. Gersonde (1998), A planktic foraminiferal transfer function for the southern South Atlantic Ocean, *Mar. Micropaleontol.*, *34*, 213–234.
- Norris, R. D., and H. Nishi (2001), Evolutionary trends in coiling of tropical Paleogene planktic foraminifera, *Paleobiology*, *27*, 327–347.
- Parker, F. L. (1962), Planktonic foraminiferal species in Pacific sediments, *Micropaleontology*, *8*, 219–254.
- Pawlowski, J., I. Bolivar, J. Fahrni, C. de Vargas, M. Gouy, and L. Zaninetti (1997), Extreme differences in rates of molecular evolution of foraminifera revealed by comparison of ribosomal DNA sequences and the fossil record, *Mol. Biol. Evol.*, *14*, 498–505.
- Pawlowski, J., M. Holzmann, C. Berney, J. Fahrni, A. J. Gooday, T. Cedhagen, A. Habura, and S. S. Bowser (2003), The evolution of early foraminifera, *Proc. Natl. Acad. Sci. U. S. A.*, *100*, 11,494–11,498.
- Pflaumann, U., J. Duprat, C. Pujol, and L. D. Labeyrie (1996), SIMMAX: A modern analog technique to deduce Atlantic sea surface temperatures from planktonic foraminifera in deep-sea sediments, *Paleoceanography*, *11*, 15–35.
- Pfuhl, H. A., and N. J. Shackleton (2004), Changes in coiling direction, habitat depth and abundance in two menardellid species, *Mar. Micropaleontol.*, *50*, 3–20.
- Reynolds, L. A., and R. C. Thunell (1986), Seasonal production and morphological variation of *Neogloboquadrina pachyderma* (Ehrenberg) in the northeast Pacific, *Micropaleontology*, *32*, 1–18.
- Saito, T. (1976), Geologic significance of coiling direction in the planktonic foraminifera *Pulleniatina*, *Geology*, *4*, 305–309.
- Saitou, N., and M. Nei (1987), The neighbor-joining method: A new method for reconstructing phylogenetic trees, *Mol. Biol. Evol.*, *4*, 406–425.
- Sautter, L. R., and R. C. Thunell (1989), Seasonal succession of planktonic foraminifera: Results from a four-year time series sediment trap experiment in the northeast Pacific, *J. Foraminiferal Res.*, *19*, 253–267.
- Sautter, L. R., and R. C. Thunell (1991), Planktonic foraminiferal response to upwelling and seasonal hydrographic conditions: Sediment trap results from San Pedro Basin, Southern California Bight, *J. Foraminiferal Res.*, *21*, 347–363.
- Schiebel, R., and C. Hemleben (2000), Inter-annual variability of planktic foraminiferal populations and test flux in the eastern North Atlantic Ocean (JGOFS), *Deep Sea Res., Part II*, *47*, 1809–1852.
- Smith, S. W., R. Overbeek, R. Woese, W. Gilbert, and P. M. Gilliuet (1994), The genetic data environment and expandable GUI for multiple sequence analysis, *Comput. Appl. Biosci.*, *10*, 671–675.
- Spencer-Cervato, C., H. R. Thierstein, D. B. Lazarus, and J.-P. Beckmann (1994), How synchronous are Neogene marine plankton events?, *Paleoceanography*, *9*, 739–763.
- Spindler, M., and G. S. Diekmann (1986), Distribution and abundance of the planktic foraminifer *Neogloboquadrina pachyderma* in sea ice of the Weddell Sea (Antarctica), *Polar Biol.*, *5*, 186–191.
- Srinivasan, M. S., and J. P. Kennett (1976), Evolution and phenotypic variation in the late Cenozoic *Neogloboquadrina dutertrei* plexus, in *Progress in Micropaleontology*, edited by Y. Takayanagi and T. Saito, pp. 329–355, Micropaleontol. Press, New York.
- Stangeew, E. (2001), Distribution and isotopic composition of living planktonic foraminifera *N. pachyderma* (sinistral) and *T. quinqueloba* in the high latitude North Atlantic, Ph.D. dissertation, Christian-Albrechts-Univ., Kiel, Germany.
- Swofford, D. L. (2003), *PAUP*: Phylogenetic Analysis Using Parsimony (and Other Methods)*, Version 4.0 [CD-ROM], Sinauer Assoc., Sunderland, Mass.

Ufkes, E., and W.-J. Zachariasse (1993), Origin of coiling differences in living neogloboquadrinids in the Walvis Bay region, off Namibia, southwest Africa, *Micropaleontology*, 39, 283–287.

Vella, P. (1974), Coiling ratios of *Neogloboquadrina pachyderma* (Ehrenberg): Variations in different size fractions, *Geol. Soc. Am. Bull.*, 85, 1421–1424.

Vincent, E., and W. H. Berger (1981), Planktonic foraminifera and their use in paleoceanography, in *The Sea*, vol. 7, *The Oceanic Lithosphere*,

edited by C. Emiliani, pp. 1025–1119, Wiley-Interscience, Hoboken, N. J.

Zaric, S., B. Donner, G. Fischer, S. Multza, and G. Wefer (2005), Sensitivity of planktic foraminifera to sea surface temperature and export production as derived from sediment trap data, *Mar. Micropaleontol.*, 55, 75–105.

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