



RESEARCH ARTICLE

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Key Points:

- Glacial *C. wuellerstorfi* and *C. kullenbergi* $\delta^{13}\text{C}$ offsets in the South Atlantic are observed
- Comparison of *Uvigerina* spp. $\delta^{13}\text{C}$ and *C. kullenbergi* $\delta^{13}\text{C}$ does not indicate strong habitat effects
- Glacial *C. kullenbergi* $\delta^{13}\text{C}$ may be biased toward lower $\delta^{13}\text{C}$, and glacial *C. wuellerstorfi* $\delta^{13}\text{C}$ may not represent average local conditions

Supporting Information:

- Supporting Information S1

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Carbon isotope offsets between benthic foraminifer species of the genus *Cibicides* (*Cibicoides*) in the glacial sub-Antarctic Atlantic

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Abstract Epibenthic foraminifer $\delta^{13}\text{C}$ measurements are valuable for reconstructing past bottom water dissolved inorganic carbon $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{DIC}}$), which are used to infer global ocean circulation patterns. Epibenthic $\delta^{13}\text{C}$, however, may also reflect the influence of ^{13}C -depleted phytodetritus, microhabitat changes, and/or variations in carbonate ion concentrations. Here we compare the $\delta^{13}\text{C}$ of two benthic foraminifer species, *Cibicides kullenbergi* and *Cibicides wuellerstorfi*, and their morphotypes, in three sub-Antarctic Atlantic sediment cores over several glacial-interglacial transitions. These species are commonly assumed to be epibenthic, living above or directly below the sediment-water interface. While this might be consistent with the small $\delta^{13}\text{C}$ offset that we observe between these species during late Pleistocene interglacial periods ($\Delta\delta^{13}\text{C} = -0.19 \pm 0.31\text{‰}$, $N=63$), it is more difficult to reconcile with the significant $\delta^{13}\text{C}$ offset that is found between these species during glacial periods ($\Delta\delta^{13}\text{C} = -0.76 \pm 0.44\text{‰}$, $N=44$). We test possible scenarios by analyzing *Uvigerina* spp. $\delta^{13}\text{C}$ and benthic foraminifer abundances: (1) *C. kullenbergi* $\delta^{13}\text{C}$ is biased to light values either due to microhabitat shifts or phytodetritus effects and (2) *C. wuellerstorfi* $\delta^{13}\text{C}$ is biased to heavy values, relative to long-term average conditions, for instance by recording the sporadic occurrence of less depleted deepwater $\delta^{13}\text{C}_{\text{DIC}}$. Neither of these scenarios can be ruled out unequivocally. However, our findings emphasize that supposedly epibenthic foraminifer $\delta^{13}\text{C}$ in the sub-Antarctic Atlantic may reflect several factors rather than being solely a function of bottom water $\delta^{13}\text{C}_{\text{DIC}}$. This could have a direct bearing on the interpretation of extremely light South Atlantic $\delta^{13}\text{C}$ values at the Last Glacial Maximum.

1. Introduction

Most species of the benthic foraminifer genera *Cibicides* and *Cibicoides* are generally believed to dwell in an epibenthic habitat [Lutze and Thiel, 1989; Jorissen et al., 1995]. The term “epibenthic” denotes a habitat directly above the sediment (sometimes referred to as “real epibenthic”) and within the sediment near the sediment-water interface [Jorissen et al., 1995]. Despite ambiguities regarding the exact average living depth that is represented by an epibenthic habitat, the term is useful to make a distinction to (infaunal/endobenthic) species living within the sediment that may have a marked subsurface abundance maximum [Jorissen et al., 1995]. Epibenthic foraminifera are often assumed to record the $\delta^{13}\text{C}$ of dissolved inorganic carbon (DIC) of the ambient (i.e., bottom) water in a roughly one-to-one relationship [Woodruff et al., 1980; Belanger et al., 1981; Graham et al., 1981; Duplessy et al., 1984; Zahn et al., 1986]. This assumption forms the basis for spatiotemporal reconstructions of DIC $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{DIC}}$) of bottom waters that are used to infer past global ocean circulation [e.g., Duplessy et al., 1988; Sarnthein et al., 1994; Ravelo and Andreasen, 2000; Bickert and Mackensen, 2003; Curry and Oppo, 2005; Gebhardt et al., 2008; Waelbroeck et al., 2011].

Past-ocean $\delta^{13}\text{C}_{\text{DIC}}$ reconstructions have shown much lower benthic $\delta^{13}\text{C}$ in the deep sub-Antarctic Atlantic than in the deep Pacific Ocean during the last glacial period (Figure 1) [Curry et al., 1988; Charles et al., 1996; Mackensen et al., 2001; Ninnemann and Charles, 2002; Hodell et al., 2003a]. The modern ocean, however, is generally characterized by a progressive decrease of $\delta^{13}\text{C}_{\text{DIC}}$ and an increase of deepwater DIC concentrations from the North Atlantic toward the North Pacific related to the steady accumulation of respired organic carbon along the flow path of deep water [Kroopnick, 1985]. The very negative benthic $\delta^{13}\text{C}$ values in the

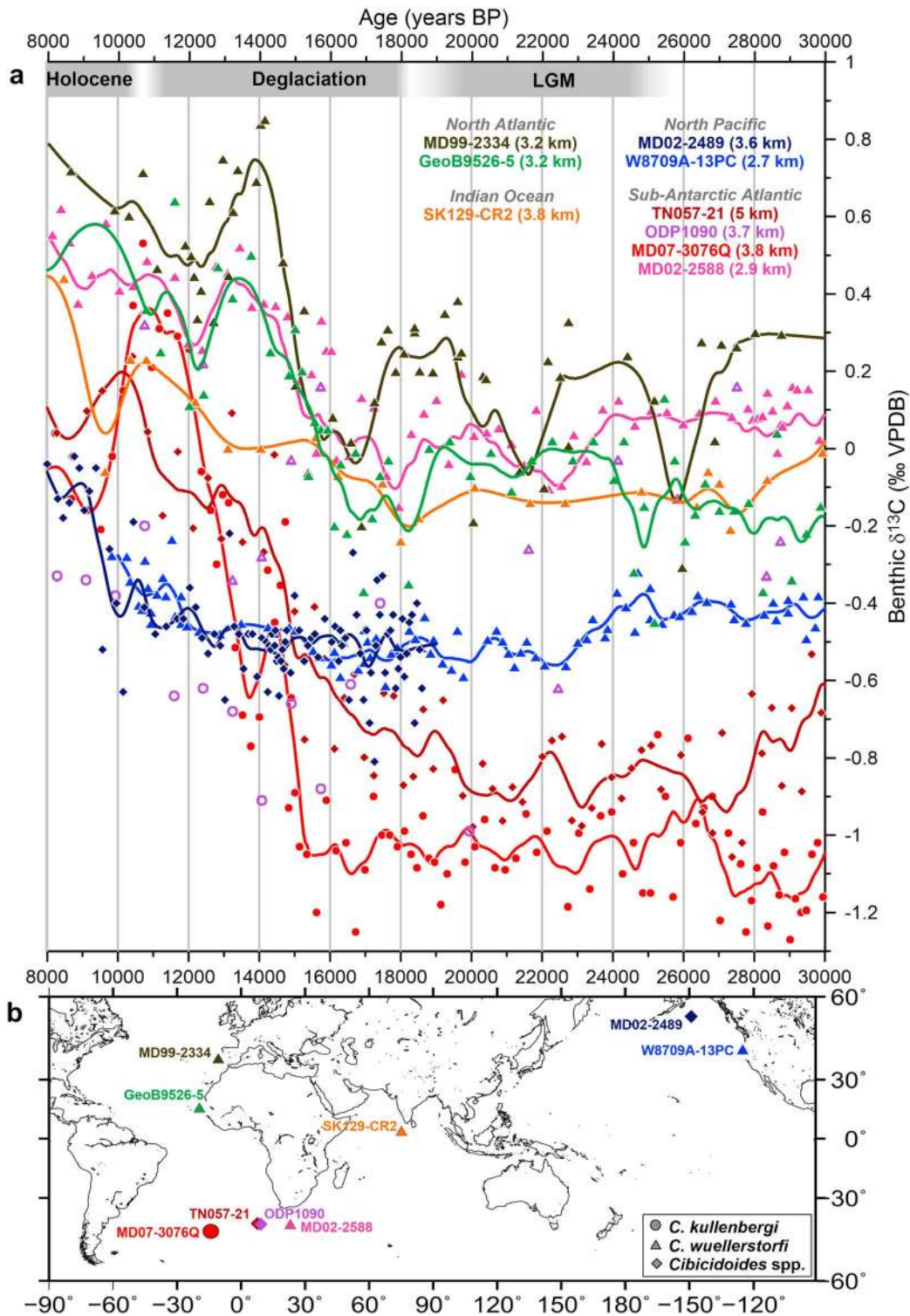


Figure 1. Deglacial benthic $\delta^{13}\text{C}$ records: (a) *Cibicides/Cibicides* $\delta^{13}\text{C}$ records (circles: *C. kullenbergi*; triangles: *C. wuellerstorfi*; diamonds: mixed *Cibicides/Cibicides* samples) from the North Atlantic (MD99-2334 [Skinner et al., 2007] and GeoB9526-5 [Zarriess and Mackensen, 2011]), the Indian Ocean (SK129-CR2 [Piotrowski et al., 2009]), the North Pacific (W8709A-13PC [Lund and Mix, 1998] and MD02-2489 [Gebhardt et al., 2008]), and the sub-Antarctic Atlantic (TN057-21 [Ninnemann et al., 1999], ODP site 1090 [Hodell et al., 2003a] (symbols only), MD07-3076Q [Waelbroeck et al., 2011], and MD02-2588 [Ziegler et al., 2013]). The numbers in the parentheses indicate the water depth at the core sites. The solid lines represent the 1000 year running averages. (b) Locations of sediment cores (Table S3 in the supporting information). The grey bars on the top indicate the Last Glacial Maximum (LGM), the deglaciation, and the Holocene periods. The benthic $\delta^{13}\text{C}$ records are shown on their previously published (^{14}C -based) age scales, except for TN057-21 [Barker and Diz, 2014] and MD99-2334 (transferred to the GICC05 chronology [Svensson et al., 2008]).

deep South Atlantic during the Last Glacial Maximum (LGM) may thus imply much higher respired carbon levels [Kroopnick, 1985], if the processes governing seawater $\delta^{13}\text{C}_{\text{DIC}}$ remained the same over glacial-interglacial cycles. This observation is important because it would imply different glacial ocean circulation patterns and/or changes in ocean carbon sequestration [Curry *et al.*, 1988; Michel *et al.*, 1995; Charles *et al.*, 1996; Ninnemann *et al.*, 1999] that may be associated with glacial atmospheric CO_2 minima [e.g., Toggweiler *et al.*, 2006]. However, the interpretation of very high respired carbon levels in the deep Southern Ocean has proven difficult to reconcile with nutrient proxy data such as benthic Cd/Ca ratios, which show little or no change in nutrient concentrations compared to Holocene levels [Boyle, 1992; Martínez-Méndez *et al.*, 2009]. Although benthic Cd/Ca ratios may also be affected by additional processes [e.g., McCorkle *et al.*, 1995], the apparent discrepancy between benthic Cd/Ca and carbon isotope ratios in the deep Southern Ocean may suggest that the mechanisms influencing deep South Atlantic $\delta^{13}\text{C}_{\text{DIC}}$ and/or benthic $\delta^{13}\text{C}$ have changed over glacial-interglacial time scales [e.g., Martínez-Méndez *et al.*, 2009; Mackensen, 2012]. However, the causes of low glacial South Atlantic benthic $\delta^{13}\text{C}$ values remain not fully understood.

Other ocean circulation proxies have been used to shed light on this conundrum and have highlighted the complexity of benthic $\delta^{13}\text{C}$ as a paleoceanographic proxy that incorporates the effects of ocean transport rates, biological export productivity, and air-sea gas exchange [e.g., Charles and Fairbanks, 1990; Lynch-Stieglitz *et al.*, 1995]. For instance, despite general agreement of millennial-scale variations in benthic $\delta^{13}\text{C}$ and the water mass provenance indicator ϵ_{Nd} , measured in sediment core TN057-21 from the Cape Basin, slight deviations between these proxies have been attributed to thermodynamic and kinetic fractionation effects on $\delta^{13}\text{C}$ during air-sea exchange of CO_2 [Piotrowski *et al.*, 2008]. These processes would have changed the preformed $\delta^{13}\text{C}$ signature of the water mass, producing changes in benthic $\delta^{13}\text{C}$ unrelated to respired carbon accumulation [Charles *et al.*, 1993; Lynch-Stieglitz *et al.*, 1995; Mackensen *et al.*, 2001]. In addition, Mackensen *et al.* [1993] demonstrated negative deviations of epibenthic $\delta^{13}\text{C}$ from bottom water $\delta^{13}\text{C}_{\text{DIC}}$ in environments with strong seasonal phytodetrital organic carbon input as the result of the incorporation of ^{13}C -depleted CO_2 into foraminiferal carbonates. It has further been suggested that benthic $\delta^{13}\text{C}$ does not only reflect changes in $\delta^{13}\text{C}_{\text{DIC}}$ of bottom waters but also variations in carbonate ion concentrations [Spero *et al.*, 1997; Mackensen and Licari, 2004]. Benthic foraminiferal $\delta^{13}\text{C}$ may also be biased if epibenthic foraminifera migrate from an elevated habitat above the sediment into the sediment and adopt a ^{13}C -depleted infaunal habitat [Corliss, 1985; McCorkle *et al.*, 1990; Rathburn *et al.*, 1996; Tachikawa and Elderfield, 2002; Hodell *et al.*, 2003a].

Here we present $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ records obtained from *Cibicides kullenbergi* and *Cibicides wuellerstorfi* during past glacial-interglacial transitions from sub-Antarctic Atlantic sediment core MD07-3076Q (44°9.19'S, 14°13.70'W; 3777m water depth) and the long piston core MD07-3077 retrieved at the same site (44°9.20'S, 14°13.69'W; 3776m water depth), as well as core TN057-6GC (42°52.7'S, 8°57.4'E; 3750m water depth). The core sites are currently bathed in Lower Circumpolar Deep Water, which is a transition zone between northern and southern sourced water masses. The goal of this study is to assess the consistency of stable isotope data for epibenthic foraminifer species and to test possible overprints. In our samples, we identify, analyze, and compare the records of distinct morphotypes of each of the species, and compare these with the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signature of *Uvigerina* spp., which we consider to consistently monitor $\delta^{13}\text{C}_{\text{DIC}}$ variations in an infaunal habitat. We discuss the general applicability of *C. kullenbergi*, *C. wuellerstorfi*, and *Cibicides/Cibicoides* spp. $\delta^{13}\text{C}$ analyses for ocean circulation reconstructions, in particular in the Atlantic sector of the Southern Ocean.

2. Modern Habitats and Morphologies

A variety of authors use different nomenclatures when referring to benthic species of the *Cibicides* and *Cibicoides* genera. Although *Cibicides* and *Cibicoides* species have been traditionally classified on the basis of their test convexity (planoconvex versus biconvex), along with wall structure and/or apertural shape [Mead, 1985; Loeblich and Tappan, 1988; Sen Gupta, 1989; Gupta, 1994], phylogenetic support for such placements is lacking [Schweizer *et al.*, 2009]. Test shape is also believed to be the expression of intraspecific ecophenotypic variations [Gupta, 1994]. We follow this notion and group both species into the single genus *Cibicides* de Montfort 1808 [de Montfort, 1808], where they were first described [Sen Gupta, 1989; Schweizer, 2006]. However, we note that *Cibicoides* is also a commonly used genus denomination (see Appendix A

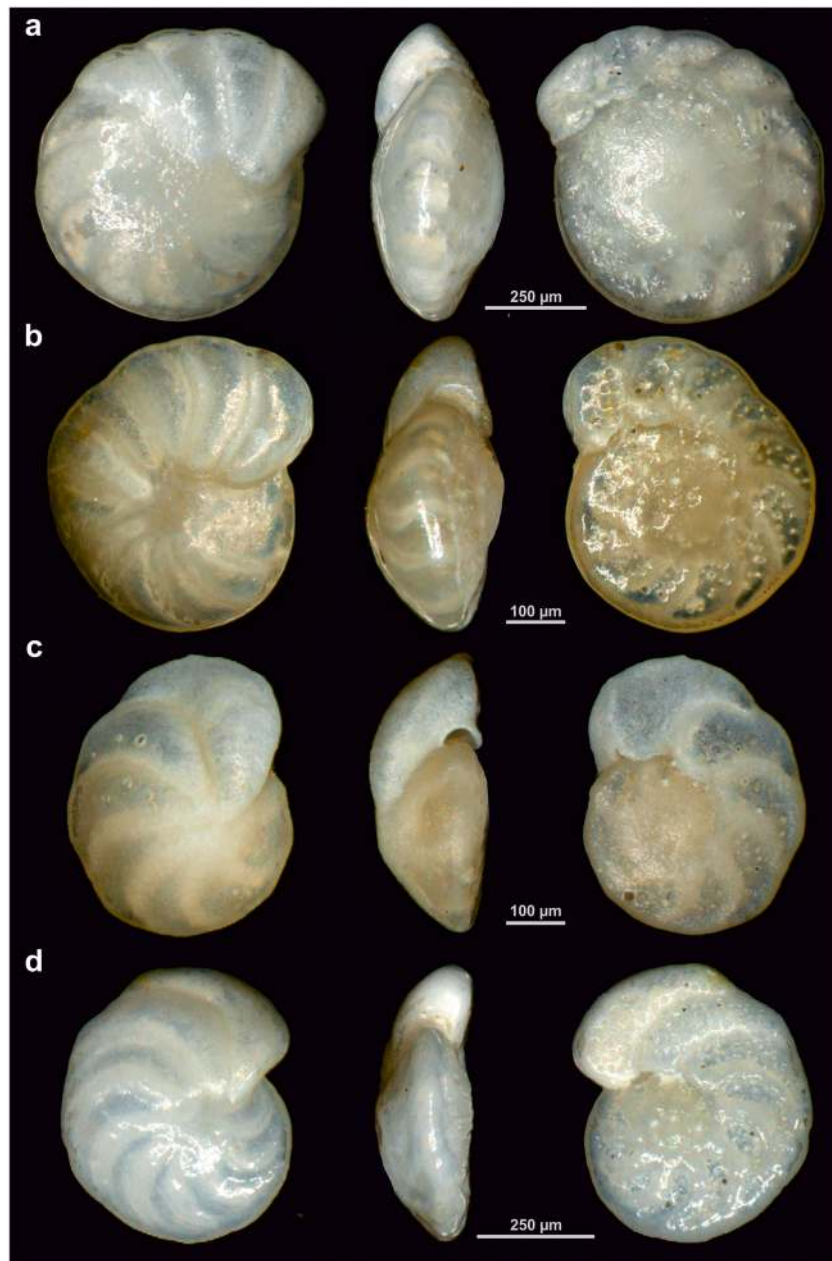


Figure 2. (left) Umbilical, (middle) lateral, and (right) spiral view of type specimens of (a) *C. kullenbergi sensu stricto*; (b) *C. kullenbergi sensu lato*; (c) *C. wuellerstorfi sensu lato*, referred to as *C. cf. wuellerstorfi* in this study; and (d) *C. wuellerstorfi sensu stricto*, photographed with the digital microscope ShuttlePix by Nikon®. These strongly resemble type specimens of *C. wuellerstorfi* and *C. kullenbergi* (called *C. mundulus*) and their morphotypes shown in Rae et al. [2011].

for taxonomic details). *Cibicides kullenbergi* Parker is generally considered a synonym for *Cibicidoides mundulus* (Brady, Parker, and Jones) [Van Morkhoven et al., 1986; Holbourn et al., 2013].

Cibicides wuellerstorfi and *C. kullenbergi* may present different morphological varieties (“morphotypes”) [e.g., Van Morkhoven et al., 1986; Hayward et al., 2010; Rae et al., 2011], which is a common feature of benthic foraminifer species (Figure 2). The subtle differences among species and morphotypes, and the occurrence of anomalous features, challenge their identification, with specimens often presenting morphological characteristics that are “intermediate” between two species [Van Morkhoven et al., 1986]. Unequivocal identification of different species from the *Cibicides* and *Cibicidoides* groups is thus difficult and, in part, subjective. We summarize the most important morphological features of *C. wuellerstorfi* and *C. kullenbergi* and of the

morphotypes we have identified in our sub-Antarctic Atlantic sediment samples and outline their main habitats (although these are not exclusive to the individual benthic foraminifer species).

2.1. *Cibicides wuellerstorfi* (Schwager), 1866

The typical features of the morphology of *C. wuellerstorfi* are shown in Figure 2 and have been described in *Loeblich and Tappan* [1988]. Its most important features include a low trochospiral and planoconvex test, 8 to 12 chambers visible in the final whorl that curve back at the periphery, strongly arched sutures, and an interiomarginal aperture (see also Figure S1 in the supporting information).

We have identified a *sensu lato* morphotype of *C. wuellerstorfi* commonly found in Southern Ocean sediments (hereafter referred to as *C. cf. wuellerstorfi*), shown in Figure 2c. The test of *C. cf. wuellerstorfi* is subcircular and planoconvex with a flat spiral side and convex umbilical side. The last whorl shows 7 to 9 chambers, which are generally wider and slightly more inflated than those of *C. wuellerstorfi*. The intercameral sutures are curved and bending toward the periphery, although not as strongly as in *C. wuellerstorfi*, and are slightly depressed. The shell has a dull reflectance (that may be an effect of preservation) and little perforation on the umbilical and spiral sides but tends to have a coarser perforation on the spiral side. The aperture may extend on the spiral side along the base of the final chambers. The morphology of *C. cf. wuellerstorfi* resembles very closely that of one holotype figure of *Anomalina wuellerstorfi* Schwager, 1866 in *Ellis and Messina* [1940].

Cibicides wuellerstorfi can live attached to benthic animals, plants, rocks, and hard substrates and is a “suspension feeder” [Lutze and Thiel, 1989]. This “real” epibenthic habitat makes *C. wuellerstorfi* a faithful recorder of bottom water $\delta^{13}\text{C}_{\text{DIC}}$ [Belanger et al., 1981; Graham et al., 1981; Duplessy et al., 1984; Zahn et al., 1986; Lutze and Thiel, 1989; Mackensen and Licari, 2004]. However, live (Rose Bengal stained) *C. wuellerstorfi* have also been found within the topmost centimeters of the sediment, suggesting that its habitat may not be restricted to an above-seafloor habitat, but may also be within the sediment [Corliss, 1985; Corliss and Emerson, 1990; Rathburn and Corliss, 1994; Jorissen et al., 1998; Wollenburg and Mackensen, 1998b; Fontanier et al., 2002]. This species is often associated with strong bottom water currents [Linke and Lutze, 1993; Mackensen et al., 1995]. It prefers a low organic carbon flux to the seafloor but withstands seasonally pulsed phytodetrital (labile) food supply [Mackensen et al., 1993, 2001; Jorissen et al., 1998]. As such, it is considered an indicator of oligotrophic conditions [Wollenburg and Mackensen, 1998a, 1998b]. *Cibicides wuellerstorfi* does not generally withstand high and sustained annual fluxes of organic carbon or perennial oxygen depletion in bottom waters [Mackensen et al., 1995]. Although *C. wuellerstorfi* specimens can be found in association with the (episodic) arrival of young, well-oxygenated water masses, as observed in the South Atlantic [Mackensen et al., 1995; Schmiedl and Mackensen, 1997], they have also been found in oxygen-poor seep environments [e.g., Rathburn et al., 2000; Burkett et al., 2015].

2.2. *Cibicides kullenbergi* Parker, 1953

The *sensu stricto* morphology of *C. kullenbergi* is shown in Figure 2a and has been described by *Loeblich and Tappan* [1988]. Important characteristics are a trochospiral and biconvex test (2.5 to 3 whorls are generally visible), 10 to 11 chambers in the final whorl, arched sutures on the spiral side, almost straight and radial sutures on the umbilical side, and a low interiomarginal aperture (see also Figure S1, in the supporting information).

In most of our sub-Antarctic Atlantic sediment samples, the morphology of *C. kullenbergi* deviates from the *sensu stricto* morphotype. This *sensu lato* morphotype of *C. kullenbergi* appears mostly convex on the umbilical side but tends to be rather flat on the spiral side and has a more subcircular test compared to *C. kullenbergi sensu stricto* (Figure 2). The chamber length-to-width ratio is also slightly greater in comparison to *C. kullenbergi sensu stricto* (Figure 2b). The spiral side of *C. kullenbergi sensu lato* is coarsely perforated, whereas perforation on the umbilical side is sparse. Furthermore, the sutures of *C. kullenbergi sensu lato* may be slightly depressed and marginally arched toward the periphery both on the spiral and umbilical sides (Figure 2b).

Cibicides kullenbergi has been suggested to dwell at the sediment-water interface and has been considered a “mud dweller” [Corliss and Emerson, 1990; Schweizer, 2006]. Live (stained) specimens are generally found in the first centimeter of the sediment [Rathburn and Corliss, 1994; Jorissen et al., 1998] and have also been extensively used to reconstruct bottom water $\delta^{13}\text{C}_{\text{DIC}}$ [e.g., Duplessy et al., 1988; Charles et al., 1996; Gebhardt et al., 2008]. In contrast to *C. wuellerstorfi*, *C. kullenbergi* is adapted to various modes of organic

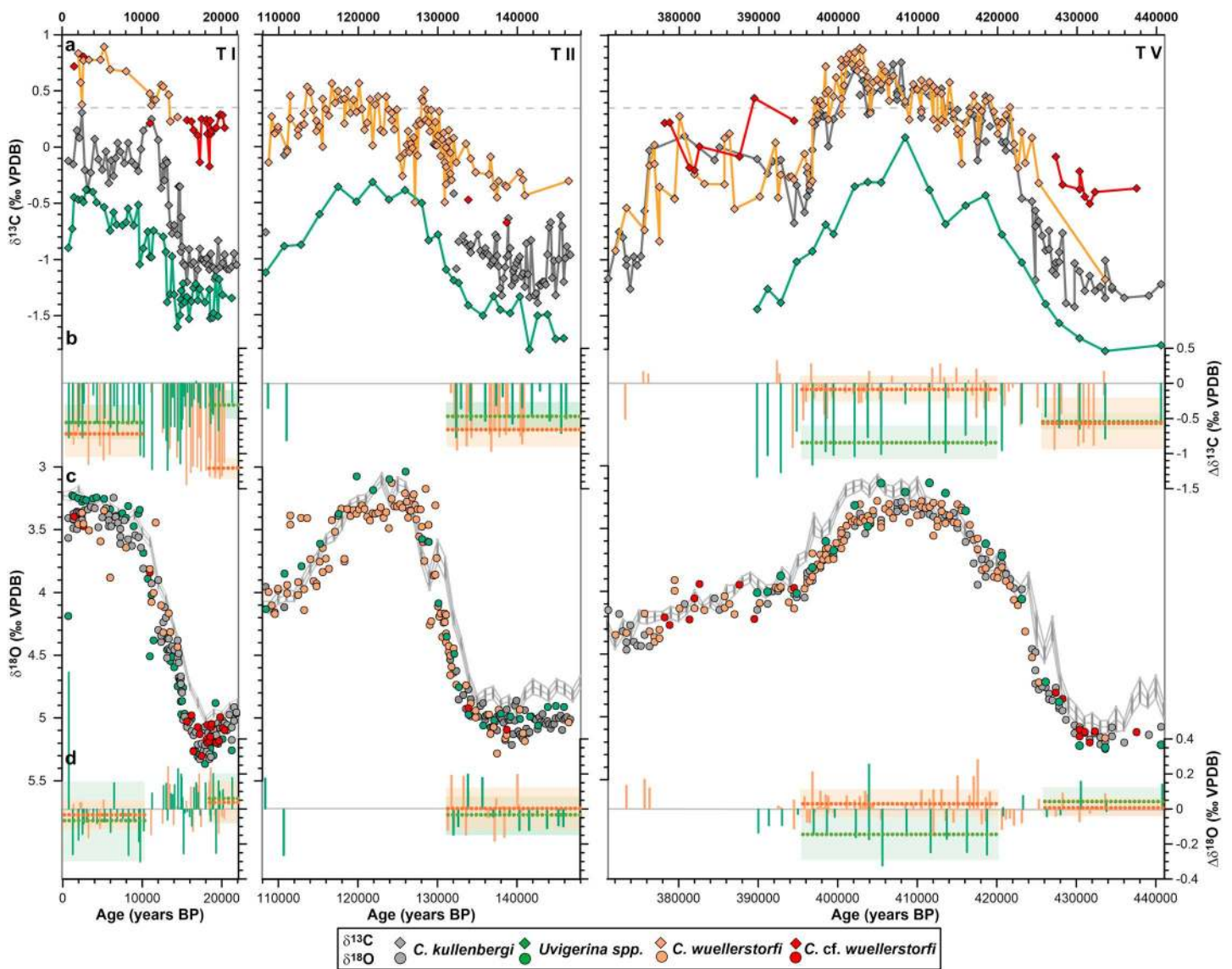


Figure 3. Mean benthic foraminifer $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ during the last deglaciation in sediment core (left) MD07-3076Q, as well as (middle) marine isotope stage (MIS) 6–5 and (right) MIS 12–11 in sediment core MD07-3077. (a) The $\delta^{13}\text{C}$ of *Uvigerina* spp. (green), *C. wuellerstorfi sensu stricto* (orange), *C. cf. wuellerstorfi* (i.e., *C. wuellerstorfi sensu lato*; red), and *C. kullenbergi sensu lato* (grey); (b) $\delta^{13}\text{C}$ gradient between *C. kullenbergi* and *C. wuellerstorfi* (s.l.) (orange), as well as between *Uvigerina* spp. and *C. kullenbergi* (green); (c) benthic $\delta^{18}\text{O}$ as in Figure 3a, shown with the global benthic $\delta^{18}\text{O}$ stack (and its standard error) of *Lisiecki and Raymo* [2005] for reference (grey); and (d) benthic $\delta^{18}\text{O}$ gradient as in Figure 3b; *C. cf. wuellerstorfi* and *C. kullenbergi* $\delta^{18}\text{O}$ data are adjusted by 0.64‰ [Shackleton and Opdyke, 1973; Duplessy et al., 1984], the stippled line in Figure 3a indicates the present-day bottom water $\delta^{13}\text{C}_{\text{DIC}}$ at the core site ($\sim -0.36\text{‰}$ VPDB) after Mackensen [2012], and the dotted lines and envelopes in Figures 3b and 3d show the mean interglacial and glacial values and their 1 σ errors, respectively (Table 1).

carbon food supply [Lutze and Coulbourn, 1984; Jorissen et al., 1998; Eberwein and Mackensen, 2006]. Although it prefers oligotrophic conditions, similar to *C. wuellerstorfi* [Fariduddin and Loubere, 1997], it may withstand a much more continuous organic carbon supply to the seafloor [Eberwein and Mackensen, 2006].

3. Methods

3.1. Stable Isotope Measurements

Stable isotope analyses in sediment cores MD07-3076Q and MD07-3077 have been performed on 1 to 4 specimens of *C. kullenbergi* (212–500 μm), *C. wuellerstorfi* (150–500 μm), and *C. cf. wuellerstorfi* (150–500 μm) as well as of *Uvigerina* spp. (mostly *U. peregrina*; 212–350 μm) on Finnigan $\Delta+$ and Elementar Isoprime mass spectrometers at the Laboratoire des Sciences du Climat et de l'Environnement (LSCE) in Gif-sur-Yvette,

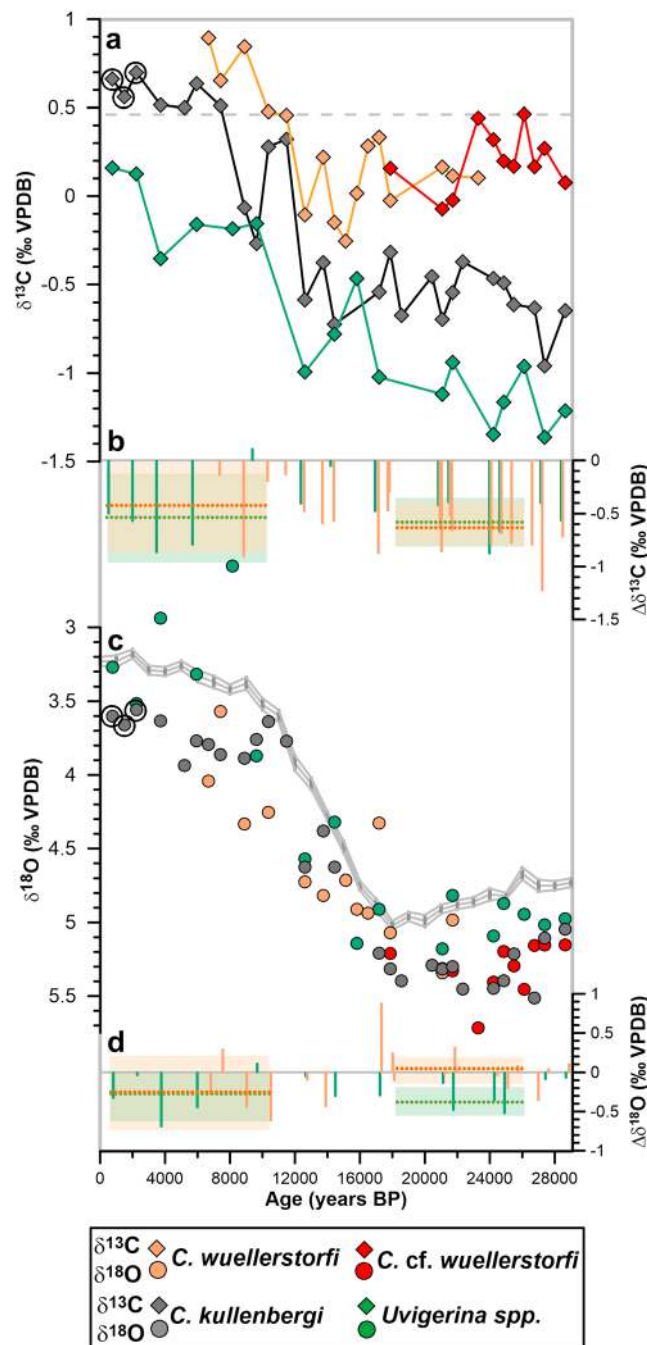


Figure 4. Benthic foraminifer $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ during the last deglaciation in sediment core TN057-6GC (symbols and lines as in Figure 3); encircled data points show the measurements on *C. kullenbergi sensu stricto* (see discussion in section 2.2), and stippled line in Figure 4a indicates the present-day bottom water $\delta^{13}\text{C}_{\text{DIC}}$ at the core site ($\sim 0.47\text{‰ VPDB}$) after Mackensen [2012].

France. Small size fractions ($<212\mu\text{m}$) were analyzed when benthic foraminifera (in particular, *C. wuellerstorfi* and *C. cf. wuellerstorfi*) were absent in the 212–500 μm fraction. Stable isotope analyses of *C. kullenbergi* in MD07-3076Q and MD07-3077 were made on the *sensu lato* morphotype (Figure 2b) because of its predominant occurrence in these cores. Benthic foraminifer stable isotopes in sediment core TN057-6GC (same size fractions as above) have been measured on ThermoFisher MAT253 mass spectrometer with an automated Kiel Device at the Godwin Laboratory for Palaeoclimate Research at the University of Cambridge (UK). Both morphotypes of *C. kullenbergi* were identified in the 212–500 μm size fraction and were measured separately.

In all cores, stable isotope analyses have been performed separately on *C. wuellerstorfi* and *C. cf. wuellerstorfi* (Figures 3–5). Paired stable isotope analyses on *C. wuellerstorfi* and *C. cf. wuellerstorfi* could not be performed, as they hardly coexist in exactly the same depth levels in our sediment cores. *Cibicides cf. wuellerstorfi* seems to be more common during glacial periods, whereas *C. wuellerstorfi* is abundant during interglacials. Although this needs to be verified by genetic characterization [e.g., Schweizer *et al.*, 2009], we treat *C. wuellerstorfi* and *C. cf. wuellerstorfi* as the same species for our purposes, hereafter abbreviated as *C. wuellerstorfi* (in a *sensu lato*; *s.l.*), owing to their close morphologies (section 2.1.) and the generally lower abundance of these foraminifera in sub-Antarctic Atlantic sediments. However, whether these two benthic foraminifera represent different species or different morphotypes does not matter for the conclusion of this study, because in practice they can be (and often are) considered as equivalents of the *sensu stricto* form.

Prior to stable isotope analyses, foraminifera were cleaned to remove organic matter and extraneous carbonates that are adsorbed or attached to the foraminiferal shells. Foraminifer samples from MD07-3076Q and MD07-3077 were rinsed with methanol, ultrasonicated for $\sim 10\text{s}$, dried at room temperature, and finally roasted under vacuum at $\sim 380^\circ\text{C}$ for 45 min. Foraminifer samples from TN057-6GC were crushed, soaked in $\sim 15\%$ hydrogen peroxide for 30 min at room temperature, rinsed in acetone, ultrasonicated for a

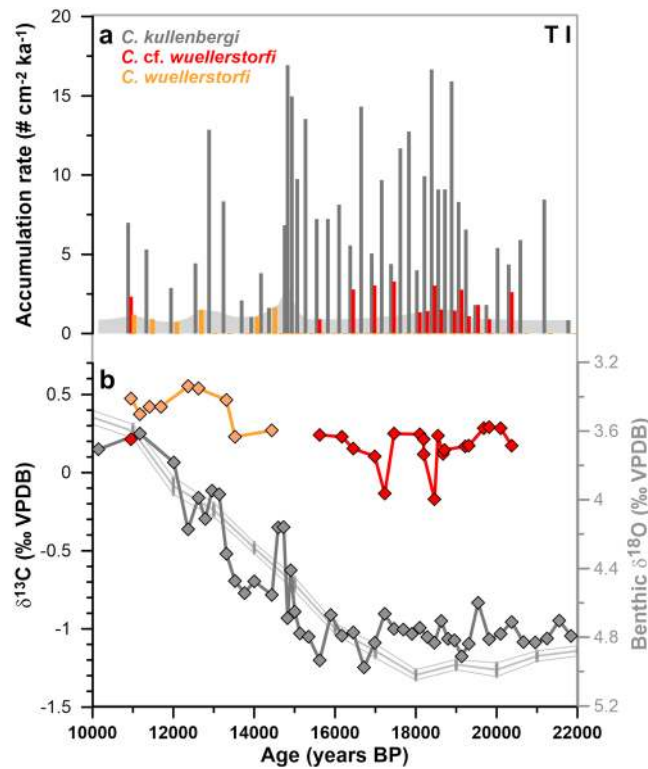


Figure 5. Benthic foraminifer accumulation rates during Termination I in core MD07-3076Q. (a) Accumulation rate of *C. kullenbergi* in grey, *C. cf. wuellerstorfi* in red, and *C. wuellerstorfi* in orange (the grey shaded area indicates the detection limit of the analyses, i.e., one foraminifer per gram dry bulk sediment times the linear sedimentation rate times the dry bulk sediment density of the 8 cm³ samples). (b) The δ¹³C of *C. wuellerstorfi* (orange), *C. cf. wuellerstorfi* (red), and *C. kullenbergi* (grey) with the global benthic δ¹⁸O stack (and its standard error) of Lisiecki and Raymo [2005] for reference in light grey.

lerstorfi and an intraspecies δ¹³C variability of 0.15±0.14‰ (N=87) for *C. kullenbergi* and 0.09±0.08‰ (N=21) for *C. wuellerstorfi*. Replicated stable isotope values are reported as mean values in our study.

Interspecies δ¹⁸O and δ¹³C offsets were estimated for interglacial periods (Holocene: last 10ka before present (B.P.), marine isotope stage (MIS) 11: 419–395ka B.P.) and for glacial periods (LGM: 25–18ka B.P., MIS 6: 149–132ka B.P., MIS 12: 448–425ka B.P.; Figures 3 and 4 and Table 1). Interspecies δ¹⁸O and δ¹³C offsets between *C. kullenbergi* and *C. wuellerstorfi* (*s.l.*) (Δδ¹⁸O_{Ck-Cw} and Δδ¹³C_{Ck-Cw}, respectively) and between *Uvigerina* spp. and *C. kullenbergi* (Δδ¹⁸O_{Uvi-Ck} and Δδ¹³C_{Uvi-Ck}, respectively) were calculated based on paired measurements from the same sediment sample and in sediment core MD07-3076Q also from consecutive sediment samples within 2cm (or <400years) of each other. The benthic interspecies δ¹⁸O_{Ck-Cw} difference obtained from adjacent sediment samples from within 2cm in MD07-3076Q is -0.01±0.13‰ (N=11) on average, which is statistically indistinguishable from the average Δδ¹⁸O_{Ck-Cw} value of 0.03±0.12‰ (N=19) obtained from the same sediment sample. We argue that this correspondence justifies the calculation of Δδ¹³C_{Ck-Cw} from adjacent sediment samples within 2cm spacing that was necessary because of low benthic foraminifer abundances in MD07-3076Q.

3.2. Benthic Foraminifer Abundances in MD07-3076Q

To quantify the abundance of *C. wuellerstorfi*, *C. cf. wuellerstorfi*, and *C. kullenbergi* during the last deglaciation in sediment core MD07-3076Q, we determined the number of specimens per gram of dry bulk sediment in discrete 8cm³ volume samples obtained from 1cm thick sediment slices. The benthic foraminifer accumulation rate (BFAR) was calculated as BFAR=#foraminifera×LSR×ρ_{dry}, where #foraminifera is the number of

few seconds, and dried in an oven at 50°C. All foraminifer samples in each individual core were pretreated equally.

The mean external reproducibility of carbonate standards of LSCE Finnigan Δ+ and Elementar Isoprime mass spectrometers (Godwin Laboratory ThermoFisher MAT253 mass spectrometer) is σ=0.05‰ (0.08‰) for δ¹⁸O and σ=0.03‰ (0.06‰) for δ¹³C. The results are reported with reference to the international Vienna Peedee Belemnite (VPDB) standard, defined with respect to the National Bureau of Standards (NBS)-19 calcite standard (δ¹⁸O=-2.20‰ and δ¹³C=+1.95‰) [Coplen, 1988]. Stable isotope analyses of the NBS-19 calcite standard and of an internal carbonate standard for the purpose of an interlaboratory comparison between Gif and Cambridge have indicated good reproducibility (Gif δ¹⁸O: -5.50±0.05‰, N=40; Cambridge δ¹⁸O: -5.52±0.07‰, N=20; Gif δ¹³C: 1.45±0.03‰, N=40; Cambridge δ¹³C: 1.44±0.02‰, N=20) and thus support consistency of stable isotope measurements between the laboratories.

Replicate measurements indicate an average intraspecies δ¹⁸O variability of 0.07±0.05‰ (N=87) for *C. kullenbergi* and 0.09±0.08‰ (N=21) for *C. wuel-*

Table 1. Summary of Observed $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ Offsets ($\pm 1\sigma$ Standard Deviation) Between *C. kullenbergi* (Ck), *C. wuellerstorfi* and *C. wuellerstorfi s.l.* (Cw), and *Uvigerina* spp. (Uvi) During Interglacial and Glacial Periods in Sediment Cores MD07-3076Q, MD07-3077, and TN057-6GC (N: Number of Observations)^a

		MD07-3076Q LGM-Hol	MD07-3077 MIS 6-MIS 5	MD07-3077 MIS 12-MIS 11	TN057-6GC LGM-Hol	Average
$\Delta\delta^{18}\text{O}_{\text{Ck-Cw}}$ (‰VPDB)	Interglacial	-0.04 ± 0.09 (N=8)	-	0.04 ± 0.08 (N=52)	-0.26 ± 0.48 (N=3)	0.01 ± 0.13 (N=63)
	Glacial	0.04 ± 0.12 (N=10)	0.00 ± 0.13 (N=16)	0.01 ± 0.05 (N=10)	0.03 ± 0.17 (N=8)	0.02 ± 0.12 (N=44)
$\Delta\delta^{18}\text{O}_{\text{Uvi-Ck}}$ (‰VPDB)	Interglacial	-0.07 ± 0.23 (N=19)	-	-0.14 ± 0.14 (N=16)	-0.28 ± 0.32 (N=5)	-0.13 ± 0.22 (N=40)
	Glacial	0.07 ± 0.14 (N=11)	-0.04 ± 0.11 (N=13)	0.05 ± 0.08 (N=9)	-0.38 ± 0.17 (N=4)	-0.02 ± 0.18 (N=37)
$\Delta\delta^{13}\text{C}_{\text{Ck-Cw}}$ (‰VPDB)	Interglacial	-0.72 ± 0.35 (N=8)	-	-0.09 ± 0.19 (N=52)	-0.42 ± 0.43 (N=3)	-0.19 ± 0.31 (N=63)
	Glacial	-1.21 ± 0.14 (N=10)	-0.67 ± 0.22 (N=16)	-0.57 ± 0.37 (N=10)	-0.61 ± 0.18 (N=8)	-0.76 ± 0.44 (N=44)
$\Delta\delta^{13}\text{C}_{\text{Uvi-Ck}}$ (‰VPDB)	Interglacial	-0.55 ± 0.26 (N=19)	-	-0.83 ± 0.23 (N=16)	-0.53 ± 0.39 (N=5)	-0.66 ± 0.29 (N=40)
	Glacial	-0.31 ± 0.20 (N=11)	-0.46 ± 0.19 (N=13)	-0.56 ± 0.12 (N=9)	-0.59 ± 0.23 (N=4)	-0.45 ± 0.21 (N=37)

^aThe interglacial and glacial periods associated with Termination (T) I refer to the Holocene (last 10ka B.P.; Hol) and the LGM (25–18ka B.P.), respectively. The glacial interval prior to TII used for our calculations is 149–132ka B.P. (within marine isotope stage (MIS) 6), whereas the intervals 419–395ka B.P. (within MIS 11) and 448–425 B.P. (within MIS 12) were chosen for the interglacial and glacial periods after and prior to TV (compare stippled lines in Figures 3 and 4). Averages were calculated based on all data from our three study cores. Benthic $\delta^{18}\text{O}$ data (excluding that of *Uvigerina* spp.) are adjusted by +0.64‰ [Shackleton and Opdyke, 1973; Duplessy et al., 1984].

benthic foraminifera per gram of dry bulk sediment, LSR is the linear sedimentation rate in cm ka^{-1} , and ρ_{dry} is the dry bulk sediment density in g cm^{-3} [Herguera and Berger, 1991]. The ρ_{dry} was calculated from the dry sediment weight of the discrete 8cm^3 samples.

3.3. Core Chronologies

The age model of sediment core MD07-3076Q is based on calibrated radiocarbon ages corrected for surface ocean reservoir age variations [Skinner et al., 2010]. Our deglacial age model applies a linear interpolation between the radiocarbon-derived age-depth tie points [Gottschalk et al., 2015] to be consistent with the age model approach used for core MD07-3077 [Vázquez Riveiros et al., 2010, 2013; this study]. However, the difference between the age models for the last 25ka B.P. using a Monte Carlo-based approach [Skinner et al., 2010] and a piecewise linear interpolation [Gottschalk et al., 2015] is small (2 ± 38 years).

The chronology of sediment core MD07-3077 during MIS 12–11 is based on the stratigraphic alignment of abundance variations of the cold-water planktonic foraminifer *Neogloboquadrina pachyderma* (sinistral) with Antarctic temperature variations [Vázquez Riveiros et al., 2010, 2013] approximated by the δD record of the Antarctic Dome C ice core (European Project for Ice Coring in Antarctica) [Jouzel et al., 2007] on the newest Antarctic Ice Core Chronology (AICC) 2012 [Bazin et al., 2013]. Six additional age-depth markers were obtained using the same approach in the MIS 6–5 interval (Figure S2 and Table S1 in the supporting information). The final chronology is based on linear interpolation between tie points.

The age model of sediment core TN057-6GC is based on the alignment of the benthic $\delta^{18}\text{O}$ record of MD07-3076Q to that of TN057-6GC (Figure S3 and Table S2 in the supporting information), justified because the cores are located in close proximity to each other. Although this provides only a rough age model, it is sufficient for comparing benthic $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values between interglacial and glacial periods, which is the aim of our study.

4. Results

4.1. Downcore $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ Variabilities

4.1.1. MD07-3076Q/MD07-3077

We observe a $\delta^{13}\text{C}$ offset between *C. wuellerstorfi* (s.l.) and *C. kullenbergi* in the sub-Antarctic Atlantic that is consistently larger during the glacial than during the succeeding interglacial periods (Figure 3 and Table 1). Also, the average Holocene *C. wuellerstorfi* (s.l.) $\delta^{13}\text{C}$ value is higher than present-day $\delta^{13}\text{C}_{\text{DIC}}$ at the core site, whereas the average *C. kullenbergi* $\delta^{13}\text{C}$ value is lower (Figure 3).

In MD07-3077, *C. wuellerstorfi* (s.l.) $\delta^{13}\text{C}$ and *C. kullenbergi* $\delta^{13}\text{C}$ values are statistically identical during MIS 11 ($\Delta\delta^{13}\text{C} = -0.09 \pm 0.19\text{‰}$, $N=52$; Figure 3). The offset between *C. kullenbergi* $\delta^{13}\text{C}$ and *C. wuellerstorfi* (s.l.) $\delta^{13}\text{C}$ during MIS 12 ($\Delta\delta^{13}\text{C}_{\text{Ck-Cw}} = -0.57 \pm 0.37\text{‰}$, $N=10$) is significantly different from the MIS 11 offset within 95% uncertainties ($p < 0.05$). The scarcity of *C. kullenbergi* during MIS 5 does not permit an estimate of $\Delta\delta^{13}\text{C}_{\text{Ck-Cw}}$ for this period. However, $\Delta\delta^{13}\text{C}_{\text{Ck-Cw}}$ values during MIS 6 ($-0.67 \pm 0.22\text{‰}$, $N=16$) are similar to

those observed during MIS 12. During the Holocene, the $\delta^{13}\text{C}$ offset between *C. wuellerstorfi* (*s.l.*) and *C. kullenbergi* is $\Delta\delta^{13}\text{C}_{\text{Ck-Cw}} = -0.72 \pm 0.35\text{‰}$ ($N=8$) on average, which is lower than last glacial values in MD07-3076Q ($\Delta\delta^{13}\text{C}_{\text{Ck-Cw}} = -1.21 \pm 0.14\text{‰}$, $N=10$), but similar to those of MIS 6 and MIS 12 in MD07-3077 (Figure 3 and Table 1). Again, a statistical t test shows that the observed LGM $\Delta\delta^{13}\text{C}_{\text{Ck-Cw}}$ values are significantly different from Holocene $\Delta\delta^{13}\text{C}_{\text{Ck-Cw}}$ estimates within 95% uncertainties ($p < 0.05$).

Despite the significant glacial $\delta^{13}\text{C}$ offset, *C. wuellerstorfi* (*s.l.*) and *C. kullenbergi* $\delta^{18}\text{O}$ values in the central sub-Antarctic Atlantic closely agree with each other throughout the studied time interval (Table 1 and Figure 3).

4.1.2. TN057-6GC

The distinct glacial-interglacial difference between *C. kullenbergi* $\delta^{13}\text{C}$ and *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ observed in MD07-3076Q/MD07-3077 agrees with results in Cape Basin sediment core TN057-6GC (Figure 4). The mean $\delta^{13}\text{C}$ offset between *C. kullenbergi* and *C. wuellerstorfi* (*s.l.*) in TN057-6GC is $\Delta\delta^{13}\text{C}_{\text{Ck-Cw}} = -0.61 \pm 0.18\text{‰}$ ($N=8$) during the LGM and $\Delta\delta^{13}\text{C}_{\text{Ck-Cw}} = -0.42 \pm 0.43\text{‰}$ ($N=3$) during the Holocene. Because of the small number of observations during these two periods, the glacial-interglacial $\Delta\delta^{13}\text{C}_{\text{Ck-Cw}}$ difference observed in TN057-6GC is not statistically significant and awaits confirmation by further analyses in other Cape Basin sediment cores. Mean Holocene *C. wuellerstorfi* (*s.l.*) and *C. kullenbergi* $\delta^{13}\text{C}$ are higher than modern $\delta^{13}\text{C}_{\text{DIC}}$ at the core site (Figure 4).

The $\delta^{18}\text{O}$ values of the different *Cibicides* species are in agreement, although the interspecies $\delta^{18}\text{O}$ variability is slightly greater in TN057-6GC than in MD07-3076Q/MD07-3077 (Table 1 and Figure 4).

4.2. Comparison of *C. kullenbergi* $\delta^{13}\text{C}$ and *Uvigerina* spp. $\delta^{13}\text{C}$

In sediment cores MD07-3076Q and MD07-3077, *Uvigerina* spp. and *C. kullenbergi* $\delta^{13}\text{C}$ differences are larger during the interglacial periods than during the glacial periods we have investigated (Table 1 and Figure 3). $\Delta\delta^{13}\text{C}_{\text{Uvi-Ck}}$ values during MIS 11 ($-0.83 \pm 0.23\text{‰}$, $N=16$) and MIS 12 ($-0.56 \pm 0.12\text{‰}$, $N=9$) are statistically distinguishable from each other ($p < 0.05$). During MIS 6 (Table 1 and Figure 3), we observe $\Delta\delta^{13}\text{C}_{\text{Uvi-Ck}}$ values of $-0.46 \pm 0.19\text{‰}$ ($N=13$), consistent with values observed during MIS 12 ($-0.56 \pm 0.12\text{‰}$, $N=9$). During the Holocene (Table 1 and Figure 3), $\Delta\delta^{13}\text{C}_{\text{Uvi-Ck}}$ is $-0.55 \pm 0.26\text{‰}$ ($N=19$), which is slightly greater although not significantly different from the LGM offset ($\Delta\delta^{13}\text{C}_{\text{Uvi-Ck}} = -0.31 \pm 0.20\text{‰}$, $N=11$; $p < 0.05$).

In Cape Basin core TN057-6GC, $\Delta\delta^{13}\text{C}_{\text{Uvi-Ck}}$ values during the Holocene ($\Delta\delta^{13}\text{C}_{\text{Uvi-Ck}} = -0.53 \pm 0.39\text{‰}$, $N=5$) and during the LGM ($\Delta\delta^{13}\text{C}_{\text{Uvi-Ck}} = -0.59 \pm 0.23\text{‰}$, $N=4$) are similar. A t test shows that these values are not significantly different from each other within the 95% confidence level.

Uvigerina spp. $\delta^{18}\text{O}$ agrees with *C. kullenbergi* $\delta^{18}\text{O}$ during interglacial ($\Delta\delta^{18}\text{O}_{\text{Uvi-Ck,mean}} = -0.13 \pm 0.22\text{‰}$, $N=40$) and glacial periods ($\Delta\delta^{18}\text{O}_{\text{Uvi-Ck,mean}} = -0.02 \pm 0.18\text{‰}$, $N=37$; Table 1), provided that an adjustment of 0.64‰ is applied to account for disequilibrium effects (Figures 3 and 4) [Shackleton and Opdyke, 1973; Duplessy et al., 1984]. Both mean interglacial and glacial $\Delta\delta^{18}\text{O}_{\text{Uvi-Ck}}$ values are statistically indistinguishable from zero within 95% confidence level ($p < 0.05$).

4.3. Benthic Foraminiferal Accumulation Rates

Benthic census counts show that *C. wuellerstorfi* is very rare in MD07-3076Q sediments of the last 22ka B.P. (Figure 5). *Cibicides* cf. *wuellerstorfi* occurs very sporadically, with a mean accumulation rate of 1 ± 1 specimen $\text{cm}^{-2} \text{ka}^{-1}$, primarily when *C. wuellerstorfi* is absent (Figure 5). *Cibicides kullenbergi* is the most abundant *Cibicides* species during the last deglaciation, with a mean accumulation rate of 7 ± 5 specimens $\text{cm}^{-2} \text{ka}^{-1}$ (Figure 5).

5. Discussion

5.1. Benthic Foraminifer Interspecies $\delta^{13}\text{C}$ Offsets

Our findings demonstrate a significant $\delta^{13}\text{C}$ difference between *C. kullenbergi* and *C. wuellerstorfi* (*s.l.*) in the sub-Antarctic Atlantic. This difference is noticeable during glacial periods ($\Delta\delta^{13}\text{C}_{\text{Ck-Cw,mean}} = -0.76 \pm 0.44\text{‰}$, $N=44$), while it is smaller during interglacial periods ($\Delta\delta^{13}\text{C}_{\text{Ck-Cw,mean}} = -0.19 \pm 0.31\text{‰}$, $N=63$). In contrast, $\delta^{18}\text{O}$ values agree between the species during both glacial and interglacial periods ($\Delta\delta^{18}\text{O}_{\text{Ck-Cw,mean}} = 0.02 \pm 0.12\text{‰}$ ($N=44$) and $\Delta\delta^{18}\text{O}_{\text{Ck-Cw,mean}} = 0.01 \pm 0.13\text{‰}$ ($N=63$), respectively; Table 1).

It has been previously shown that *C. kullenbergi* and *C. wuellerstorfi* $\delta^{13}\text{C}$ values are nearly identical in globally distributed core tops or in down-core sediments [Graham et al., 1981; Duplessy et al., 1984], which agrees with paired *C. kullenbergi* and *C. wuellerstorfi* (s.l.) $\delta^{13}\text{C}$ measurements in MIS 11 in core MD07-3077 (Figure 3). In contrast, core top studies from the upwelling region off the Moroccan margin show a significant $\delta^{13}\text{C}$ offset between *C. kullenbergi* and *C. wuellerstorfi* [Eberwein and Mackensen, 2006] that has also been observed in a downcore record from the high-productivity coastal area off Chile over both glacial and interglacial intervals of the last 1 Myr ($\Delta\delta^{13}\text{C}_{\text{Ck-Cw}} = -0.16 \pm 0.16\text{‰}$, $N = 114$; statistically significant within 95% confidence, $p < 0.05$) [Martínez-Méndez et al., 2013]. The glacial offsets we have found are much larger and similar to glacial $\delta^{13}\text{C}_{\text{Ck-Cw}}$ offsets in the deep, south Cape Basin [Hodell et al., 2003a] and in the Northeast Atlantic [Hodell et al., 2001]. Our comparison suggests that during interglacials, *C. wuellerstorfi* (s.l.) and *C. kullenbergi* $\delta^{13}\text{C}$ generally reflect bottom water $\delta^{13}\text{C}_{\text{DIC}}$ with uncertainties of a few tenths of per mil, while during glacial periods *C. wuellerstorfi* (s.l.) $\delta^{13}\text{C}$ and/or *C. kullenbergi* $\delta^{13}\text{C}$ may be significantly shifted away from bottom water $\delta^{13}\text{C}_{\text{DIC}}$.

The fact that specimens of *C. kullenbergi* and *C. wuellerstorfi* (s.l.) are neither consistently smaller nor larger during glacial periods compared to interglacials and that species of the genera *Cibicides* and *Cibicidoides* generally lack a significant $\delta^{13}\text{C}$ response to varying respiration rates [Corliss et al., 2002; Franco-Fraguas et al., 2011; Theodor et al., 2016] rules out a bias of observed $\Delta\delta^{13}\text{C}_{\text{Ck-Cw}}$ values due to ontogenetic isotope effects. We therefore explore two possible scenarios that could explain our data: (1) *C. kullenbergi* $\delta^{13}\text{C}$ has been biased toward light values relative to average deepwater $\delta^{13}\text{C}_{\text{DIC}}$, either due to a shift to a shallow infaunal microhabitat or due to phytodetritus effects that do not significantly affect *C. wuellerstorfi*, and/or (2) *C. wuellerstorfi* $\delta^{13}\text{C}$ is biased to heavy values, relative to long-term average conditions, by recording the sporadic (seasonal to centennial) occurrence of less depleted deepwater $\delta^{13}\text{C}_{\text{DIC}}$ at our core sites or by reflecting $\delta^{13}\text{C}_{\text{DIC}}$ from a different location.

5.2. Potential Biases of *C. kullenbergi* $\delta^{13}\text{C}$ from Bottom Water $\delta^{13}\text{C}_{\text{DIC}}$

A significant negative offset of glacial *C. kullenbergi* $\delta^{13}\text{C}$ from contemporaneous bottom water $\delta^{13}\text{C}_{\text{DIC}}$ may result from a microhabitat differentiation of *C. kullenbergi* and *C. wuellerstorfi*, which has been previously proposed [Hodell et al., 2001, 2003a], and/or from variations in the pore water $\delta^{13}\text{C}_{\text{DIC}}$ gradient. Even small microhabitat changes may have a significant influence on epibenthic foraminifer $\delta^{13}\text{C}$, because vertical pore water $\delta^{13}\text{C}_{\text{DIC}}$ gradients in marine sediments are large and vary depending on organic carbon rain rates and bottom water oxygen concentrations (Figure 6) [McCorkle and Emerson, 1988; McCorkle et al., 1997; Tachikawa and Elderfield, 2002]. These gradients may reach up to -1‰cm^{-1} , in particular near the surface [McCorkle et al., 1985], and can be accompanied by pore water carbonate ion variations that may have an additional (potentially counteracting) influence on benthic $\delta^{13}\text{C}$ [Spero et al., 1997; Bemis et al., 1998]; however, a carbonate ion-dependent carbon isotope effect on benthic foraminifera remains to be demonstrated and quantified. Small increases in the calcite precipitation depth of *C. kullenbergi* within the sediment may explain the observed glacial $\delta^{13}\text{C}_{\text{Ck-Cw}}$ gradient, if the microhabitat of *C. wuellerstorfi* (s.l.) did not shift simultaneously in the same direction (or by a lesser amount) and remained epibenthic.

Benthic faunal analyses off West Africa have suggested that the microhabitat of (epi)benthic foraminifera may shift deeper into the sediment depending on the availability of food [Linke and Lutze, 1993; Licari and Mackensen, 2005; Licari, 2006]. These studies indicate that the average living depth of benthic foraminifera, i.e., *Cibicides pachyderma* and *Cibicides lobatulus*, correlates with the $\delta^{13}\text{C}$ offset from bottom water $\delta^{13}\text{C}_{\text{DIC}}$, which ranges between -0.4 and 0‰ and may reach extremes of -0.8‰ owing to the effect of ^{13}C -depleted pore waters. It is possible that this adaptable behavior also applies to *C. kullenbergi* in the glacial sub-Antarctic Atlantic.

In order to test whether *C. kullenbergi* $\delta^{13}\text{C}$ reflects the $\delta^{13}\text{C}_{\text{DIC}}$ of an infaunal habitat rather than that of bottom water, we compare *C. kullenbergi* $\delta^{13}\text{C}$ with *Uvigerina* spp. $\delta^{13}\text{C}$. Most benthic foraminifera of the genus *Uvigerina*, including *Uvigerina peregrina*, are considered a shallow infaunal species [Zahn et al., 1986; Mackensen and Licari, 2004; Schweizer, 2006], as their highest abundance often occurs in the first two centimeters of the sediment [Corliss and Emerson, 1990; McCorkle et al., 1990, 1997; Jorissen et al., 1998; Fontanier et al., 2002; Mackensen and Licari, 2004]. These benthic foraminifera prefer moderate and perennial fluxes of organic matter [Lutze and Coulbourn, 1984; Zahn et al., 1986; Rathburn and Corliss, 1994] but have also been characterized as opportunistic species that may thrive under the supply of labile phytodetritus

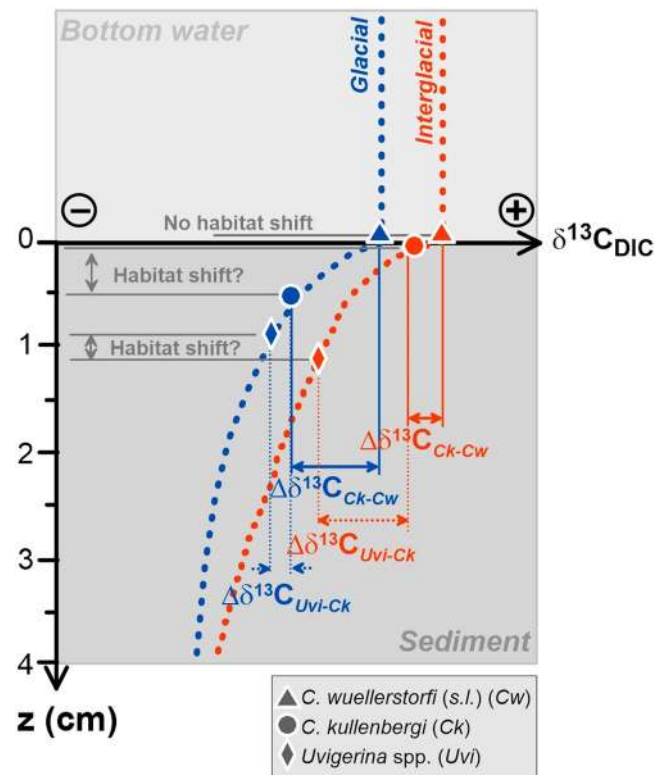


Figure 6. Potential scenarios of foraminiferal habitat shifts over glacial-interglacial cycles and the associated effects on their shell $\delta^{13}\text{C}$ values in the sub-Antarctic Atlantic. The symbols represent the average living depth (ALD) of the discussed benthic foraminifera (the microhabitat distribution of infaunal species likely resembles a Gaussian distribution). Glacial (blue) and interglacial (orange) pore water $\delta^{13}\text{C}_{\text{DIC}}$ gradients that would be caused by changes in bottom water $\delta^{13}\text{C}_{\text{DIC}}$ due to variations in bottom water oxygenation and changes in organic carbon fluxes are schematized after *McCorkle and Emerson [1988]*. Shifts of the calcification depth/ALD of *C. kullenbergi* (toward that of *Uvigerina* spp.) may be one explanation of observed glacial interspecies $\delta^{13}\text{C}$ offsets in the deep sub-Antarctic Atlantic. It is equally likely that significant offsets of *C. kullenbergi* $\delta^{13}\text{C}$ from bottom water $\delta^{13}\text{C}_{\text{DIC}}$ are caused by glacial-interglacial changes of the pore water $\delta^{13}\text{C}_{\text{DIC}}$ gradient with no change of an infaunal habitat depth of *C. kullenbergi*.

$\delta^{13}\text{C}$ offsets despite a common microhabitat [*Schmiedl et al., 2004; Theodor et al., 2016*], a significant glacial $\Delta\delta^{13}\text{C}_{\text{Uvi-Ck}}$ value is consistent among our core sites and over several past glacial periods (Figures 3 and 4). We therefore conclude that if *C. kullenbergi* had an endobenthic habitat during glacials, it would have been shallower than that of *Uvigerina* spp., limiting the possible microhabitat effect, and thus the offset from $\delta^{13}\text{C}_{\text{DIC}}$ of the overlying bottom water during these time intervals. A negative bias due to ^{13}C -depleted pore water is supported by the observation of lower Holocene *C. kullenbergi* $\delta^{13}\text{C}$ than modern $\delta^{13}\text{C}_{\text{DIC}}$ at the MD07-3076Q core site (Figure 3), which may have been larger during last glacial periods, for instance as a response to enhanced glacial organic carbon fluxes [*Anderson et al., 2014; Gottschalk et al., 2016*]. However, a close match of *C. kullenbergi* and *C. wuellerstorfi* $\delta^{13}\text{C}$ during MIS11 (-0.09 ± 0.19 , $N=52$) suggest that this bias was negligible during some interglacials.

Cibicides kullenbergi $\delta^{13}\text{C}$ may also significantly deviate from bottom water $\delta^{13}\text{C}_{\text{DIC}}$ during glacials if it calcified in a ^{13}C -depleted phytodetritus layer forming at the seafloor [*Mackensen et al., 1993*]. This would explain observed glacial $\Delta\delta^{13}\text{C}_{\text{Ck-Cw}}$, provided that *C. wuellerstorfi* (s.l.) was not affected by it (for instance owing to having an habitat above the phytodetritus layer and/or living at a time different from *C. kullenbergi* within the ~200–400-year time span that one sediment sample represents). The overprint of epibenthic foraminifer

[e.g., *Fontanier et al., 2002*]. Owing to their slightly deeper microhabitat, *Uvigerina* spp. $\delta^{13}\text{C}$ shows lower $\delta^{13}\text{C}$ values than epibenthic foraminifera [e.g., *Tachikawa and Elderfield, 2002*], and this gradient reflects changes in the organic carbon supply to the seafloor [*Zahn et al., 1986; McCorkle et al., 1990*]. Although the exact position of *Uvigerina* spp. in the upper sediment column throughout the intervals investigated remains unknown, we assume here that *Uvigerina* spp. $\delta^{13}\text{C}$ consistently monitors $\delta^{13}\text{C}_{\text{DIC}}$ of an infaunal habitat in the sub-Antarctic Atlantic (i.e., within the upper ~2 to 3 cm of the sediment [e.g., *McCorkle et al., 1997; Jorissen et al., 1998; Fontanier et al., 2002*]) and provides a benchmark of an *Uvigerina*-like, endobenthic habitat for a comparison with *C. kullenbergi* $\delta^{13}\text{C}$.

Our data indicate that *C. kullenbergi* $\delta^{13}\text{C}$ was mostly higher than *Uvigerina* spp. $\delta^{13}\text{C}$ during the studied time intervals. The $\delta^{13}\text{C}$ gradient between *C. kullenbergi* and *Uvigerina* spp. remained constant during glacial and interglacial periods (Figures 3 and 4 and Table 1); only during MIS 12 $\Delta\delta^{13}\text{C}_{\text{Uvi-Ck}}$ was significantly smaller than during MIS 11 ($p=0.01$). Although the uncertainty of our *Uvigerina* spp. $\delta^{13}\text{C}$ record owing to possible ontogenetic size effects within our narrow fraction of 212–350 μm may be up to 0.4‰ [*Schumacher et al., 2010; Theodor et al., 2016*] and benthic foraminifera of the genus *Uvigerina* may have species-specific

$\delta^{13}\text{C}$ caused by the incorporation of ^{13}C -depleted CO_2 that accumulates in these phytodetritus layers is suggested to be 0.4‰ on average, but negative deviations of up to 0.9‰ have also been observed [Mackensen *et al.*, 1993; Mackensen and Bickert, 1999]. Although the average phytodetritus effect of 0.4‰ is smaller than the mean glacial difference between *C. kullenbergi* and *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ and was primarily shown for *C. wuellerstorfi* in the South Atlantic [e.g., Mackensen *et al.*, 1993], we cannot rule out that it was not exceptionally strong (unprecedented) for *C. kullenbergi* at our core sites during past glacials, explaining deviations of up to $-1.21 \pm 0.14\text{‰}$ (Table 1).

5.3. Potential Bias of *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ from Bottom Water $\delta^{13}\text{C}_{\text{DIC}}$

We now assess the possibility that glacial *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ is positively offset from average bottom water $\delta^{13}\text{C}_{\text{DIC}}$ due to an allochthonous nature of *C. wuellerstorfi* (*s.l.*) specimens or due to calcification in a short-term ^{13}C -enriched environment. We make use of benthic foraminifer abundance variations to discuss these two effects.

As Figure 5 shows, *C. wuellerstorfi* (*s.l.*) is scarce in MD07-3076Q. This may be an indication that specimens found in this core are allochthonous, being transported post mortem to our study site via bottom water currents or nepheloid layers along the mid-ocean ridge from shallower water levels. If *C. wuellerstorfi* (*s.l.*) lives elevated above the sediment [Lutze and Thiel, 1989], it may be particularly sensitive to these processes. This scenario is in line with similar benthic foraminifer $\delta^{18}\text{O}$ and higher $\delta^{13}\text{C}$ found at the crest of the sub-Antarctic mid-ocean ridge (~2.7 km water depth) [Mackensen *et al.*, 2001], from where we would expect allochthonous *C. wuellerstorfi* (*s.l.*) in MD07-3076Q and MD07-3077 to originate. However, this explanation requires a very fortuitous situation both in the central and southeast sub-Antarctic Atlantic, i.e., net volume transport by bottom currents toward our core sites, very high current velocities, and a sufficient number of specimens with elevated habitat to be transported downslope. Although the impact of this scenario on observed $\Delta\delta^{13}\text{C}_{\text{CK-CW}}$ during past glacials is therefore likely small, it may be relevant for other study sites, in particular near or at continental slopes [e.g., Duros *et al.*, 2012].

Abundances of benthic foraminifera in marine sediments also reflect the extent to what they are adapted to the prevailing ecological and hydrographic conditions [Loubere and Fariduddin, 2003]. High accumulation rates of *C. kullenbergi* in MD07-3076Q imply that this species may cope best with the prevailing seasonal to multidecadal ecological conditions, e.g., higher export production rates during glacial periods, which may have been unfavorable for *C. wuellerstorfi* (*s.l.*) at our core sites (Figure 5). The sparse occurrence of *C. wuellerstorfi* and *C. cf. wuellerstorfi* in core MD07-3076Q (Figure 5) might therefore indicate that its $\delta^{13}\text{C}$ reflects only short-term (annual or seasonal) environmental conditions that deviate from average (long-term) bottom water $\delta^{13}\text{C}_{\text{DIC}}$. Such temporally constrained conditions may be related to short-term (seasonal) changes in the amount or quality of carbon exported [Diz and Barker, 2016] and with higher bottom water oxygen levels, for instance during the incursion of well-ventilated water masses, such as North Atlantic Deep Water (NADW) or unmixed Antarctic Bottom Water [e.g., Mackensen and Bickert, 1999], induced by turbulent mixing or frontal instabilities in this region [e.g., Naveira Garabato *et al.*, 2004; Sheen *et al.*, 2012, 2014]. The latter is only suitable to explain $\Delta\delta^{13}\text{C}_{\text{CK-CW}}$ if the $\delta^{18}\text{O}$ of the sporadically admixed waters was not very different from the waters that bathed our core sites in the long-term (Figures 3 and 4), making temporal changes in the carbon export explaining our data more likely. These effects may also explain the deviation of Holocene *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ from modern $\delta^{13}\text{C}_{\text{DIC}}$ at the MD07-3076Q core site (Figure 3) and may have been more pronounced during glacial intervals. However, as short-term environments are difficult to reconstruct from the available sedimentary records, their impact on sub-Antarctic Atlantic glacial $\Delta\delta^{13}\text{C}_{\text{CK-CW}}$ values remains to be shown.

6. Implications for Paleooceanographic Reconstructions

6.1. Bottom Water $\delta^{13}\text{C}_{\text{DIC}}$ Reconstructions Based on *Cibicidoides* spp. $\delta^{13}\text{C}$

Many paleooceanographic reconstructions rely on a combination of different species of the *Cibicidoides* and *Cibicides* genera (e.g., "*Cibicidoides* spp.") to compensate for the scarcity of each species in marine sediment cores (Figure 7) [e.g., Mackensen *et al.*, 2001; Hodell *et al.*, 2003a; Gebhardt *et al.*, 2008; Hoffman and Lund, 2012]. For example, *Cibicidoides* spp. $\delta^{13}\text{C}$ data from the Brazil margin (~30°S) below 3.5 km water depth [Hoffman and Lund, 2012] show a mean 1 σ standard deviation of replicate measurements

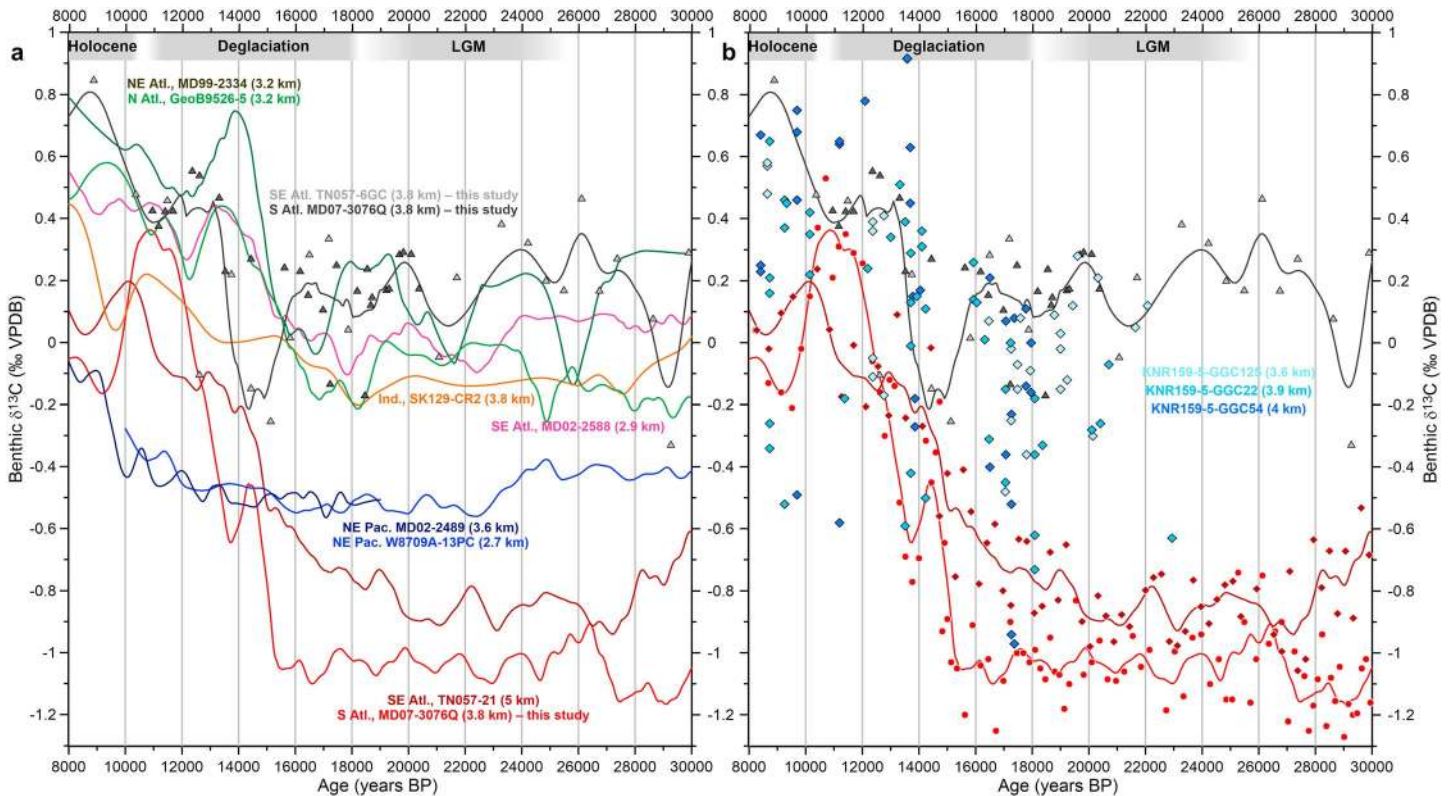


Figure 7. (a) Composite *C. wuellerstorfi* and *C. cf. wuellerstorfi* $\delta^{13}\text{C}$ record obtained from TN057-6GC (light grey) and MD07-3076Q (dark grey) (the black line represents the 1000-year running average) in comparison to benthic $\delta^{13}\text{C}$ from other ocean regions as in Figure 1 (only 1000-year running averages are shown). (b) Comparison of the *Cibicidoides* spp. $\delta^{13}\text{C}$ record from TN057-21 (dark red) [Ninnemann et al., 1999], *C. kullenbergi* $\delta^{13}\text{C}$ from MD07-3076Q (red) [Waelbroeck et al., 2011], the composite *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ record obtained from TN057-6GC and MD07-3076Q (black lines and grey symbols as in Figure 7a), and *Cibicidoides* spp. $\delta^{13}\text{C}$ data from the Brazil margin (light to dark blue) [Hoffman and Lund, 2012]; locations of the cores are given in Table S3 in the supporting information.

(KNR159-5-22GGC: $0.31 \pm 0.19\text{‰}$, $N=12$; KNR159-5-54GGC: $0.35 \pm 0.24\text{‰}$, $N=11$) that exceeds the intraspecies *C. kullenbergi* ($0.15 \pm 0.13\text{‰}$, $N=129$) and *C. wuellerstorfi* $\delta^{13}\text{C}$ variability ($0.09 \pm 0.08\text{‰}$, $N=21$) observed in MD07-3076Q and MD07-3077 by more than a factor of 2 (Figure 7b). The upper limit of these Brazil margin $\delta^{13}\text{C}$ data broadly coincides with the composite *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ record of the deep sub-Antarctic Atlantic, whereas the lower limit broadly matches *C. kullenbergi* $\delta^{13}\text{C}$ from the deep sub-Antarctic Atlantic (Figure 7b). The large spread of Brazil margin $\delta^{13}\text{C}$ values may be significantly influenced by mixed analyses of “low- $\delta^{13}\text{C}$ ” *C. kullenbergi* and/or “high- $\delta^{13}\text{C}$ ” *C. wuellerstorfi* (*s.l.*), as well as by bioturbational sediment mixing and variations in bottom water $\delta^{13}\text{C}_{\text{DIC}}$. Marked interspecies offsets may increase the uncertainty of Atlantic seawater $\delta^{13}\text{C}_{\text{DIC}}$ reconstructions based on benthic $\delta^{13}\text{C}$ compilations that incorporate mixed-species (*Cibicides/Cibicidoides* spp.) $\delta^{13}\text{C}$ [e.g., Duplessy et al., 1988; Sarthein et al., 1994; Curry and Oppo, 2005; Oliver et al., 2010; Hesse et al., 2011; Peterson et al., 2014].

6.2. Bottom Water $\delta^{13}\text{C}_{\text{DIC}}$ Reconstructions Based on *C. wuellerstorfi* and *C. cf. wuellerstorfi* $\delta^{13}\text{C}$

High glacial *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ values of a deep sub-Antarctic Atlantic composite record combining MD07-3076Q and TN057-6GC records are broadly consistent with data from the deep Brazil Margin (not shown) [Oppo and Horowitz, 2000; Lund et al., 2015], the central South Atlantic (not shown) [Jonkers et al., 2015], the deep northern Cape Basin (not shown) [Bickert and Wefer, 1999; Wei et al., 2015], the deep Iberian Margin [Shackleton et al., 2000; Skinner et al., 2007], and the Agulhas Plateau [Ziegler et al., 2013] (Figure 7a). The similarity of the deep sub-Antarctic Atlantic *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ and data from north of the sub-Antarctic Front, in particular from the Iberian Margin, may support the notion that occasional southward incursions of well-ventilated and ^{13}C -rich water masses, such as NADW from just north of the core sites, may influence the *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ records, although it falls short of proving it. The assumption that *C. wuellerstorfi* (*s.l.*) may respond to a particular (seasonal) flux or quality of carbon exported and/or to a

particular oceanographic setting may be an explanation for its relative low abundance in the sediment during the last deglaciation and calls for caution in interpreting $\delta^{13}\text{C}$ of very low abundant benthic foraminifer species in general.

6.3. Bottom Water $\delta^{13}\text{C}_{\text{DIC}}$ Reconstructions Based on *C. kullenbergi* $\delta^{13}\text{C}$

Negative "*Cibicidoides* spp." $\delta^{13}\text{C}$ values similar to *C. kullenbergi* $\delta^{13}\text{C}$ in our study cores have been observed in last glacial sediments throughout the sub-Antarctic zone (between the sub-Antarctic and sub-Tropical Fronts; Figure S4 in the supporting information) [e.g., Charles *et al.*, 1996; Ninnemann *et al.*, 1999; Mackensen *et al.*, 2001]. These values remain among the most negative values observed in the entire last glacial ocean [e.g., Hesse *et al.*, 2011; Peterson *et al.*, 2014]. Possible explanations for lower $\delta^{13}\text{C}_{\text{DIC}}$ reconstructed in the deep sub-Antarctic Atlantic than in the North Pacific include (i) glacial changes in ocean circulation and in deep-water formation sites [Michel *et al.*, 1995; Ninnemann and Charles, 2002; Toggweiler *et al.*, 2006], (ii) a strong glacial density stratification of the ocean interior in the southern high-latitude Atlantic [Adkins *et al.*, 2002; Bouttes *et al.*, 2011], (iii) significant preformed bottom water $\delta^{13}\text{C}$ variations due to alternating modes of formation of Southern Ocean deep waters [Mackensen *et al.*, 2001; Martínez-Méndez *et al.*, 2009; Mackensen, 2012] or different source regions of southern sourced deep waters along the Antarctic coast [McCave *et al.*, 2008], and (iv) a large interbasin redistribution of DIC from the Pacific to the Atlantic Ocean over glacial-interglacial transitions [Schmittner *et al.*, 2007]. However, these explanations assume a reliable representation of bottom water $\delta^{13}\text{C}_{\text{DIC}}$ by *Cibicidoides* spp. and *C. kullenbergi* $\delta^{13}\text{C}$. Above we have discussed some hypotheses why this one-to-one representation may be flawed—some of which have been discussed earlier [Ninnemann and Charles, 2002]. We conclude that the magnitude and significance of a bias of *C. kullenbergi* $\delta^{13}\text{C}$ and/or *C. wuellerstorfi* (*s.l.*) $\delta^{13}\text{C}$ from bottom water $\delta^{13}\text{C}_{\text{DIC}}$ cannot be unambiguously resolved based on presented data from our study cores.

Two arguments have been previously advanced to emphasize the validity of South Atlantic *C. kullenbergi* (or synonymously, *C. mundulus*) and *Cibicides/Cibicidoides* spp. $\delta^{13}\text{C}$ as an indicator of low glacial bottom water $\delta^{13}\text{C}_{\text{DIC}}$ [Ninnemann and Charles, 2002], although other influences have been acknowledged [Charles *et al.*, 1996]. First, low last glacial benthic $\delta^{13}\text{C}$ values can be reproduced spatially (Figure S4 in the supporting information) and also temporally during older glacial Pleistocene periods [e.g., Oppo *et al.*, 1990; Hodell *et al.*, 2003a]. Second, the characteristic low glacial *C. kullenbergi* $\delta^{13}\text{C}$ is also mirrored in planktonic (*N. pachyderma* s.) $\delta^{13}\text{C}$ in the Cape Basin [Hodell *et al.*, 2003a], suggesting that the planktonic record reflects bottom water $\delta^{13}\text{C}_{\text{DIC}}$ that is recorded in benthic foraminifer $\delta^{13}\text{C}$ [Ninnemann and Charles, 2002]. We discuss these arguments below.

Most core sites with low benthic $\delta^{13}\text{C}$ during the last glacial period are located near or within the sub-Antarctic zone (Figure S4 in the supporting information). North of this zone, higher glacial benthic $\delta^{13}\text{C}$ values ($> -0.6\text{‰}$) are observed [e.g., Oppo *et al.*, 1990; Bickert and Wefer, 1999; Hodell *et al.*, 2003a; Martínez-Méndez *et al.*, 2009; Hoffman and Lund, 2012]. Proxy data indicate that increases in aeolian dust supply caused an increase in organic carbon fluxes throughout the sub-Antarctic Atlantic during the LGM [e.g., Anderson *et al.*, 2014], and bottom water oxygen levels have declined in the southern high-latitude Atlantic during this interval [Gottschalk *et al.*, 2016]. If active shifts of the microhabitat or changes within the (infaunal) microhabitat of *C. kullenbergi* are ecologically motivated (for instance, as a response to increased organic carbon fluxes or the seasonal supply of labile food sources) [e.g., Licari, 2006] and *C. kullenbergi* dominates the *Cibicides/Cibicidoides* population, a bias of *C. kullenbergi* and *Cibicides/Cibicidoides* spp. $\delta^{13}\text{C}$ may be possible during glacial periods throughout the (sub-)Antarctic zone. This contention, however, remains to be tested.

Planktonic $\delta^{13}\text{C}$ records have been used to suggest that the benthic $\delta^{13}\text{C}$ signal in the sub-Antarctic Atlantic is not spurious [Ninnemann and Charles, 2002; Hodell *et al.*, 2003a], although vital effects render a direct comparison of planktonic $\delta^{13}\text{C}$ and benthic $\delta^{13}\text{C}$ difficult [Kohfeld *et al.*, 2000; Gottschalk *et al.*, 2015]. However, two observations may support this suggestion: (1) benthic and planktonic $\delta^{13}\text{C}$ values in the Cape Basin resemble each other, reflecting the influence of bottom water $\delta^{13}\text{C}_{\text{DIC}}$, and (2) the relative magnitude of glacial-interglacial changes in planktonic $\delta^{13}\text{C}$ south of the Polar Front in the Antarctic divergence zone, where vertical mixing of the water column is expected and deep waters may reach the surface [Mackensen *et al.*, 1994; Hodell *et al.*, 2003b], is close to glacial-interglacial *C. kullenbergi* (or *Cibicidoides* spp.) $\delta^{13}\text{C}$ changes in the sub-Antarctic [Ninnemann and Charles, 2002; this study]. However, planktonic $\delta^{13}\text{C}$ records do not reproduce the low benthic $\delta^{13}\text{C}$ values at all sites [e.g., Michel *et al.*, 1995; Charles *et al.*, 1996; Gottschalk *et al.*, 2015],

and in MD07-3076Q, *N. pachyderma* (s.) $\delta^{13}\text{C}$ closely resembles high *C. wuellerstorfi* (s.l.) $\delta^{13}\text{C}$ rather than the low *C. kullenbergi* $\delta^{13}\text{C}$ record [Gottschalk et al., 2015]. This shows that a better understanding of the controls governing sub-Antarctic Atlantic planktonic foraminifer $\delta^{13}\text{C}$ (e.g., export production, air-sea gas exchange, and vertical mixing) is required to reconcile the observed benthic $\delta^{13}\text{C}$ patterns and to validate low glacial sub-Antarctic bottom water $\delta^{13}\text{C}_{\text{DIC}}$.

7. Conclusions

Paired *C. kullenbergi* and *C. wuellerstorfi* (s.l.) $\delta^{13}\text{C}$ analyses in several sub-Antarctic Atlantic sediment cores over three glacial-interglacial cycles show a significant $\delta^{13}\text{C}$ difference during glacial periods of $\Delta\delta^{13}\text{C}_{\text{CK-CW}} = -0.76 \pm 0.44\text{‰}$, despite a very close agreement of their $\delta^{18}\text{O}$ values. This offset is significantly higher than the average interglacial offset ($\Delta\delta^{13}\text{C}_{\text{CK-CW}} = -0.19 \pm 0.31\text{‰}$). We have ruled out ontogenetic effects as cause of our observations and have subsequently discussed several possible scenarios: (1) *C. kullenbergi* $\delta^{13}\text{C}$ is biased toward lighter values owing to the influence of low $\delta^{13}\text{C}_{\text{DIC}}$ in an infaunal microhabitat or in a benthic phytodetritus layer, while *C. wuellerstorfi* (s.l.) is not affected, and (2) *C. wuellerstorfi* (s.l.) $\delta^{13}\text{C}$ is biased to heavy values, by being transported from elsewhere (downslope) or by recording the sporadic occurrence of a microenvironment with higher $\delta^{13}\text{C}_{\text{DIC}}$, while *C. kullenbergi* is not affected. We found that neither of these explanations can be ruled out unequivocally. However, our observations are important for glacial $\delta^{13}\text{C}$ interpretations and raise important questions on the universal consistency of benthic $\delta^{13}\text{C}$ as indicator of long-term average bottom water $\delta^{13}\text{C}_{\text{DIC}}$.

Due to the complexity of *Cibicides* morphotypes presented here, and the inherent subjectivity of the process of picking foraminifera, we recommend the careful documentation of selected specimens of a given species or morphotype, when possible, for example by supplying photographs together with the respective $\delta^{13}\text{C}$ data or a detailed taxonomic list. The observed divergence of $\delta^{13}\text{C}$ measured in apparently epibenthic foraminifera in the sub-Antarctic Atlantic underscores the need for multiproxy approaches for the reconstruction of ocean circulation changes in the past. In order to avoid adding different biases, stable $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ measurements should be performed on monospecific benthic foraminifer samples only, whenever possible. This will allow a clearer picture of the reconstructed benthic and/or bottom water $\delta^{13}\text{C}$ variability.

Notwithstanding the possible caveats of benthic $\delta^{13}\text{C}$ in the cores we have studied, we suggest that benthic $\delta^{13}\text{C}$ of abundant *Cibicides* species likely remains a good proxy for bottom water $\delta^{13}\text{C}_{\text{DIC}}$ in the deep sub-Antarctic Atlantic, although it may be associated with a larger uncertainty than previously assumed. It remains to be shown which benthic foraminifer species is the most trustworthy in representing bottom water $\delta^{13}\text{C}_{\text{DIC}}$ in particular in the sub-Antarctic Atlantic.

Appendix A

Cibicides wuellerstorfi (Schwager), 1866

- *Anomalina wuellerstorfi* Schwager, 1866, p. 258, pl. 7, Figures 105 and 107.
- *Truncatulina wuellerstorfi* (Schwager) [Brady, 1884], p. 662, pl. 93, Figure 9.
- *Planulina wuellerstorfi* (Schwager) [Phleger and Parker, 1951], p. 33, pl. 18, Figure 11.
- *Planulina wuellerstorfi* (Schwager) [Phleger et al., 1953], p. 49, pl. 11, Figures 1 and 2.
- *Cibicides wuellerstorfi* (Schwager) [Parker, 1958], p. 275, pl. 4, Figures 41 and 42.
- *Cibicidoides wuellerstorfi* (Schwager) [Parker, 1964], pp. 624–625, pl. 100, Figure 29.
- *Cibicides wuellerstorfi* (Schwager) [Boltovskoy, 1978], pl. 3, Figures 19–21.
- *Planulina wuellerstorfi* (Schwager) [Corliss, 1979], pp. 7–8, pl. 2, Figures 13–16.
- *Cibicidoides wuellerstorfi* (Schwager) [Mead, 1985], pl. 6, Figures 1 and 2.
- *Planulina wuellerstorfi* (Schwager) [Van Morkhoven et al., 1986], pp. 48, 50, pl. 14, Figures 1 and 2.
- *Fontbotia wuellerstorfi* (Schwager) [Loeblich and Tappan, 1988], p. 583, pl. 634, Figures 10–12; pl. 635, Figures 1–3.
- *Cibicides wuellerstorfi* (Schwager) [Sen Gupta, 1989], p. 706, Figures 1–7.
- *Planulina wuellerstorfi* (Schwager) [Corliss, 1991], pl. 1, Figures 1, 2, and 5.
- *Cibicides wuellerstorfi* (Schwager) [Gupta, 1994], pl. 5, Figures 8 and 9.
- *Cibicides wuellerstorfi* (Schwager) [Schweizer, 2006], pl. 11a–11l.

Cibicides kullenbergi Parker, 1953

- *Cibicides kullenbergi* Parker [Phleger et al., 1953], p. 49, pl. 11, Figures 7 and 8.
- *Cibicides kullenbergi* Parker [Pflum and Frerichs, 1976], pl. 2, Figures 6–8.
- *Cibicidoides kullenbergi* (Parker) [Lohmann, 1978], p. 29, pl. 2, Figures 5–7.
- *Cibicidoides kullenbergi* (Parker) [Corliss, 1979], p. 10, pl. 3, Figures 4–6.
- *Cibicidoides cf. kullenbergi* (Parker) [Mead, 1985], p. 242, pl. 6, Figures 6a and 6b.
- *Cibicidoides mundulus* (Brady, Parker, and Jones) [Loeblich and Tappan, 1988], p. 572, pl. 626, Figures 1–3.
- *Cibicidoides kullenbergi* (Parker) [Corliss, 1991], pl. 1, Figures 6, 8, and 9.
- *Cibicides kullenbergi* Parker [Gupta, 1994], pl. 1, Figures 6, 8, and 9.
- *Cibicides kullenbergi* Parker [Schweizer, 2006], pl. 4a–4m.

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