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A resolution for the coiling direction paradox in Neogloboquadrina pachyderma

Kate F. Darling, Michal Kucera, Dick Kroon, and Christopher M. Wade

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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.


1. Introduction

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; Bolvoskov, 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 foraminifers 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.

The neogloboquadrinid clade exhibits a strong preferential coiling direction, approaching 100%. The tropical and warmer water morphospecies Neogloboquadrina dutertrei and Pseudonaiadina 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; Be and Hamlin, 1967; Kennett, 1968; Arikawa, 1983; Reynolds and Thunell, 1986]. The significance of the distinct distribution of the two coiling types has
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 [Yell, 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* 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. Paleoceneanographers 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

[8] 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 [Swoford, 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...
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/~cns/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 foraminifers are shown within a background of benthic morphospecies sequenced by Pawłowski et al. [1997] and rooted on the benthic foraminifer Allogromia, an early evolving group in the history of the foraminiferal clade [Pawłowski 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 foraminifers 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].
The evolutionary relationships within the Neogloboquadrina clade are shown in Figure 2. The phylogeny is based on 685 nucleotide sites and is rooted on \textit{G. inflata} which shared a common ancestor with the \textit{Neogloboquadrina} lineage in the late Oligocene [Kennett and Srinivasan, 1983]. The tree includes all genetic types of \textit{N. pachyderma} sequenced to date [Darling et al., 2003, 2004]. The predominantly right coiling genotypes of \textit{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 \textit{N. pachyderma}.

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 \textit{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 \textit{N. pachyderma}, \textit{G. glutinata}, and \textit{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, \textit{Globigerinella}; Or, \textit{Orbulina}; Gs, \textit{Globigerinoides}; Gb, \textit{Globigerina}; Tu, \textit{Turborotalita}; Ha, \textit{Hastigerina}; Ne, \textit{Neogloboquadrina}; Pu, \textit{Pulleniatina}; Gr, \textit{Globorotalia}; and Ga, \textit{Globigerinita}. 

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 \textit{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 \textit{N. pachyderma}, \textit{G. glutinata}, and \textit{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, \textit{Globigerinella}; Or, \textit{Orbulina}; Gs, \textit{Globigerinoides}; Gb, \textit{Globigerina}; Tu, \textit{Turborotalita}; Ha, \textit{Hastigerina}; Ne, \textit{Neogloboquadrina}; Pu, \textit{Pulleniatina}; Gr, \textit{Globorotalia}; and Ga, \textit{Globigerinita}. 

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5 changes per 100 nucleotide positions
3.2. Biogeography of Left Coiling N. pachyderma Genotypes in the Atlantic Ocean and the Antarctic

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

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 opposed 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 12.0°–14.5°C (eastern North Pacific; n = 20) and 14.0°–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

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.

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].
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*

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).

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

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°C–10°C) takes place over a slightly narrower range of temperatures than in the South Atlantic (4°C–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°C and 12°C.

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**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.

[19] Assemblies 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).

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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

<table>
<thead>
<tr>
<th>Region</th>
<th>Foraminiferal Province</th>
<th>Collection Method</th>
<th>Total Left Coiling</th>
<th>Total Right Coiling</th>
<th>Right Coiling, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctic</td>
<td>Greenland Sea</td>
<td>polar [Stangeew, 2001]</td>
<td>58,895</td>
<td>1,237</td>
<td>2.1</td>
</tr>
<tr>
<td>Antarctic</td>
<td>Weddell Sea</td>
<td>polar (this study)</td>
<td>718</td>
<td>22</td>
<td>3.1</td>
</tr>
<tr>
<td>North Pacific</td>
<td>San Pedro Basin</td>
<td>transitional [Sautter and Thunell, 1991]</td>
<td>47</td>
<td>4,611</td>
<td>99.0</td>
</tr>
<tr>
<td>S. Californian Bight</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
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.

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.

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*

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 *Aristerospira 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.
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.

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°39′N/69°33′W) within the predominantly right coiling province.

All paratypes of N. incompta illustrated by Cifelli [1961] are clearly morphologically nonspinose 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 nonspinose 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 nonspinose, 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

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.

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 nonspinose neogloboquadrinid wall structure.
clearly no possibility of confusion between the genotypes of these morphospecies.

[30] 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 opposed 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; Malgrngren 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; Zarić 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 [McIntrye 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 endemicism 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 foraminiferal 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 forms reappeared in the Atlantic after 1.2 Myr following the closure of the Panama Isthmus but both coiling types are genetically identical and should thus reflect 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.

36] 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.
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

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.

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 to as *N. incompta*, and all left coiling specimens should be referred to as *N. incompta* (sinistral). Ne is *Neogloboquadrina*.

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