

## PLANKTONIC FORAMINIFERAL ENDEMISM AT SOUTHERN HIGH LATITUDES FOLLOWING THE TERMINAL CRETACEOUS EXTINCTION

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### ABSTRACT

Austral planktonic foraminiferal assemblages from immediately above the Cretaceous/Paleogene (K/Pg) boundary at Ocean Drilling Program Hole 690C (Maud Rise, Weddell Sea) and International Ocean Drilling Program Hole U1514C (southeast Indian Ocean) show a much different record of post-extinction recovery than anywhere outside the circum-Antarctic region. Species of *Woodringina* and *Parvularugoglobigerina*, genera with well-documented evolutionary successions within the early Danian P0 and P $\alpha$  biozones at tropical/subtropical and mid-latitude localities, are absent from southern high latitude sequences. This study proposes new criteria for biostratigraphic correlation of the lowermost Danian Antarctic Paleocene AP0 and AP1 Zones using stratophenetic observations from Scanning Electron Microscope images of lower Danian planktonic foraminifera at deep-sea sites in the southern South Atlantic and southern Indian Ocean. The small but distinctive species *Turborotalita nikolasi* (Koutsoukos) is a highly reliable index species for the lowermost Danian as it consistently occurs immediately above the K/Pg boundary at multiple southern high latitude sites, which is consistent with its distribution at middle and low latitudes. Also useful for cross-latitude correlation is *Parasubbotina neanika* n. sp., which first appears within the lowermost Danian worldwide. The geographic distribution of the New Zealand species *Antarcticella pauciloculata* (Jenkins) and *Zeauvigerina waiparaensis* (Jenkins), as well as *Eoglobigerina maudrisensis* n. sp. from just above the K/Pg in the southern South Atlantic and southern Indian Ocean, helps define the extent of the Austral Biogeographic Province and provides evidence for marine communication via marine seaways across Antarctica. While *An. pauciloculata* was previously considered a benthic species, new stable isotope evidence demonstrates that it lived a planktonic mode of life. It is possible this species evolved from a benthic ancestor and that the benthic to planktonic transition occurred through an intermediate tychoepelagic lifestyle at a time when calcareous plankton were less abundant as a result of the terminal Cretaceous mass extinction.

### INTRODUCTION

The mass extinction at the end of the Cretaceous resulted in the abrupt loss of over 90% of Maastrichtian species of planktonic foraminifera (e.g., Smit, 1982; D'Hondt et al.,

1996; Schulte et al., 2010) and calcareous nannofossils (e.g., Pospichal, 1996; Bernaola & Monechi, 2007). The change in carbon cycling associated with these extinctions led to a rapid collapse in the surface to deep ocean carbon isotopic gradient, which signifies a drop in the flux of organic matter to the seafloor (D'Hondt et al., 1998; Coxall et al., 2006; Birch et al., 2016). The calcareous plankton extinctions also led to an immediate decrease in carbonate accumulation rates (e.g., D'Hondt, 2005). Absence of extinctions among deep-sea benthic foraminifera across the Cretaceous-Paleogene (K/Pg) boundary and minimal changes in their community structure (Alegret & Thomas, 2007, 2013), as well as geochemical indicators of continued surface water productivity at some sites during the early Danian (Hull & Norris, 2011), indicate that a post-impact decrease in export productivity did not occur everywhere in the world ocean. Restoration of the biological pump to pre-impact levels is thought to have taken at least 1.8 m.y. (Birch et al., 2016).

According to Olsson et al. (1999), all Cenozoic lineages that radiated after the K/Pg extinction were descended from three Cretaceous species: *Guembelitra cretacea*, *Muricohedbergella holmdelensis*, and *Mu. monmouthensis*. Although additional Cretaceous species may have survived the extinction event (e.g., Arenillas & Arz, 2017), gaps in their lower Danian stratigraphic ranges and strongly diachronous highest occurrences within the Danian suggest some or most of these post-impact distributions could be an artifact of sediment reworking and/or bioturbation (e.g., Huber, 1996; MacLeod & Huber, 1996). If additional species did survive the K/Pg extinction, there is no evidence that they were ancestral to any of the Cenozoic planktonic foraminiferal lineages.

Studies of low to mid-latitude sites indicate that post-impact planktonic foraminiferal diversification was rapid, with at least 18 species belonging to eight genera appearing within the first 300 kyr after the impact (Coxall et al., 2006). According to a detailed taxonomic study by Koutsoukos (2014), at least six new species assigned to three genera appeared within Zone P0 (*sensu* Berggren et al., 1995), which spans the first 40 kyr of the Danian (Ogg et al., 2016). Species diversity did not return to pre-extinction levels until the Paleocene-Eocene boundary, ~10 m.y. after the extinction (Coxall et al., 2006).

The record of post-impact recovery of planktonic foraminifera at southern high latitudes differs from the record at lower latitudes most notably in the absence of several taxa, including species used to biostratigraphically subdivide the Danian. The most complete austral deep-sea K/Pg boundary sequences drilled by the Ocean Drilling Program (ODP) include one on Maud Rise in the southern South Atlantic (ODP Hole 690C; Stott & Kennett, 1990) and the other on Kerguelen Plateau in the southern Indian Ocean (ODP Hole 738C; Huber, 1991). Both sequences yielded Ir enrichment peaks at the biostratigraphically

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defined boundary (Michel et al., 1990; Schmitz et al., 1991). At both locations the zonal marker species for the standard Pa Zone of Berggren et al. (1995), *Parvularugoglobigerina eugubina*, is absent as are other species of *Parvularugoglobigerina* and species of *Woodringina*. To facilitate correlation among the southern high latitude deep-sea sites, Huber & Quillevéré (2005) erected a separate Antarctic Paleocene (AP) zonal scheme using distinctive species that can be reliably correlated among the distant circum-Antarctic sites. Their definitions for lower Danian Zones AP0 and AP1 are used herein and are discussed below.

The main objective of the present study is to document planktonic foraminiferal distributions across the K/Pg boundary at high southern latitudes using samples from a recently drilled site in the southeast Indian Ocean (IODP Site U1514) and reexamination of species distributions in existing samples from a southern South Atlantic site (ODP Site 690). These observations provide a basis for revising the biostratigraphic scheme for circum-Antarctic correlation of the lower Danian. Paleobiogeographic implications for the species distributions at these and additional circum-Antarctic sites are also discussed. Scanning Electron Microscope imaging was extensively employed for specimens from lowermost Danian samples to ensure accurate species identification of the small-sized tests. Additional imaging using 2D nannoCT technology and comparison of oxygen and carbon isotopic values among co-occurring planktonic and benthic species were undertaken to try to determine whether the enigmatic austral species *Antarcticella pauciloculata* lived a planktonic or benthic mode of life.

## MATERIAL AND METHODS

Our study primarily focuses on K/Pg samples from two sites: IODP Hole U1514C, drilled in 3,850 m water depth on the Mentelle Basin southwest of Australia (33°7.2327'S, 113°5.4672'E) and ODP Hole 690C, drilled on Maud Rise in the southern South Atlantic (65°10'S, 1°12'E). These and additional sites discussed in this study were located between 60°S and 65°S paleolatitude (Fig. 1). Sample depths for these sites are expressed as meters below seafloor (mbsf) and sample IDs use standard DSDP/ODP/IODP conventions listing, in order: site, hole, core-section [including core-catcher (CC)], and cm interval.

Samples from Hole U1514C were soaked in tap water, washed over a 38- $\mu$ m sieve, and dried at 50°C. Foraminifera in the washed residue were identified and picked under a stereomicroscope and placed on microslides. Abundance counts of planktonic vs. benthic foraminifera (Table 1; Fig. 2) were made on the >38- $\mu$ m fraction by microsplitting samples with the goal of obtaining at least 300 planktonic specimens; in samples with <300 planktonic specimens, all individuals present were counted. Abundance counts for planktonic species are expressed as percentages relative to the sum of planktonic and benthic specimens. Qualitative abundance values for foraminifera, calcispheres, and fish teeth relative to sediment particles in the >38- $\mu$ m fraction are presented as follows: A = abundant (>30%), C = common (10–30%), F = few (5–10%), R = rare (<5%), B = barren (none). Qualitative planktonic foraminiferal abundance estimates relative to the total plankton assemblage are presented as follows:

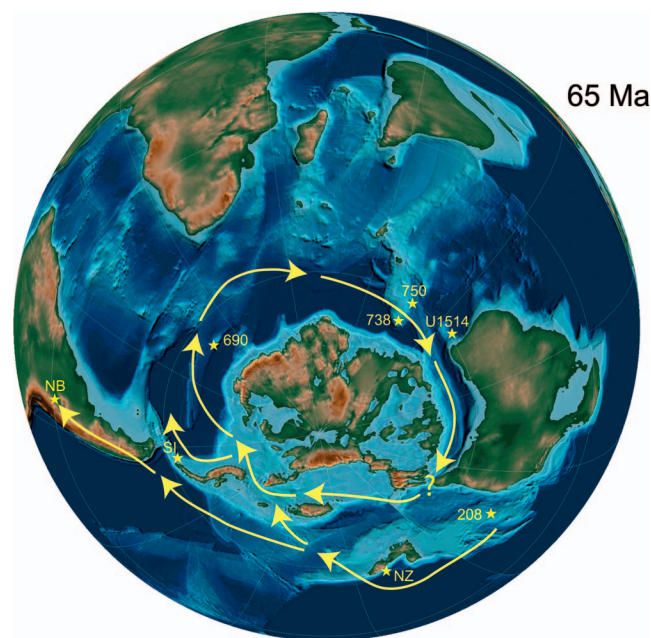


FIGURE 1. Paleogeographic map from Scotese (2016) for 65 Ma showing location of sites discussed in this study. NB = Neuquén Basin; NZ = New Zealand; SI = Seymour Island.

A = abundant (>20%), C = common (10–20%), F = few (5–10%), R = rare (1–5%), and P = present. Foraminiferal preservation as viewed under the light microscope was recorded as: E = excellent [most specimens have a “glassy” appearance indicating little recrystallization or evidence of overgrowth, dissolution, or infilling and abrasion]; G = good [some specimens show minor evidence of diagenetic overgrowth, dissolution, or abrasion; recrystallization may or may not have occurred]; M = moderate [most specimens show evidence of overgrowth, dissolution, and abrasion; tests infilled with cement or indurated sediment obscuring apertures]; P = poor [most or all specimens show substantial diagenetic overgrowth (including infilling), dissolution, and abrasion; foraminifera can be fragmentary and difficult to identify because of major overgrowth and/or dissolution].

Lower Danian samples from Hole 690C were obtained from washed residues previously used by Thomas (1990) and Stott & Kennett (1990). These and Maastrichtian samples studied by Huber (1990) were all washed over a 63- $\mu$ m sieve. Because specimens had been previously removed from these samples, species distributions are shown only as presence/absence records (Table 2).

Qualitative spot analyses of major and trace elements on whole specimens were conducted using a ThermoFisher Scientific Apreo field emission scanning electron microscope (ThermoFisher Scientific, Brno, Czech Republic) operated at 35 pa low vacuum, 15 kV, and 1.6 nA current, coupled to a Edax Octane energy-dispersive X-ray fluorescence spectrometer (EDS) with Silicon Drift Detector (SDD). Weight percentages were standardized relative to potassium content. Positions of spot analyses on target grains are shown in Figure 3, and relative weight percent data are presented in Table 2.

Holotypes and paratypes are housed in the Cushman Collection of Foraminifera at the Smithsonian Institution's

TABLE 1. Maastrichtian and lower Danian foraminiferal and other microfossil distributions in IODP Hole U1514C. Calcareous nannofossil zones from Huber et al. (2019). See Methods section for explanation of preservation and abundance estimates.

| U1514C         | Midpoint Depth [mbsf] | Age          | Planktic Foraminiferal Zone | Calcareous nannofossil Zone | Foraminiferal Preservation | Calcsphere abundance | Fish teeth | Foram abundance | <i>Archaeoglobigerina australis</i> | <i>"Globigerinelloides" asper</i> | <i>"Globigerinelloides" subcarinatus</i> | <i>Muricohed. monmouthensis</i> | <i>Globotruncana arca</i> | <i>Globotruncana bulloides</i> | <i>Globotruncanella havanensis</i> | <i>Gublerina rajagopalani</i> | <i>Laeviheterohelix dentata</i> | <i>Plancheterohelix globulosa</i> | <i>Plancheterohelix planata</i> | <i>Pseudoguemb. haryanaensis</i> | <i>Pseudotextularia elegans</i> | <i>Guenbellia cretacea</i> | <i>Chiloguembel. morsei</i> | <i>Eoglobigerina eobulloides</i> | <i>Turbotalitella nikolasi</i> | <i>Eoglobigerina maudrisensis</i> | <i>Parasubbotina nearika</i> | <i>Zeauvigerina walpapaensis</i> | <i>Antarcticella pauciloculata</i> | Biseriata | Planispirals | Trochospirals | Indeterminate | Benthics | %Planktics |       |       |
|----------------|-----------------------|--------------|-----------------------------|-----------------------------|----------------------------|----------------------|------------|-----------------|-------------------------------------|-----------------------------------|------------------------------------------|---------------------------------|---------------------------|--------------------------------|------------------------------------|-------------------------------|---------------------------------|-----------------------------------|---------------------------------|----------------------------------|---------------------------------|----------------------------|-----------------------------|----------------------------------|--------------------------------|-----------------------------------|------------------------------|----------------------------------|------------------------------------|-----------|--------------|---------------|---------------|----------|------------|-------|-------|
| 22R-CC         | 390.66                | early Danian | Barren                      | Barren                      | —                          | —                    | —          | B               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-1, 2-4     | 392.03                |              | Barren                      | Barren                      | —                          | —                    | —          | B               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            | 0.00% |       |
| 23R-1, 10-12   | 392.11                |              | Barren                      | CP2                         | —                          | —                    | —          | B               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            | 0.00% |       |
| 23R-1, 24-26   | 392.25                |              | Barren                      | CP1b                        | —                          | —                    | —          | B               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            | 0.00% |       |
| 23R-1, 35-37   | 392.36                |              | Barren                      | Barren                      | —                          | B                    | B          | B               | B                                   |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            | 0.00% |       |
| 23R-1, 60-62   | 392.61                |              | AP0                         | CP1a                        | P-G                        | C                    | B          | R               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 | rw                                |                                 |                                  |                                 |                            |                             |                                  |                                | F                                 |                              |                                  | P                                  | P         | 10           | 25            |               | 144      | 19.6%      |       |       |
| 23R-1, 90-92   | 392.91                |              | AP0                         | CP1a                        | P-G                        | C                    | B          | F               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 | rw                                |                                 |                                  |                                 |                            |                             | F                                | P                              | C                                 |                              |                                  | F                                  | P         | 24           | 67            |               | 58       | 61.1%      |       |       |
| 23R-1, 101-103 | 393.03                |              | AP0                         | CP1a                        | P                          | C                    | B          | R               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 | rw                                |                                 | rw                               |                                 |                            | P                           | P                                | P                              | C                                 |                              |                                  | P                                  | P         |              |               |               |          | 0.00%      |       |       |
| 23R-1, 110-112 | 393.11                |              | AP0                         | CP1a                        | P                          | R                    | B          | R               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                | C                                 |                              |                                  | P                                  | P         | 27           | 123           | 17            | 248      | 37.7%      |       |       |
| 23R-1, 120-122 | 393.21                |              | AP0                         | CP1a                        | M-G                        | F                    | B          | A               |                                     | rw                                |                                          |                                 |                           |                                |                                    |                               |                                 |                                   | rw                              | rw                               |                                 |                            |                             |                                  | P                              | F                                 | C                            |                                  | C                                  | P         | 26           | 335           | 218           | 218      | 62.3%      |       |       |
| 23R-1, 126-128 | 393.27                |              | AP0                         | CP1a                        | M                          | R                    | B          | C               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 | rw                                | rw                              |                                  |                                 |                            |                             |                                  | P                              |                                   |                              | C                                | P                                  | 18        | 333          | 12            | 94            | 78.9%    |            |       |       |
| 23R-1, 139-140 | 393.40                | AP0          | CP1a                        | M-G                         | R                          | B                    | A          |                 |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             | P                                |                                |                                   | F                            | P                                | P                                  |           | 53           | 3             | 438           | 10.8%    |            |       |       |
| 23R-1, 147-149 | 393.48                | AP0          | CP1a                        | M-G                         | A                          | B                    | R          | rw              | rw                                  |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  | A                              |                                   |                              | P                                | P                                  | 300       | 259          | 213           |               | 72.4%    |            |       |       |
| 23R-2, 2.5-3   | 393.53                |              | AP0                         | CP1a                        | P                          | A                    | B          | F               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              | P                                | P                                  | 0         | 15           |               |               | 0.00%    |            |       |       |
| 23R-2, 3-5     | 393.54                |              | AP0/Psg. haryanaensis       | --                          | P                          | F                    | B          | B               |                                     |                                   |                                          | P                               | P                         |                                |                                    | P                             | P                               |                                   |                                 |                                  | P                               |                            |                             |                                  |                                | F                                 | P                            |                                  | P                                  |           | 9            | 3             | 44            | 17.0%    |            |       |       |
| 23R-2, 7-8     | 393.58                | I. Maas.     |                             |                             | M                          | A                    | R          | R               | rw                                  | rw                                |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-2, 9-10    | 393.60                |              |                             |                             | M                          | A                    | B          | F               | P                                   | P                                 | P                                        | P                               | P                         |                                |                                    |                               |                                 | P                                 | P                               |                                  | P                               | P                          |                             |                                  |                                |                                   |                              |                                  |                                    |           | 17           | 3             | 34            | 5        | 129        | 28.3% |       |
| 23R-2, 11-13   | 393.63                |              |                             |                             | P-M                        | A                    | R          | F               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            | 0.00% |       |
| 23R-2, 17-19   | 393.69                |              |                             |                             | M-G                        | A                    | R          | R               |                                     |                                   | P                                        |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           | 0            | 0             |               |          | 83         |       | 0.00% |
| 23R-2, 23-25   | 393.73                |              |                             |                             | P                          | C                    | R          | R               |                                     |                                   | P                                        |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            | 0.00% |       |
| 23R-2, 38-41   | 393.91                |              |                             |                             | P                          | A                    | P          | P               |                                     |                                   | P                                        |                                 |                           |                                |                                    |                               | P                               |                                   |                                 |                                  | P                               | P                          | P                           |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-2, 60-62   | 394.11                |              |                             | Barren                      |                            | M-G                  | A          | F               | R                                   |                                   |                                          |                                 |                           |                                |                                    |                               | P                               |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            | 0.00% |       |
| 23R-2, 73-75   | 393.72                |              |                             | Barren                      |                            | P                    | C          | R               | R                                   |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            | 0.00% |       |
| 23R-2, 90-92   | 394.41                |              |                             | Barren                      |                            | P-M                  | R          | B               | R                                   |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            | 0.00% |       |
| 23R-3, 8-10    | 394.70                |              |                             | Barren                      |                            | M-G                  | C          | R               | R                                   |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            | 0.00% |       |
| 23R-3, 50-52   | 395.12                |              | Barren                      |                             | P-M                        | A                    | R          | R               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-3, 70-72   | 395.32                |              | Barren                      |                             | M-G                        | A                    | R          | R               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-3, 91-93   | 395.53                |              | Barren                      |                             | M-G                        | A                    | R          | F               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-3, 110-112 | 395.72                |              | Barren                      |                             | P                          | C                    | F          | R               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-4, 77-80   | 396.55                |              | Barren                      |                             | M-G                        | A                    | F          | C               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-5, 29-31   | 397.70                |              | Barren                      |                             | M-G                        | A                    | F          | C               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-5, 57-60   | 397.99                |              | ?                           |                             | P-M                        | A                    | R          | C               |                                     | P                                 |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-5, 101-104 | 398.42                |              | Barren                      |                             | M-G                        | A                    | R          | C               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 23R-CC         | 398.89                |              | Barren                      |                             | —                          | B                    | B          | B               |                                     |                                   |                                          |                                 |                           |                                |                                    |                               |                                 |                                   |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          | 0.00%      |       |       |
| 24R-2, 37-40   | 402.90                |              | ?                           |                             | M-G                        | A                    | B          | C               | P                                   |                                   |                                          | P                               |                           |                                |                                    |                               |                                 | P                                 |                                 |                                  |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    | 1         | 2            | 8             | 101           |          | 8.2%       |       |       |
| 24R-CC         | 406.22                | I. Ca.       | <i>Archaeo. australis</i>   | CC24a                       | M                          | A                    | B          | C               | F                                   | P                                 |                                          |                                 |                           |                                | F                                  | R                             | F                               | P                                 | P                               | F                                |                                 |                            |                             |                                  |                                |                                   |                              |                                  |                                    |           |              |               |               |          |            |       |       |

National Museum of Natural History (NMNH; Washington, D.C.) and are assigned USNM (United States National Museum) catalogue numbers. The pforams@mikrotax database (Huber et al., 2016) provides species authors/dates, type descriptions, and illustrations for all previously described species discussed in the present study.

Stable isotope samples were measured on a Kiel III carbonate device/Delta Plus IRMS at the University of Missouri. Measurement error is +/- 0.04‰ and +/- 0.06‰ for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  (1 std. dev.), respectively, based on replicate

analyses of NBS-19 run over the course of this study. Values are reported on the Vienna-PDB (VPDB) scale.

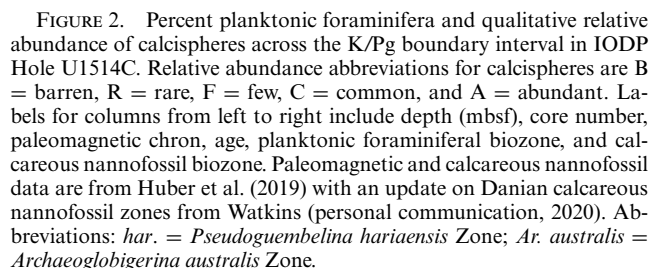
## RESULTS

### HOLE U1514C

Details on drilling operations, logging, physical properties, magnetostratigraphy, geochemistry, and sedimentology for Site U1514 are presented in the Expedition 369

TABLE 2. Qualitative estimates of elemental weight percentages for Expedition U1514C >38- $\mu\text{m}$  sieved residue sediment grains above and below the K/Pg boundary obtained from energy-dispersive X-ray fluorescence spectrometer analyses.

| A: 23R-1, 24-26 cm |          | B: 23R-1, 24-26 cm |          | C: 23R-3, 110-112 cm |          | D: 23R-3, 110-112 cm |          |
|--------------------|----------|--------------------|----------|----------------------|----------|----------------------|----------|
| Element            | Weight % | Element            | Weight % | Element              | Weight % | Element              | Weight % |
| O                  | 31.4     | C                  | 20.2     | C                    | 21.0     | C                    | 11.4     |
| Mg                 | 1.3      | O                  | 29.9     | O                    | 32.4     | O                    | 46.0     |
| Al                 | 9.4      | Mg                 | 0.9      | Mg                   | 0.4      | Mg                   | 0.2      |
| Si                 | 37.5     | Al                 | 6.2      | Al                   | 6.6      | Al                   | 0.8      |
| K                  | 3.1      | Si                 | 30.7     | Si                   | 30.8     | Si                   | 3.3      |
| Ca                 | 3.0      | K                  | 2.8      | K                    | 3.1      | Ca                   | 38.3     |
| Fe                 | 14.4     | Ca                 | 1.6      | Ca                   | 3.4      |                      |          |
|                    |          | Fe                 | 7.8      | Fe                   | 2.2      |                      |          |



Planktonic foraminiferal counts were only possible in samples immediately above and below the K/Pg boundary and in a few upper Campanian-Maastrichtian samples. Between 398.89 and 393.63 mbsf (Sample 23R-CC to 22R-2, 11 cm), most samples are barren of planktonic foraminifera or yielded very few specimens and those were only of particularly robust planktonic species. A number of samples without planktonic foraminifera, though, contain well preserved calcareous and agglutinated benthic foraminifera as well as pithonellid calcispheres (Table 1, Fig. 2), and some contain only agglutinated benthics. Preservation in the counted samples is generally moderate to poor for planktonic specimens, with tests showing cement infilling, fragmentation, and moderate to severe recrystallization. Benthic specimens tend to be better preserved than co-occurring planktonics, with some tests showing glassy preservation in more clay-rich samples immediately above and below the K/Pg and in the upper Campanian samples.

The lowest consistent occurrence of Danian planktonic foraminifera is in Sample U1514C-23R-2, 3–5 cm (mid-point depth 393.54 mbsf) within a heavily bioturbated interval where uppermost Maastrichtian light gray chalk is overlain by Paleocene greenish gray claystone (Fig. 3). At this level is the lowest occurrence (LO) of *Turborotalita nikolsai*, which is a very small, four-chambered cancellate-walled species (Figs. 4.9–4.10) that has been identified in the lowermost Danian at a number of southern mid- and high-latitude locations (Koutsoukos, 2014). This species is consistently the most common species in samples between the K/Pg boundary and the upper barren interval, which begins at Sample U1514C-23R-1, 35–37 cm. In addition to *Tu. nikolsai*, two other unusual forms absent from the Cretaceous (*Eoglobigerina maudrisensis* n. sp.: Fig. 5; *Zeauvigerina waiparaensis*: Figs. 4.8a, b) are found in samples from just above the boundary. Several Cretaceous species occur above our proposed level of the K/Pg boundary in Hole U1514C, probably because of reworking due to strong bioturbation (Table 1, Fig. 3). The LO of the lower Danian species *Chiloguembelina morsei* is in Sample U1514C-23R-1, 126–128 cm. Placement of the K/Pg within the upper 3.5 cm of Section U1514C-

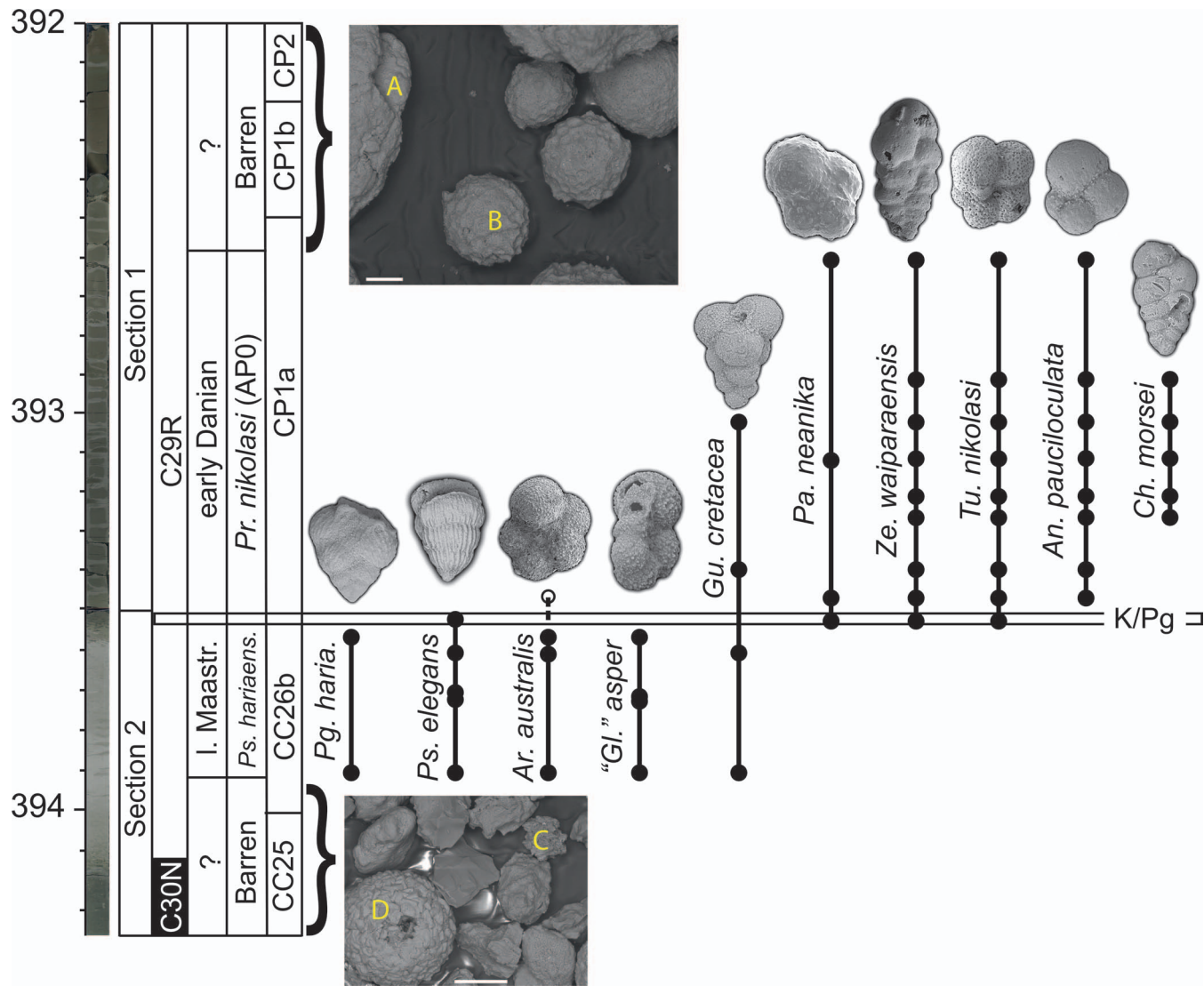


FIGURE 3. Planktonic foraminiferal distributions and washed sieved residues across the K/Pg boundary sequence recovered from IODP Hole U1514C. Composite core photos to left show lithologic changes. See Figure 2 caption for explanation of columns to left and data sources. Hollow circle represents inferred reworking. SEM images of sediment grains show locations of EDS spot elemental analyses; see elemental weight percent estimates in Table 2. A: probable grain of cristobalite; B: radiolarian; C: probable grain of cristobalite; D: pithonellid calcisphere. Scale bars represent 50 μm.

23R-2 is consistent with the lowest occurrence of the calcareous nannofossil *Biantholithus sparsus* used to denote the base of lower Danian Zone CP1a, identified in the top 1 cm of Section U1514C-23R-2 (Table 1; Huber et al., 2019). It is also consistent with a peak in the concentration of platinum group element concentrations (Ru, Pd, Os, Ir, and Pt) and a peak in the radiogenic isotopic composition of Os ( $^{187}\text{Os}/^{188}\text{Os}$ ) observed at 393.52 mbsf (Ota et al., 2020).

Planktonic foraminiferal diversity in the immediately overlying lowermost Danian samples from Section U1514C-23R-1 slightly increases with the LO of the unusual endemic taxon *Antarcticella pauciloculata* (Fig. 6), rare occurrences of *Guembelitra cretacea* (Fig. 4.1), and rare to few occurrences of *Parasubbotina neanika* n. sp. and *Chiloguembelina morsei*. Consistently present in all samples through

Sample 1514C-23R-1, 60–62 cm *Turborotalita nikolasi*, *Ze. waiparaensis*, and *An. pauciloculata* (Table 1. Fig. 3).

No specimens of *An. pauciloculata* were found in the lowermost 8 cm of the Danian samples despite an extensive search including SEM observations to verify light microscope identifications of morphologically similar taxa (Table 1). This species is consistently present but very rare up to Sample U1514C-23R-1, 60–62 cm, which is the highest Danian sample below the upper barren interval and is still within Zone AP0 judging from the absence of *Globocoma daubjergensis*.

Conspicuously absent from the sequence, but commonly found in the lowermost Danian P0 and Pa Zones at lower latitudes, are *Woodringina* spp. and *Parvularugoglobigerina* spp., including *Pa. eugubina*, the nominate species of Zone

P $\alpha$  used in tropical/subtropical zonal schemes (e.g., Wade et al., 2011).

#### HOLE 690C

The K/Pg boundary at Hole 690C is placed at an Ir peak in Sample 15X-4, 39–40 cm (247.80 mbsf; Michel et al., 1990) within a strongly bioturbated, white to pinkish-white nannofossil chalk and ooze that grades into a pale brown Danian clay-rich nannofossil ooze (Barker et al., 1988). Magnetostratigraphic results place this level within but near the top of Chron 29R (Hamilton, 1990). Bioturbation carried Danian planktonic foraminifera and calcareous nannofossils as much as 1.3 m below the Ir peak and complicates precisely placing the level of the K/Pg boundary. That level was approximated from nannofossils by Pospichal & Wise (1990) at the LO of *Biantholithus sparsus* which occurs between 247.82 and 247.89 mbsf (690C-15X-4, 41–50 cm) and from foraminifera by Stott & Kennett (1990) at the point where the percent Paleogene planktonic foraminiferal exceeds that of Cretaceous species between 247.85 and 247.75 mbsf (690C-15X-4, 35–45 cm; Fig. 7).

Preservation of Danian foraminifera in Hole 690C is good throughout the studied interval, with essentially no cement infilling of the tests and minor shell wall recrystallization. Tests with glassy (optically translucent) preservation were not observed in any sample.

Analysis of the Danian planktonic foraminiferal assemblages from within 5 m above the K/Pg of Hole 690C reveals several striking similarities and differences with the correlative interval in Hole U1514C. The first similarity is the distinctive presence of *Tu. nikolasi*, *Pa. neanika* (Fig. 8), and *Eo. maudrisensis* immediately above the boundary level and *Ze. waiparaensis* and *An. pauciloculata* at slightly higher levels starting at 0.58 m and 1.49 m above the boundary, respectively (Table 3, Fig. 7). The second similarity is the absence of *Woodringina* spp. and *Parvularugoglobigerina* spp., which first appear in the early Danian within Chron C29r at the base of Zone P $\alpha$  at lower latitudes (Olsson et al., 1999). The main difference from Hole U1514C is the presence of numerous additional taxa including *Eoglobigerina* spp., *Globoconusa daubjergensis*, *Globanomalina planocompressa*, and *Chiloguembelina midwayensis*. However, despite the higher diversity in Hole 690C compared to Site U1514, species of *Parvularugoglobigerina* and *Woodringina* are still absent from the lower Danian samples.

#### STABLE ISOTOPE RESULTS

To provide an independent perspective on the depth ecology of *Antarcticella pauciloculata*, oxygen and carbon isotope values were measured on separates of this species as well as separates of the planktonic foraminiferal species *Globanomalina planocompressa* and *Eoglobigerina eobulloides* and the benthic species *Gavelinella beccariiiformis* for three lower Danian samples from Hole 690C between 246.15 and 245.57 mbsf (690C-15X-3, 25 cm; 690C-15X-2, 140 cm; and 690C-15X-2, 117 cm). The lowermost sample is positioned 1.6 m above the K/Pg boundary. Rarity of specimens prevented acquisition of data from all samples containing *Antarcticella pauciloculata* in Hole 690C.

There are consistent offsets in both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  between the benthic taxon *Ga. beccariiiformis* and the other taxa analyzed; values for *An. pauciloculata* are quite similar to the values for the two known planktonic taxa (Table 4, Fig. 9). The  $\delta^{13}\text{C}$  offsets between *Ga. beccariiiformis* and the other taxa match expected surface to seafloor gradients assuming an active biological pump. The  $\delta^{18}\text{O}$  offsets, though, are opposite expectations with generally lower  $\delta^{18}\text{O}$  values in the benthic taxon which suggest warmer waters at the seafloor than at the sea surface. The  $\delta^{18}\text{O}$  measurements from *Ga. beccariiiformis* average 0.10‰, and values for *Gl. planocompressa*, *Eo. eobulloides*, and *An. pauciloculata* average 0.36‰, 0.42‰, and 0.39‰, respectively. Pairwise offsets between *Ga. beccariiiformis* and the other species within the same sample ranges average 0.33‰ and range from -0.04‰ to 0.47‰. The  $\delta^{13}\text{C}$  measurements from *Ga. beccariiiformis* average 1.41‰, and values for *Gl. planocompressa*, *Eo. eobulloides*, and *An. pauciloculata* average 2.19‰, 2.06‰, and 1.91‰, respectively. Pairwise offsets between *Ga. beccariiiformis* and the other species within the same sample average 0.60‰ and range from 0.31‰ to 0.92‰. There is no clear stratigraphic shift in  $\delta^{18}\text{O}$  or  $\delta^{13}\text{C}$  values among the species analyzed.

#### DISCUSSION

##### REVISED DEFINITION OF THE AP0 ZONE

Stott & Kennett (1990) were the first to define a separate planktonic foraminiferal biozonation for the Paleogene at southern high latitudes addressing the problem of biostratigraphically subdividing the interval despite the absence of standard zonal marker species used in low latitude schemes. Their scheme, which used AP as a prefix for the Antarctic Paleogene, was significantly revised by Huber & Quillévère (2005) following study of additional circum-Antarctic deep-sea sites. The latter authors defined the lowermost Danian AP0 Zone (*Guembelitra cretacea* Partial Range Zone) as the interval from the HO of Cretaceous planktonic foraminifera to the LO of *Globoconusa daubjergensis*, but they did not declare characteristic species that can be used to identify the zone.

We herein revise the AP0 Zone by designating *Turborotalita nikolasi* as the nominate species because of its easy identification and consistent occurrence in samples that range from immediately above the K/Pg boundary (defined by a platinum group element concentration peak) to the LO of *Globoconusa daubjergensis*, which defines the base of the overlying AP1 Zone. Additional characteristic species occurring within the AP0 zone include *Eoglobigerina eobulloides*, *Eo. maudrisensis* n. sp., *Parasubbotina neanika* n. sp., and *Antarcticella antarctica*. The duration of the AP0 Zone is estimated as 240 kyr, based on the Beggren et al. (1995) datum age for the LO of *Globoconusa daubjergensis*.

##### DISTRIBUTION AND DEPTH ECOLOGY OF *ANTARCTICELLA PAUCILOCOLATA*

*Antarcticella pauciloculata* was originally described from the lower Teurian Stage (Danian) in the Middle Waipara section on South Island, New Zealand (Jenkins, 1966). It was placed in the planktonic foraminiferal genus

TABLE 3. Presence/absence distributions for planktonic foraminifera from the lower Danian of ODP Hole 690C. *A. may.* = *Abathomphalus mayaroensis*; x = present; rw = reworked; ? = questionably present.

| 690C           | Depth (mbsf) | Age          | Zone           | <i>Archaeoglobigerina australis</i> | <i>"Globigerinelloides" subcarinatus</i> | <i>Muricohedbergella sliteri</i> | <i>Abathomphalus intermedius</i> | <i>Abathomphalus mayaroensis</i> | <i>Guembelitra cretacea</i> | <i>Parasubbotina neanika</i> | <i>Turbototalia nikolasi</i> | <i>Eoglobigerina eobulloides</i> | <i>Eoglobigerina maudrisensis</i> | <i>Eoglobigerina quadrata</i> | <i>Zenaidgerina waiparaensis</i> | <i>Globocosa daubjerjensis</i> | <i>Chiloguembelina midwayensis</i> | <i>Chiloguembelina morsei</i> | <i>Subbotina trivialis</i> | <i>Antaricella pauciloculata</i> | <i>Subbotina triloculoides</i> | <i>Globanomalina planocompressa</i> | <i>Parasubbotina pseudobulloides</i> | <i>Parasubbotina varianta</i> |
|----------------|--------------|--------------|----------------|-------------------------------------|------------------------------------------|----------------------------------|----------------------------------|----------------------------------|-----------------------------|------------------------------|------------------------------|----------------------------------|-----------------------------------|-------------------------------|----------------------------------|--------------------------------|------------------------------------|-------------------------------|----------------------------|----------------------------------|--------------------------------|-------------------------------------|--------------------------------------|-------------------------------|
| 15X-1, 67-69   | 243.47       | early Danian | AP1b           |                                     |                                          |                                  |                                  |                                  | x                           |                              |                              | x                                |                                   |                               |                                  | x                              | x                                  | x                             |                            |                                  | x                              |                                     | x                                    |                               |
| 15X-1, 120-122 | 244.00       |              | AP1b           |                                     |                                          |                                  |                                  |                                  | x                           |                              |                              |                                  | x                                 | x                             |                                  |                                | x                                  | x                             | x                          |                                  | x                              | x                                   |                                      |                               |
| 15X-2, 17-19   | 244.47       |              | AP1b           |                                     |                                          |                                  |                                  |                                  |                             |                              | x                            |                                  | x                                 | x                             |                                  | x                              | x                                  | x                             | x                          | x                                | x                              | x                                   |                                      |                               |
| 15X-2, 62-69   | 245.02       |              | AP1b           |                                     |                                          |                                  |                                  |                                  | x                           | x                            |                              |                                  | x                                 | x                             |                                  | x                              | x                                  | x                             | x                          | x                                | x                              | x                                   | x                                    |                               |
| 15X-2, 117-119 | 245.57       |              | AP1b           |                                     |                                          |                                  |                                  |                                  |                             |                              |                              |                                  | x                                 | x                             |                                  |                                | x                                  | x                             | x                          | x                                | x                              | x                                   |                                      |                               |
| 15X-2, 140-142 | 245.80       |              | AP1b           |                                     |                                          | rw                               |                                  |                                  |                             | x                            | x                            |                                  | x                                 | x                             |                                  |                                | x                                  | x                             | x                          | x                                | x                              | x                                   | x                                    |                               |
| 15X-3, 25-29   | 246.15       |              | AP1b           |                                     |                                          |                                  |                                  |                                  |                             |                              | x                            |                                  | x                                 | x                             |                                  |                                | x                                  | x                             |                            | x                                | x                              | x                                   | x                                    |                               |
| 15X-3, 41-46   | 246.31       |              | AP1b           | rw                                  | rw                                       |                                  |                                  |                                  |                             | x                            | x                            | x                                | x                                 | x                             |                                  |                                | x                                  | x                             | x                          | x                                | x                              | x                                   |                                      |                               |
| 15X-3, 95-97   | 246.85       |              | AP1a           |                                     |                                          |                                  |                                  | rw                               |                             |                              | x                            | x                                | x                                 | x                             | x                                | x                              | x                                  | x                             |                            | x                                | x                              |                                     |                                      |                               |
| 15X-3, 132-136 | 247.22       |              | AP1a           |                                     |                                          | rw                               | rw                               |                                  |                             |                              | x                            | x                                | x                                 | x                             |                                  | x                              | x                                  | x                             | x                          |                                  |                                |                                     |                                      |                               |
| 15X-4, 28-30   | 247.68       | Maas.        | AP0            | rw                                  | rw                                       |                                  |                                  | rw                               |                             | x                            | x                            | x                                | x                                 | x                             |                                  | x                              | x                                  |                               |                            |                                  |                                |                                     |                                      |                               |
| 15X-4, 35-37   | 247.75       |              | AP0            | rw                                  | rw                                       | rw                               | rw                               | rw                               |                             | x                            | x                            | x                                |                                   | x                             |                                  |                                |                                    |                               |                            |                                  |                                |                                     |                                      |                               |
| 15X-4, 40-41   | 247.80       |              | <i>A. may.</i> | x                                   | x                                        | x                                | x                                | x                                | x                           | x                            |                              |                                  |                                   |                               |                                  |                                |                                    |                               |                            |                                  |                                |                                     |                                      |                               |
| 15X-4, 84-86   | 248.24       |              | <i>A. may.</i> | x                                   | x                                        | x                                | x                                | x                                | x                           |                              |                              |                                  |                                   |                               |                                  |                                |                                    |                               |                            |                                  |                                |                                     |                                      |                               |
| 15X-4, 128-130 | 248.68       |              | <i>A. may.</i> | x                                   | x                                        | x                                | x                                | x                                | x                           |                              |                              |                                  |                                   |                               |                                  |                                |                                    |                               |                            |                                  |                                |                                     |                                      |                               |

TABLE 4. Stable isotopes of benthic (*Gavelinella beccariiiformis*), planktonic *Globanomalina planocompressa*; *Eoglobigerina eobulloides*) for comparison with the possibly tychoepelagic species *Antarcticella pauciloculata*.

| Hole 690C      | mbsf   | <i>Ga. beccariiiformis</i> |                       | <i>Gl. planocompressa</i> |                       | <i>Eo. eobulloides</i> |                       | <i>An. pauciloculata</i> |                       |
|----------------|--------|----------------------------|-----------------------|---------------------------|-----------------------|------------------------|-----------------------|--------------------------|-----------------------|
|                |        | $\delta^{13}\text{C}$      | $\delta^{18}\text{O}$ | $\delta^{13}\text{C}$     | $\delta^{18}\text{O}$ | $\delta^{13}\text{C}$  | $\delta^{18}\text{O}$ | $\delta^{13}\text{C}$    | $\delta^{18}\text{O}$ |
| 15X-2, 117-119 | 245.57 | 1.28                       | 0.27                  |                           |                       | 2.20                   | 0.23                  | 2.07                     | 0.31                  |
| 15X-2, 117-119 | 245.57 | 1.44                       | 0.09                  |                           |                       | 2.16                   | 0.36                  |                          |                       |
| 15X-2, 117-119 | 245.57 | 1.51                       | 0.01                  |                           |                       |                        |                       |                          |                       |
| 15X-2, 140-142 | 245.80 | 1.39                       | 0.08                  | 2.17                      | 0.33                  | 2.15                   | 0.55                  | 1.93                     | 0.40                  |
| 15X-2, 140-142 | 245.80 |                            |                       | 2.20                      | 0.34                  | 2.19                   | 0.52                  |                          |                       |
| 15X-3, 25-27   | 246.15 | 1.55                       | 0.06                  | 2.20                      | 0.41                  | 1.86                   | 0.33                  | 1.89                     | 0.38                  |
| 15X-3, 25-27   | 246.15 | 1.43                       | 0.00                  |                           |                       | 1.91                   | 0.47                  |                          |                       |

*Globigerina*, and its biostratigraphic importance for correlation of the lower Teurian was such that Jenkins (1971) used it as the nominate species of the *Globigerina* (*G*) *pauciloculata* Zone. Although this species has a rounded and inflated test typical of planktonic foraminifera, the obscured sutural apertures, large (40  $\mu\text{m}$ ) proloculus described from the type specimens (more than twice the diameter of typical planktonic species), and concentration of pustules along the umbilical chamber sutures are characteristics that do not match those of any of the Cenozoic planktonic lineages.

In an effort to clarify the taxonomic status of this species, Liu et al. (1998) investigated its biogeographic and biostratigraphic distribution and its most likely phylogenetic relationships. These authors documented occurrences of *An. pauciloculata* in the lower Danian of Seymour Island, Antarctica and Maud Rise Hole 690C based on re-examination and classification of specimens that had been incorrectly identified in previous publications (see Systematic Taxonomy section below). That study concluded, based on morphologic criteria, that *An. pauciloculata* probably evolved from a benthic ancestor and considered *Praepararotalia cretacea* as the most likely ancestral species, although no intermediate forms linking the two species were identified.

The presence of *An. pauciloculata* in lower Danian samples from Hole U1514C expands the known distribution of the species to the high latitude Indian Ocean. Although poorly preserved (Figs. 5.8–5.10), with careful observations the species can be confidently identified. In samples from Hole U1514C, it is restricted to an interval starting 8 cm above the K/Pg and continuing to the base of the upper barren zone (Fig. 3). Its lowest occurrence in New Zealand (within 0.23 m above the K/Pg boundary in the Mid-Waipara River section) is in sediments assigned to Zone P $\alpha$ , and its highest occurrence in the Danian sequence was assigned an age of 62 Ma (Hollis & Strong, 2003). In Hole 690C, the stratigraphic gap between the K/Pg level and its lowest occurrence is greater at 90 cm (Fig. 7). On Seymour Island (where average sedimentation rates are  $\sim 175$  m/m.y.; Dutton et al., 2007), the lowest occurrence of *An. pauciloculata* (originally identified as *Globastica daubjergensis*; see Huber, 1988, figs. 32.10–32.11) is  $\sim 20$  m above the K/Pg, but its absence in the intervening sediments may be a preservation artifact (Huber, 1988). The only record of *An. pauciloculata* outside the circum-Antarctic region and New Zealand is in the Jagüel Fm. In the Nequén Basin of central Argentina (Ballent et al., 2011; Malumán & Nández, 2011), which was

located at 30°S paleolatitude (Fig. 1). It is particularly abundant in the first meter of Danian mudstones at the Bajada del Jagüel section (Ballent, 1999, p. 515). It is not clear if its range at that location is within the lowermost Danian because of absence of the P $\alpha$  marker species *Pv. eugubina*.

*Antarcticella pauciloculata*  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values from the lower Danian of Hole 690C cluster with values for co-occurring planktonic species (*Gl. planocompressa*, *Eo. eobulloides*) and are separate from the cluster of values for the benthic species *Ga. beccariiiformis* from the same samples (Table 4, Fig. 9). These results provide clues to foraminiferal paleoecology and to local and regional paleoceanography that while outside the focus of this study still deserve mention. The presence of an  $\sim 0.5\text{‰}$   $\delta^{13}\text{C}$  gradient between planktonic and benthic species suggests at least modest export of new organic matter from surface waters within 1 m.y. after the K/Pg in austral seas. The inversion of the  $\delta^{18}\text{O}$  gradient with lower and thus apparently warmer values in *Ga. beccariiiformis* relative to the planktonic species requires more consideration. *Gavelinella beccariiiformis* is thought to record equilibrium  $\delta^{18}\text{O}$  values (Katz et al., 2003), making any invocation of ‘vital effects’ to explain away the anomalous gradient *ad hoc*. Similarly, invoking a diagenetic overprint, shifting  $\delta^{18}\text{O}$  values of planktonic species to values higher than recorded by the benthic taxon (Huber et al., 2011), is difficult to reconcile with: (1) the consistently good preservation (especially the lack of overgrowths) among all taxa; (2) the considerable size difference between *An. pauciloculata* and the other planktonic taxa; and (3) difficulty in proposing a reasonable location within the sediment column where more diagenetically susceptible planktonic specimens (an assumption required in this scenario) would experience cooler temperatures than those at which the assumed less diagenetically sensitive *Ga. beccariiiformis* individuals grew. In contrast, if the southwest Pacific was a dominant site of contemporary bottom water formation, as has been proposed for the Maastrichtian from neodymium isotopic data and modeling studies (Haynes et al., 2020; Ladant et al., 2020), the reversed planktonic-benthic  $\delta^{18}\text{O}$  gradient in Hole 690C would be explained by the higher temperature and higher salinities of sinking water in the southwest Pacific compared to surface waters in the Maud Rise region. Uncertainty in regional paleoceanographic interpretations aside, similarity among values for *An. pauciloculata* and the two planktonic reference taxa, and the difference of this cluster of values to those measured on the benthic taxon *Ga. beccariiiformis*, indicate a planktonic lifestyle for *An.*

*pauciloculata* contrary to the benthic lifestyle proposed in Liu et al. (1998).

This finding does not clarify the evolutionary origin of *An. pauciloculata*. There are no planktonic foraminiferal survivors of the K/Pg extinction event or post-K/Pg species with enough shared morphologic characteristics to suggest an ancestor-descendent relationship. Although the globular, strongly inflated chambers present throughout *An. pauciloculata*'s ontogeny (Figs. 6.4d, 6.5d, 6.6d, 6.7d) are typical of planktonic species, several features are unlike any other planktonic species from the late Maastrichtian or early Danian, including: (1) occasional occurrence of specimens with a megalospheric proloculus, (2) concentration of pustules along the umbilical sutures with a microporulate test ultrastructure, and (3) absence of a visible aperture.

It seems more likely that this species evolved from a benthic ancestor, perhaps *Praepararotalia cretacea* as was suggested by Liu et al. (1998). Studies of wall microstructure, interspecies comparison of stable isotopes, and DNA sequencing indicate that this is one of many invasions of the plankton by different benthic species that resulted in the evolution of at least 12 separate planktonic foraminiferal lineages during the Mesozoic and Cenozoic (Leckie, 2009). Adoption of a wholly planktonic lifestyle would have required achieving positive buoyancy in adult forms, an ability to feed in the pelagic environment, and completion of an entire life cycle in the pelagic environment (Darling et al., 2009; Kucera et al., 2017). This shift probably occurred through an intermediate tychoipelagic lifestyle perhaps facilitated by the fact that calcareous plankton were less abundant as a result of the terminal Cretaceous mass extinction.

The idea that earliest Danian planktonic foraminifera evolved from a benthic ancestor was postulated by Brinkhuis & Zachariasse (1988), who suggested the benthic buliminid genus *Caucasina* as the likely ancestor. Arenillas & Arz (2017) took this idea a step further by proposing that the *Parvularugoglobigerina*, *Woodringina*, and *Chiloguembelina* lineages all evolved from a *Caucasina* ancestor via the benthic and then planktonic lineages *Pseudocaucasina* and *Palaeoglobigerina*, respectively. These authors also suggested *An. pauciloculata* as a possible ancestor to the parvularugoglobigerinids. Although the caucasinids share some morphologic similarity to early parvularugoglobigerinid species, absence of pore mounds among caucasinids and in *An. pauciloculata* makes it unlikely that either taxon was ancestral to parvularugoglobigerinids. In addition, strong differences in test morphology argue against a phylogenetic link between *An. pauciloculata* and caucasinids.

#### PROVINCIALITY OF LATE MAASTRICHTIAN-DANIAN AUSTRAL PLANKTONIC FORAMINIFERAL ASSEMBLAGES

The concept of a southern high-latitude biogeographic province with shared taxonomic affinities among late Mesozoic and Paleogene terrestrial and marine organisms has been around for many decades with names such as Palaeoaustral (Fleming, 1962; Stevens, 1980) Weddellian Province (Zinsmeister, 1982; Macellari, 1985, 1987), and Austral Province (Scheibnerová, 1971; Kauffman, 1973; Sliter, 1977; Huber, 1992) applied to different taxonomic groups in the circum-Antarctic region. Initially the Austral

Province was applied to Cretaceous foraminifera at southern high latitudes based on the dominance of agglutinated and calcareous benthic foraminifer assemblages "bearing clear features of forms living in cool environments" (Scheibnerová, 1971). Later the term was also applied to Cretaceous planktonic foraminiferal assemblages that were low in taxonomic diversity without Tethyan zonal marker taxa (Sliter, 1977; Krashennikov & Basov, 1983) and that included endemic species (Huber, 1992; Huber & Watkins, 1992).

Confinement of multiple planktonic and benthic foraminiferal species to the Austral Province at locations shown in Figure 1 became most apparent during the late Campanian and continued through the Maastrichtian with increasing rarity of thermophilic taxa and increased appearance of species not found outside the circum-Antarctic region (Sliter, 1977; Huber, 1988, 1992). Petrizzo et al. (2020) discuss links between changes in planktonic foraminiferal species distribution patterns, vertical stratification of surface waters, and climate that led to development of the Austral Province.

The northern limit of the Austral Province has generally been considered as ~50°S (Huber & Watkins, 1992; Fig. 1). Reasons cited for the poleward loss of thermophilic species and increased taxonomic endemism primarily include: (1) reduced differentiation of vertical niches and reduced depth of the thermocline, excluding deeper dwelling planktonic species that required a well-stratified water column; (2) climatic cooling through the Late Cretaceous and increasing thermal isolation of higher latitude surface waters; and (3) the possible existence of marine gateways across Antarctica and the Tasman Rise, providing avenues for genetic communication among all sites promoting regional similarities. Absence from the circum-Antarctic region of *Parvularugoglobigerina* spp. and *Woodringina* spp., which are widely used as early Danian index species, is puzzling since they occur in a wide range of depositional settings at middle and low latitudes and are generally considered as opportunistic species (Olsson et al., 1999).

Evidence for marine communication routes across West Antarctica and possibly through the Tasmanian Gateway during the Maastrichtian and earliest Danian is based not only on the circum-Antarctic distribution of Austral endemic species, but also on tectonic and sedimentologic observations. The existence of seaways shown in the Scotese (2016) reconstruction of West Antarctica for 65 Ma (Fig. 1) is based on the subglacial topography map of Antarctica, which indicates that large regions of West Antarctica were below sea level before growth of a continental ice sheet (Drewry, 1983). Dinoflagellate biogeography and sea-surface temperature estimates from locations in the Tasmanian Gateway region indicate that strong current flow between Antarctica and SE Australia was not established until ~49.5 Ma (Bijl et al., 2013). Nonetheless, the presence of Maastrichtian calcareous nannofossil and planktonic foraminiferal assemblages and Paleocene-Eocene marginal marine dinoflagellates at sites drilled on submerged continental blocks in the Tasmanian Gateway region during ODP Leg 189 (Shipboard Party, 2001; Brinkhuis et al., 2003; Exon et al., 2004) suggest that routes for shallow marine communication probably existed at least as far back as the Maastrichtian.

## CONCLUSIONS

Study of planktonic foraminiferal assemblages from the K/Pg boundary interval at southern high-latitude sites in the southern South Atlantic (ODP Hole 690C) and SE Indian Ocean (IODP Hole U1514C) reveals important site similarities. Observations presented provide the basis for a proposed inter-regional correlation and paleogeographic interpretations for a circum-Antarctic biogeographic region. Consistent presence of *Turborotalita nikolasi* in samples immediately above the boundary level from Zones AP0–AP1 in both regions compares well with records of its occurrence in Zones P0–P1a at lower latitudes and enables unequivocal correlation of the lowermost Danian across latitudes. Also valuable for global correlation of the lowermost Danian is the new species *Parasubbotina neanika*, which first occurs immediately above the K/Pg impact bed at ODP Hole 690C and IODP Hole 1514C. The distinctive new species *Eoglobigerina maudrisensis* also ranges from Zone AP0 through Zone AP1 at Sites 690 and U1514 and is considered useful as a lower Danian biostratigraphic marker species.

Identification of the enigmatic species *Antarcticella pauciloculata* in the lower Danian of Hole U1514C extends its known geographic distribution into the southern Indian Ocean after having been recorded in the lower Danian of New Zealand, in the southern South Atlantic (ODP Site 690) and in Argentina. Comparisons of stable isotopic ratios in this species with several taxa of known depth ecology suggest a planktonic mode of life for *An pauciloculata*. Presence of this and several other endemic benthic and planktonic foraminifera throughout the Austral Biogeographic Province during the Maastrichtian and early Danian required continuous gene flow among those sites, which could only have occurred if the southern South Pacific, southern South Atlantic, and southern Indian Ocean regions were oceanographically linked. We suggest that shallow marine circulation routes existed across West Antarctica during the Maastrichtian and early Danian (Fig. 1) based on tectonic reconstructions depicting a large portion of West Antarctica and some portions of East Antarctica below sea level during pre-glacial times (Drewry, 1983; Scotese, 2016). The presence of open-ocean marine microfossils in Maastrichtian cores from the east Tasman Plateau and marginal marine microfossils in Paleocene to early Eocene cores recovered from other Tasman Rise sites drilled during ODP Leg 189 (Shipboard Scientific Party, 2001; Brinkhuis et al., 2003; Exon et al., 2003) suggest a possible additional route for shallow marine circulation at that time.

## SYSTEMATIC TAXONOMY

Apart from the taxonomic revisions discussed below, our foraminiferal taxonomy is based on the pforams@mikrotax database (Huber et al., 2016). The planispiral genus *Globigerinelloides* is placed in quotes in the text and figures because it is polyphyletic and currently under taxonomic revision (see discussion in Petrizzo et al., 2017).

Order FORAMINIFERIDA d'Orbigny, 1826  
Superfamily ROTALIODEA Ehrenberg, 1839  
Family ROTALIIDAE Ehrenberg, 1839

Subfamily PARAROTALIINAE Reiss, 1963  
Genus *Antarcticella* Loeblich & Tappan, 1988  
Type Species: *Candeina antarctica* Leckie & Webb, 1985

**Remarks.** The genus *Antarcticella* was defined by Loeblich & Tappan (1988) to include microporifate species previously placed in *Candeina* but without true supplementary apertures along the umbilical and spiral chamber sutures, which is a distinctive feature of *Candeina*. The aperture on the final chamber of *Antarcticella* is hidden by bridge-like projections across the umbilicus and the intercameral suture and blunt pustules occur on and between the sutural projections.

*Antarcticella pauciloculata* (Jenkins, 1966)  
Figs. 6.1–6.10

*Globigerina pauciloculata* Jenkins, 1966, p. 1106, figs. 3(7–15), 3(16–41), 4(42) [lower Danian, New Zealand].  
*Globastica daubjergensis* (Brönnimann). Huber, 1988, figs. 32(10–11) [lower Danian, Seymour Island, Antarctica].  
*Eoglobigerina edita* (Subbotina). Stott & Kennett, pl. 1, figs. 9–10 [lower Danian, ODP Hole 690C, Maud Rise].  
*Antarcticella pauciloculata* (Jenkins). Liu et al., 1998, p. 15 [refigured illustrations]. Hollis & Strong, 2003, p. 249 [Middle Waipara River Gorge, South Island, New Zealand, lower Danian Zones P $\alpha$  – P1b]. Malumian & Nández, 2011, fig. 5.2 [lower Danian, Jagüel Fm., sample OP 10, Neuquén Basin, Argentina]; Ballent et al., 2011, figs. 14.6–14.7 [lower Danian, Jagüel Fm., sample SGN 2904-05, Neuquén Basin, Argentina].

**Remarks.** Although *An. pauciloculata* was originally described as having a test wall with small hexagonal pores, SEM examination of topotype specimens (e.g., Fig. 6.2) reveals a smooth test surface. Measurement of test wall pores from Maud Rise specimens (e.g., Fig. 6.4e) demonstrates that the wall is microporifate with pores diameters ranging from 0.3 to 0.7  $\mu$ m. The test size and morphology are quite variable with the maximum test diameter ranging from 94 to 182  $\mu$ m, proloculus diameters ranging from 23 to 40  $\mu$ m, the final chamber number ranging from 3 to 5, and the total chamber number ranging from 8 to 10. Some forms have kummerform final chambers (e.g., Fig. 6.6a); some forms have narrow cover plates over the umbilical sutures (Figs. 6.4a, 6.5a, 6.6a, 6.7a) while others do not (e.g., Figs. 6.8–6.10). Some forms have a regular and rapid chamber area increase (Figs. 6.8, 6.9, 6.10) while others show a slower and more irregular chamber growth rate (Figs. 6.4, 6.5).

Liu et al. (1998, pl. 3, figs. 1–7) provided SEM illustrations of a serially dissected topotype specimen of *Candeina antarctica* revealing ontogenetic changes in the aperture, which shifted from a continuous extraumbilical slit in the juvenile growth stage to a multiple aperture along the base of the chamber face in neanic chambers and then became hidden under the bridge-like extensions on the final kummerform chamber. The dissections also revealed that concentration of blunt pustules in the umbilical region early in ontogeny shifted to concentration along the umbilical sutures between the adult chambers. The SEM illustration of a topotype specimen of *Globigerina pauciloculata* by Liu

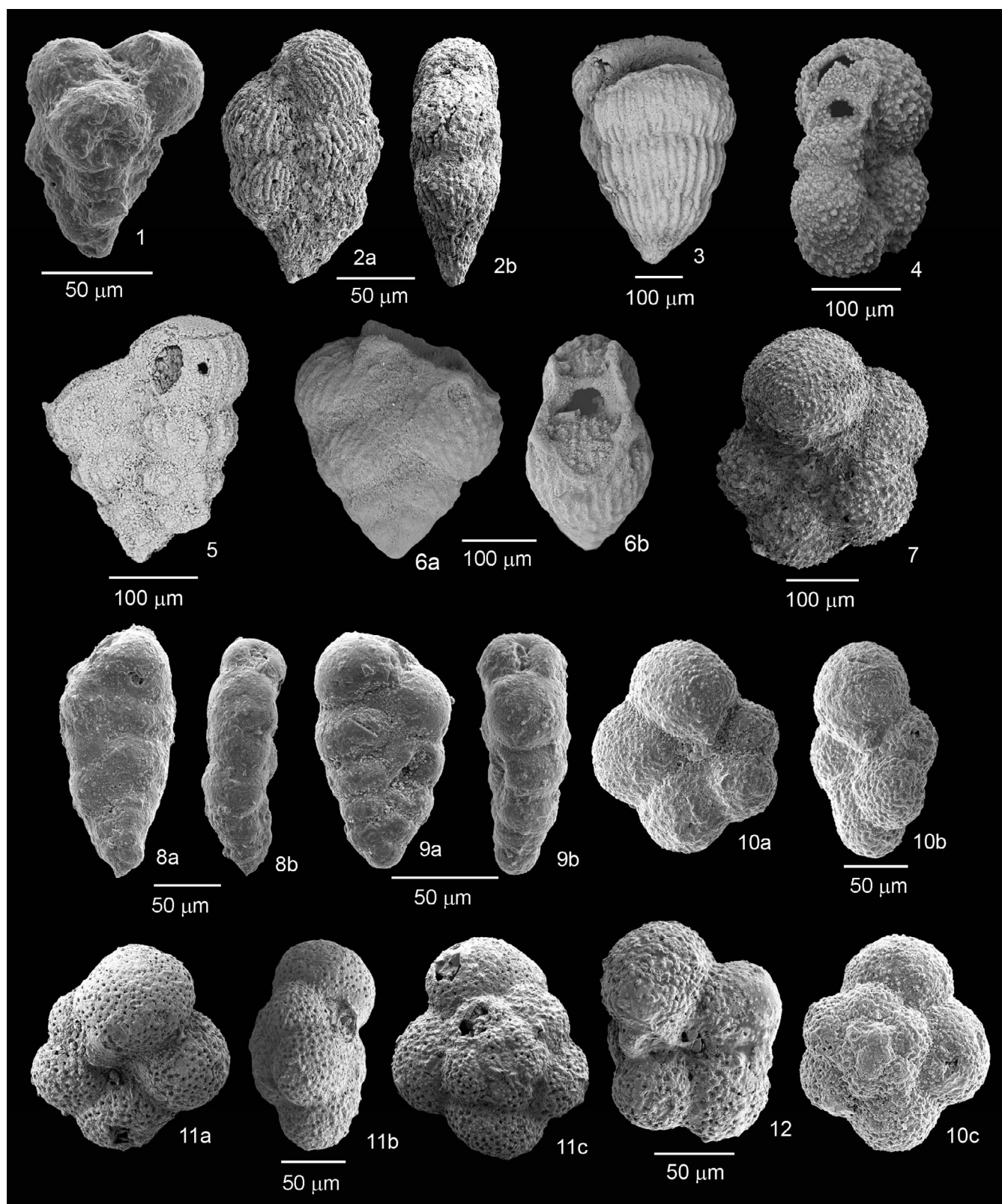


FIGURE 4. Upper Maastrichtian and lower Danian planktonic foraminifera from IODP Hole U1514C. 1 *Guembelitra cretacea*, Sample 1514C-23R-1, 139–140 cm; 2 *Planoheterohelix globulosa*, Sample 1514C-23R-2, 9–10 cm; 3 *Pseudotextularia elegans*, Sample U1514C-23R-2, 23–25 cm; 4 “*Globigerinelloides*” *asper*, Sample U1514C-23R-5, 57–60 cm; 5 *Gublerina rajagopalani*, Sample U1514C-23R-2, 23–25 cm; 6 *Pseudoguembelina hariaensis*, Sample U1514C-23R-2, 38–41 cm; 7 *Archaeoglobigerina australis*, Sample 1514C-23R-1, 147–149 cm; 8 *Zeauvigerina waiparaensis*, Sample 1514C-23R-2, 3–5 cm; 9 *Chiloguembelina morsei*, Sample 1514C-23R-1, 101–103 cm; 10 *Turborotalita nikolasi*, Sample 1514C-23R-1, 101–103 cm; 11 *Turborotalita nikolasi*, Sample 1514C-23R-1, 147–149 cm; 12 *Turborotalita nikolasi*, Sample 1514C-23R-1, 147–149 cm.

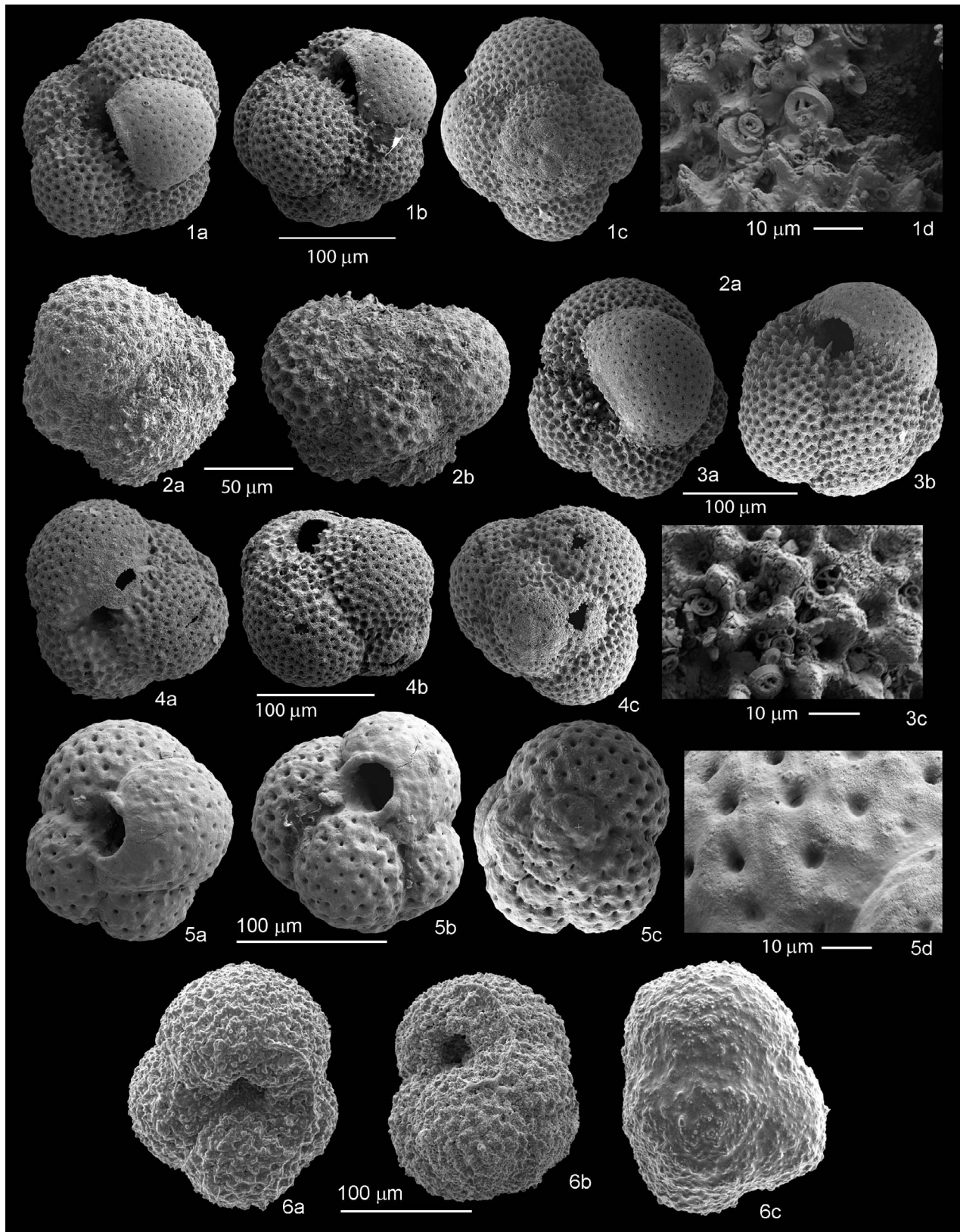


FIGURE 5. *Eoglobigerina maudrisensis* Huber & Petrizzo, n. sp. **1a–d** Holotype USNM 770857: umbilical, edge, spiral, and high magnification wall views, Sample 690C-15X-3, 132–136 cm; **2a–b** Umbilical and edge views, Sample 690C-15X-4, 25–28 cm; **3a–b** Sample 690C-15X-4, 28–30 cm; **4a–d** Paratype USNM 770858: umbilical, edge, spiral, and high magnification wall views, Sample 690C-15X-4, 25–28 cm; **5a–d** Paratype USNM 770859: Sample 690C-15X-4, 25–28 cm; **6a–c** Sample 1514C-23R-2, 3–5 cm.

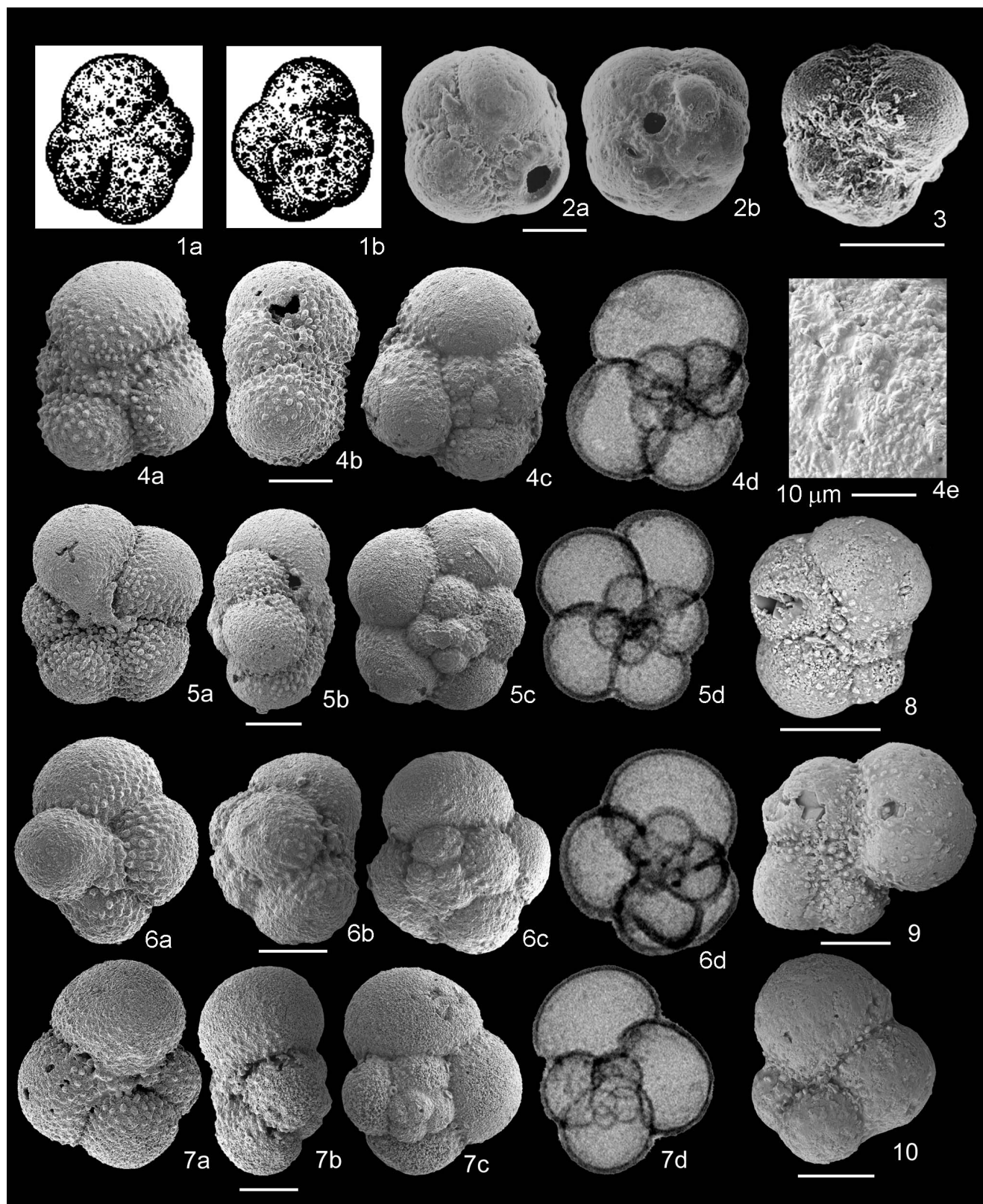


FIGURE 6. *Antarcticella pauciloculata*. **1a, b** Holotype illustration from Jenkyns, 1966; **2a, b** topotype New Zealand Geological Survey specimen S68 197, M34/7197; **3** Specimen from Seymour Island, Antarctica identified as *Globastica daubjergensis* by Huber (1988, fig. 32-10); **4a–d** Umbilical, edge, spiral and nannoCT x-ray of specimen from Sample 690C-15X-3, 95–97 cm; **5a–d** Umbilical, edge, spiral and nannoCT x-ray of specimen from Sample 690C-15X-3, 41–46 cm; **6a–d** Umbilical, edge, spiral and nannoCT x-ray of specimen from Sample 690C-15X-3, 95–97 cm; **7a–d** Umbilical, edge, spiral and nannoCT x-ray of specimen from Sample 690C-15X-3, 41–46 cm; **8** Sample U1514C-23R-1, 101–103 cm; **9** Sample 1514C-23R-1, 126–128 cm; **10** Sample U1514C-23R-1, 126–128 cm. Scale bars represent 50 µm unless otherwise noted.

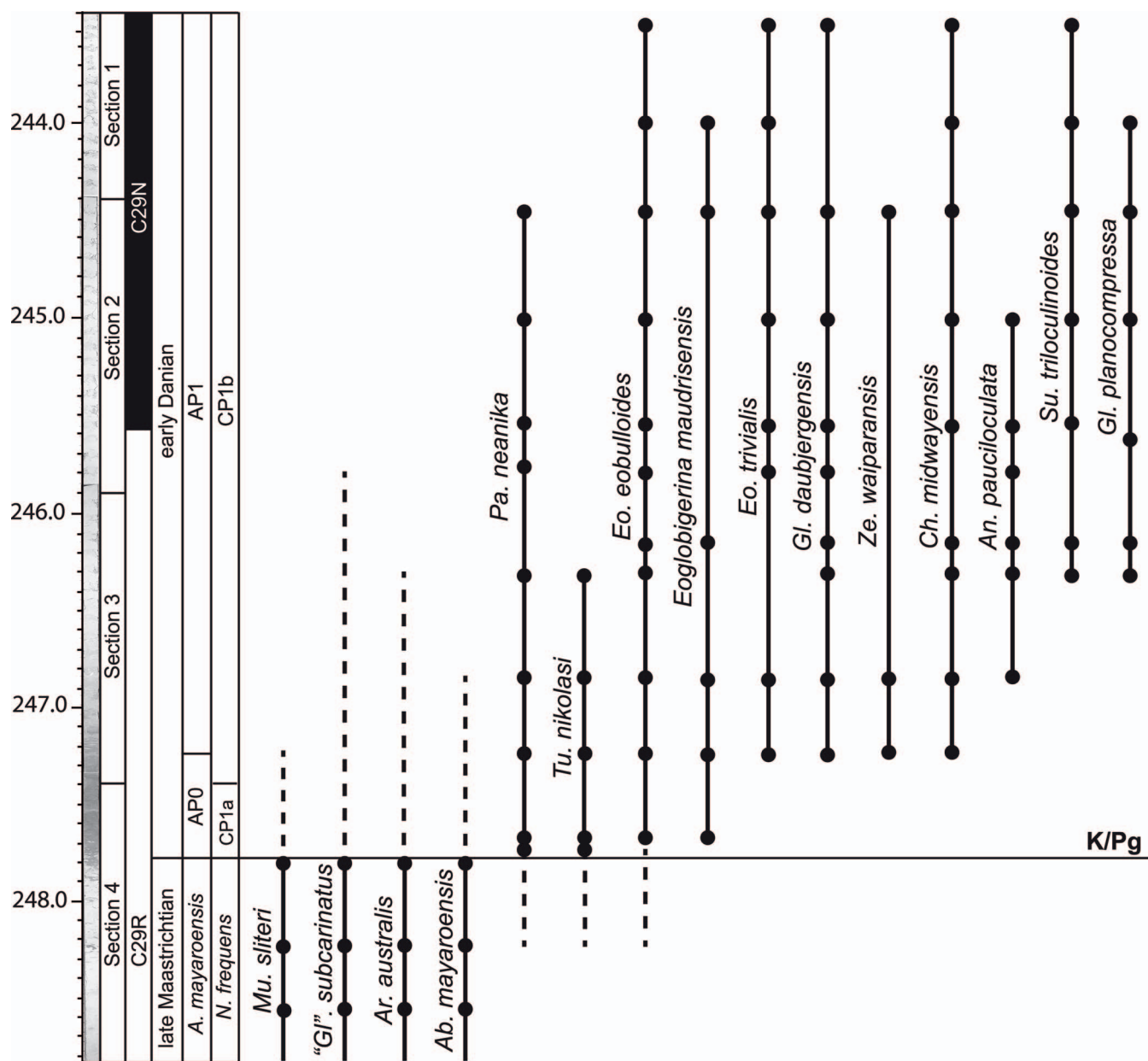


FIGURE 7. Distribution of planktonic foraminiferal across the K/Pg boundary interval in ODP Hole 690C. Composite core photos used to show changes in core lithology. Vertical dashed line represents specimen reworking. See Figure 2 caption for explanation of columns to left. Magnetostratigraphy from Hamilton (1990) and calcareous nannofossil biostratigraphy from Pospichal & Wise (1990).

et al. (1998, pl. 3, fig. 8) revealed that the species has the same distinct bridge-like extensions obscuring the primary apertures, presence of a microperforate wall, and a similar chamber arrangement and morphology, providing justification for placing *Gl. pauciloculata* in *Antarcticella*, and they considered it to be the earliest ancestor of the lineage. As noted by Liu et al. (1998), *Antarcticella pauciloculata* has less distinct sutural apertures than *An. antarctica* and *An. zeocenica* (Hornibrook & Jenkins); it differs from *An. zeocenica* (Hornibrook & Jenkins) by possessing a lower trochospire. Jenkins (1966) placed *An. pauciloculata* in *Globigerina* because of its globular, inflated chambers. Re-evaluation of the taxonomic status of the species by Liu

et al. (1998) revealed that there was no likely planktonic ancestor among the known survivors of the K/Pg extinction event. For this reason and because of differences from typical planktonic morphologies, including (1) absence of a primary aperture, (2) concentration of pustules only along umbilical chamber sutures, and (3) distributions restricted to southern high-latitude localities and mostly shallow water habitats, Liu et al. (1998) concluded that the species descended from a benthic ancestor and probably lived a benthic mode of life. However, comparison of stable isotope measurements from Maud Rise specimens of *An. pauciloculata*, planktonic specimens of *Globanomalina planocompressa* and *Eoglobigerina eobulloides*, and the

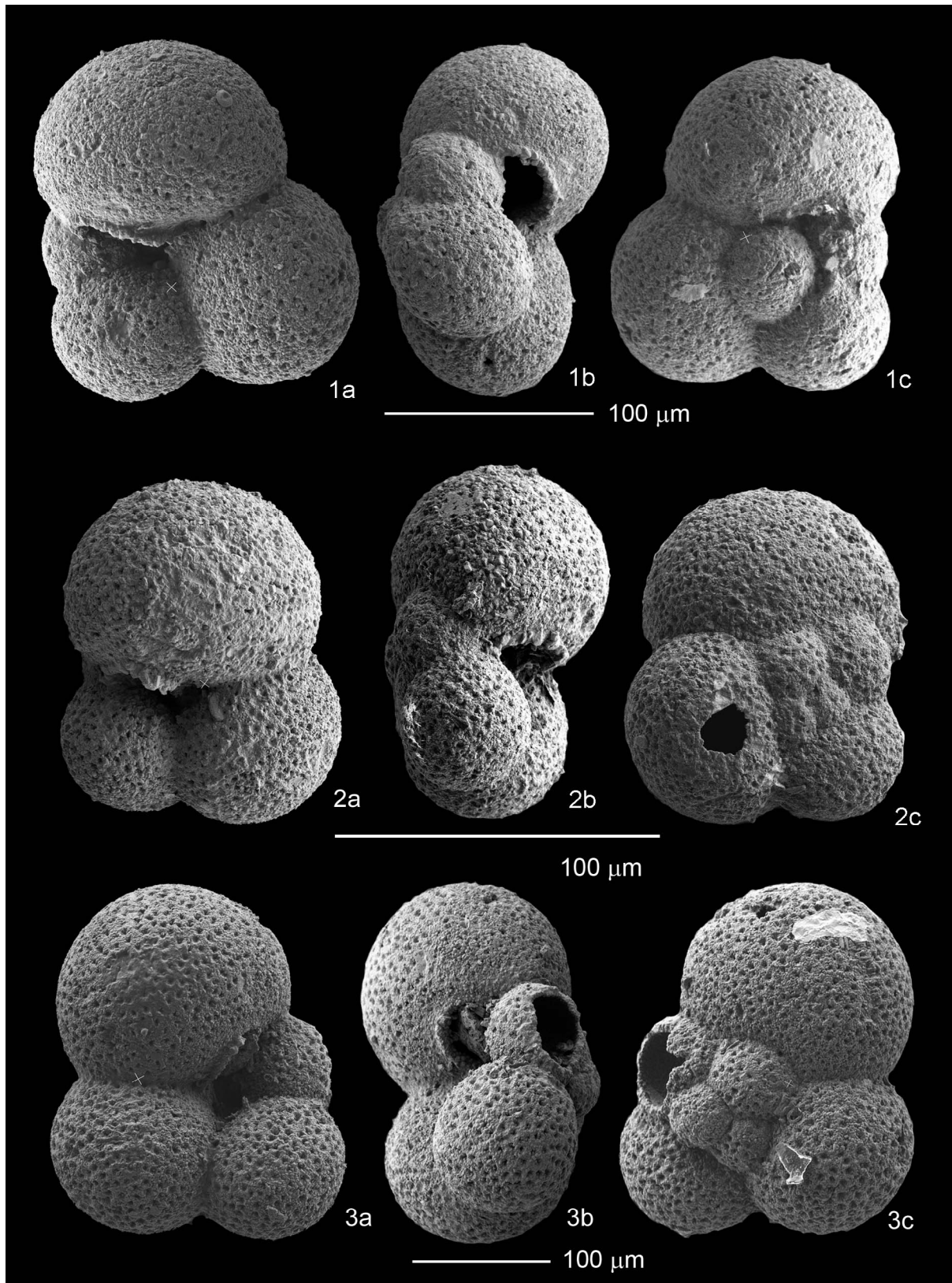


FIGURE 8. *Parasubbotina neanika* Huber and Petrizzo n. sp. **1a–c** Holotype, USNM 770854, Sample 690C-15X-4, 25–28 cm; **2a–c** Paratype, USNM 770855, Sample Paratype 690C-15X-4, 25–28 cm; **3a–c** Paratype USNM 770856, Sample 690C-15X-4, 28–30 cm.

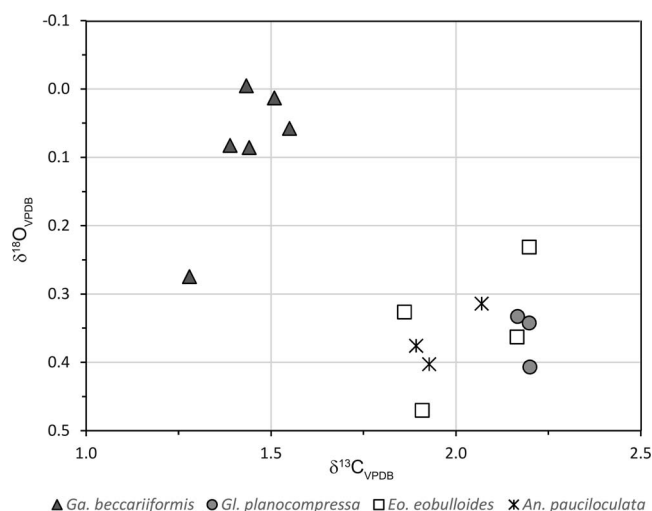


FIGURE 9. Foraminiferal oxygen and carbon isotope plots for *Gavelinella beccariiiformis* (benthic foraminifer), *Globanomalina planocompressa* and *Eoglobigerina eobulloides* (planktic foraminifera), and *Antarcticella pauciloculata* (previously considered a benthic foraminifer).

benthic species *Gavelinella beccariiiformis* (Table 4, Fig. 9) establishes that it lived a planktonic not benthic mode of life since its  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values group with co-occurring planktonic species for multiple samples. Liu et al. (1998) postulated that *An. pauciloculata* evolved from a benthic ancestor, perhaps *Praepararotalia cretacea*, and adapted to a tychoelagic or wholly planktonic life mode.

Superfamily GLOBIGERINACEAE Carpenter, Parker & Jones, 1862

Family GLOBIGERINIDAE Carpenter, Parker & Jones, 1862

Genus PARASUBBOTINA Olsson, Hemleben, Berggren & Liu, 1992

Type species: *Globigerina pseudobulloides* Plummer, 1927

**Remarks.** This genus is characterized by having a very low trochospiral test with 4.0–5.0 globular chambers in the final whorl increasing rapidly in size with the final one or two chambers sometimes offset toward the umbilicus. It has a highly arched umbilical-extraumbilical aperture bordered by a thin lip, and the wall texture shows weakly cancellate with spine holes observed along the cancellate ridges on well preserved specimens (Olsson et al., 1992).

*Parasubbotina neanika* Huber & Petrizzo, n. sp.  
Figs. 8.1–8.3

*Parasubbotina* aff. *Pa. pseudobulloides* (Plummer). Olsson et al., 1992, p. 197, pl. 4, figs. 1–4 [lower Danian, lower Zone P $\alpha$ , Clayton Basal Sands, Millers Ferry, Alabama]; Olsson et al., 1999, p. 25, 26, pl. 22, figs. 1–5 [lower Danian, Zone P $\alpha$ , Clayton Basal Sands, Millers Ferry, Alabama]; Koutsoukos, 2014, p. 127, figs. 12.9, 12.10 [lower Danian, lower Zone P $\alpha$ , piston core from 2809 water depth, core depth 132–134 cm, Campos Basin, offshore Brazil]; Rostami & Balmaki, 2018, pl. 6, figs. 4, 5 [lower Danian, Ziarat-Kola section, northern Iran].

*Parasubbotina* cf. *pseudobulloides* (Plummer, 1927). Koutsoukos, 1996, pl. 4, figs. 6–8 [lower Danian, upper P $\alpha$  Zone, Poty core #1, 487–489 cm, Pernambuco, NE Brazil].

*Eoglobigerina fringa* (Subbotina). Koutsoukos, 1996, pl. 3, fig. 11 [lower Danian, upper P $\alpha$  Zone, Poty core #1, 487–489 cm, Pernambuco, NE Brazil]; Arenillas & Arz, 2013, fig. 8.1 [lower Danian, *Eoglobigerina simplicissima* Subzone, El Kef, Tunisia].

Ex interc. *Eoglobigerina fringa* (Subbotina) and *Parasubbotina* cf. *pseudobulloides* (Plummer), Koutsoukos, 1996, pl. 3, figs. 12–13 [lower Danian, upper P $\alpha$  Zone, Poty core #1, 439.5–442.0 cm, Pernambuco, NE Brazil].

**Description.** Test small, ranging from 0.11 to 0.28 mm in maximum diameter, breadth 0.07–0.18  $\mu\text{m}$ , breadth:diameter ratio from 0.58 to 0.64; low trochospiral, with 5 to 10 total subglobular chambers increasing moderately in size, 3.25 to 5.0 chambers in the final whorl; proloculus varying in size from microspheric (minimum 14  $\mu\text{m}$ ) to large (maximum 50  $\mu\text{m}$ ). Equatorial periphery moderately to strongly lobate, axial periphery rounded to slightly compressed. Umbilicus is very small, moderately depressed. Spiral chambers rounded to radially elongate, slightly inflated, with final chamber showing slight elongation in the coiling direction, sutures radial and moderately depressed; umbilical chambers rounded to radially elongate, moderately to strongly inflated, sutures radial and depressed. Aperture umbilical-extraumbilical, highly arched, bordered by a thin imperforate lip. Wall calcareous, weakly cancellate, and finely perforate with circular pores that range from 1.2 to 1.8  $\mu\text{m}$  with spine holes apparent on well preserved specimens (e.g., Olsson et al., 1999, pl. 22, fig. 5).

Holotype (USNM 770854; Fig. 8.1a–c): maximum diameter 184  $\mu\text{m}$ , breadth 106  $\mu\text{m}$ , proloculus diameter 45  $\mu\text{m}$ ; paratypes (USNM 770855 and 770856) diameter 109–280  $\mu\text{m}$ , breadth 70–175  $\mu\text{m}$ , proloculus diameter 14–50  $\mu\text{m}$ .

**Remarks.** Morphotypes included in this species were referred to as *Parasubbotina* aff. *Pa. pseudobulloides* by Olsson et al. (1992, 1999) and Koutsoukos (2014) who characterized it as having a smaller and more tightly coiled test with a more finely cancellate wall than *Pa. pseudobulloides*. This *affinis* morphotype was considered as ancestral to *Pa. pseudobulloides*, the nominate species of Zone P1a, by Olsson et al. (1999) who noted that occurrence intermediate forms between *Pa. pseudobulloides* s.s. and *Pa. aff. Pseudobulloides* has impeded consistent identification of the base of Zone P1a (Olsson et al., 1999).

A specimen identified by Arenillas & Arz (2013, fig. 8.1) as *Eoglobigerina fringa* is here considered synonymous with *Pa. neanika* because of its small size, four-chambered morphology, and weakly cancellate wall texture. A second form identified by the same authors as *Eo. fringa* (Arenillas & Arz, fig. 8.2) has a more cancellate wall texture that more strongly resembles the *Eo. fringa* holotype.

Specimens of *Pa. neanika* from Hole 690C tend to be more tightly coiled with fewer chambers in the final whorl (3.25 to 3.75) compared to other locations where up to five chambers in the final whorl have been recorded. The Hole 690C specimens also have fewer total chambers (5–7) than elsewhere (typically 8–10 total chambers).

This species was placed in *Parasubbotina* based on observation of spine holes in well-preserved Zone P $\alpha$  specimens from the Millers Ferry core (see Olsson et al., 1992). Specimens observed from Site 690 are too recrystallized to identify spine holes. It differs from *Eoglobigerina fringa* (Subbotina, 1950) by having a much less cancellate wall texture.

**Etymology.** Derived from the Greek term “neanikus” meaning youthful referring to the pre-adult appearance of the test.

**Phylogenetic relationships.** Koutsoukos (2014) suggested that *Pa. neanika* may have evolved from *Tu. nikolasi* in Zone P $\alpha$ . Olsson et al. (1992, 1999) suggested that *Pa. neanika* (= *Pa. aff. pseudobulloides*) is directly ancestral to *Pa. pseudobulloides*.

**Repository.** Holotype USNM 770854 and paratypes USNM 770855 and 770856 are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

**Stratigraphic range.** Upper Zone P0 through Zone P $\alpha$  at lower latitudes, Zone AP0–AP1 at Maud Rise.

**Geographic distribution.** Cosmopolitan.

**Stable isotope paleobiology.** No data available.

Genus *Eoglobigerina* Morozova, 1959

Type species: *Globigerina* (*Eoglobigerina*) *eobulloides* Morozova, 1959, emended

**Remarks.** This genus includes species with 10–16 total chambers and 4–5 chambers in the final whorl with relatively tight coiling around a narrow umbilicus and a moderate to high trochospire. It is also characterized by having a cancellate wall texture with spine holes observed along cancellate ridges on well preserved specimens and by a low aperture umbilical to slightly extraumbilical in position and bordered by a thin, narrow lip (Olsson et al., 1999).

*Eoglobigerina maudrisensis* Huber & Petizzo, n. sp.  
Figs. 5.1–5.6

*Subbotina moskovini* [misspelling of *Subbotina moskvini* (Shutsкая, 1953)]. Stott & Kennett, 1990, p. 559, pl. 1, figs. 3, 4 [lower Danian, Zone AP0, ODP Hole 690C, Sample 690C-15X-4, 28–30 cm, Maud Rise, Weddell Sea].

**Description.** Test small, maximum diameter ranging from 0.12–0.20 mm, breadth ranging from 0.11–0.17 mm, breadth:diameter ratio ranging from 0.88 to 0.96; high trochospiral with 9 to 13 total globular chambers increasing moderately in size and 3.5 to 4.25 chambers in the final whorl; proloculus size uncertain. Equatorial periphery moderately lobate, axial periphery rounded. Spiral chambers rounded to radially elongate, slightly inflated, with final chamber showing slight elongation in the coiling direction, sutures radial and weakly depressed; umbilical chambers rounded to radially elongate, moderately to strongly inflated, sutures radial and moderately depressed. Final chamber bulge and directed over and obscuring the umbilicus; aperture umbilical-extraumbilical, highly arched, bordered by a narrow imperforate lip and sometimes flaps extending to previous chamber. Wall calcareous, cancellate, nonspinose, and macroperforate with circular pores that range from 2.2 to 3.7  $\mu$ m in diameter and may have elongated muricate concentrated in the umbilical region (e.g., Figs. 5.1b, 5.3b).

Holotype (USNM 770857; Figs. 5.1a–d): maximum diameter 202  $\mu$ m, breadth 172  $\mu$ m, proloculus diameter uncertain; paratypes (USNM 770858 and 770859; Figs. 5.4a–d, 5.5a–d): diameter 124–202  $\mu$ m, breadth 109–175  $\mu$ m, proloculus diameter uncertain.

**Remarks.** *Eoglobigerina maudrisensis* was identified as *Subbotina moskovini* (Shutsкая, 1953) by Stott & Kennett (1990, Pl. 1, figs. 3–4), which is a misspelling of *Globigerina moskvini* Shutsкая, 1953. The latter species now considered as a junior synonym of *Pa. pseudobulloides* (according to mikrotax.org/pforams/). It is distinguished from other early Danian species by its small test with a very high trochospire, coarse cancellate wall texture, and kummerform final chamber that covers part or all of the umbilicus. The species is included in *Eoglobigerina* because of the coarsely cancellate wall texture, tightness of coiling around a narrow umbilicus, and presence of an aperture that is mostly umbilical in position and bordered by a narrow lip. It differs from other species of *Eoglobigerina* by the presence of muricae that are enlarged along the umbilical sutures and absence of evidence for shell spines (e.g., Figs 5.1d, 5.3c, 5.5d), although this may be an artifact of preservation.

The specimen illustrated in Figure 5.5 is considered a juvenile morphotype because of its small size and weak development of the cancellate wall texture. The specimen illustrated from the lowermost Danian of Hole U1514C (Fig. 5.6) is strongly recrystallized and therefore shows a coarser wall texture than expected, but the compact coiling, high trochospire, and remnant suture showing former presence of a kummerform chamber justify inclusion in *Eo. maudrisensis*.

**Repository.** Holotype (USNM 770857) and paratypes (USNM 770858 and 770859) are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

**Etymology.** Named for Maud Rise, a submarine plateau drilled during ODP Leg 113 where it was first found.

**Phylogenetic relationships.** Ancestral species uncertain; possible direct ancestor of *Eoglobigerina eobulloides* and other species included in the *Eoglobigerina* lineage.

**Stratigraphic range.** Zone AP0–AP1 at Maud Rise Site 690 and Zone AP0 at Mentelle Basin Site U1514. Poor preservation in the lower Danian at Hole U1514C precludes determination of its stratigraphic range at that site above its single occurrence in the lowermost Danian sample.

**Geographic distribution.** Restricted to southern high latitudes with occurrences at ODP Site 690 (Weddell Sea, southern South Atlantic) and IODP Site U1514 (Mentelle Basin, SE Indian Ocean).

**Stable isotope paleobiology.** No data available.

Genus *Turborotalita* Blow & Banner, 1962, emend. Pearson & Kučera, 2018

Type species: *Truncatulina humilis* Brady, 1884

**Remarks.** Blow & Banner (1962) distinguished *Turborotalita* from other planktonic foraminiferal genera by its small, flattened test with 4.5–5.0 chambers in the final whorl, a spinose, normal perforate wall structure, and presence of a bulla. However, Pearson & Kučera (2018) observed that rather than having a bulla, as currently defined

*sensu* Hottinger (2006), the final chamber is often kummerform and ampullate in shape, with a tendency of being displaced toward the umbilicus, which is often covered by a broad apertural flap. Using their criteria for defining the genus, Pearson & Kučera (2018) reassigned *Praemurica nikolasi* Koutsoukos to *Turborotalita*, extending the genus range across the entire Cenozoic. This taxonomic revision is further supported by the genetic study of *Tu. quinqueloba* (Natland) by Aurahs et al. (2009), who suggested a deep phylogenetic divergence for the *Turborotalita* lineage.

*Turborotalita nikolasi* Koutsoukos, 2014  
Figs. 4.9–4.10

*Globigerina fringa* Subbotina. Smit, 1982, p. 339, pl. 2, figs. 11A–C [lower Danian, Zone P $\alpha$ , El Kef, Tunisia].

“*Globorotalia*” (*Turborotalia*) cf. *tetragona* (Morozova). Stott & Kennett, 1990, p. 559, pl. 1, figs. 12–13 [lower Danian, Zone AP1, ODP Sample 690C-15X-4, 28–30 cm, Maud Rise, Weddell Sea].

*Eoglobigerina fringa* (Subbotina). Huber, 1991, p. 461, pl. 2, fig. 8 [lower Danian, Zone AP0, ODP Sample 738C-20R-5, 91–92 cm].

*Praemurica nikolasi* Koutsoukos, 2014, p. 129–132, figs. 13.1–13.8, 14.1–14.9 [lower Danian, lower Zone P $\alpha$ , piston core from 2809 m water depth, core depth 132–153 cm, Campos Basin, offshore Brazil].

**Remarks.** This species is characterized by its very small size (maximum diameter 130–170  $\mu$ m), low to moderately trochospiral test with 4.5–5.0 subglobular chambers in the final whorl and presence of an ampullate final chamber with an umbilical-extraumbilical aperture and a thin apertural flap that projects toward and sometimes obscures the umbilicus. The test wall is non-spinose with a weakly cancellate, microperforate wall and circular wall pores that range from 0.3–1.0  $\mu$ m in diameter. The range of morphologic variation is comparable at all low and high latitude sites where it has been reported.

Pearson & Kučera (2018) transferred *Praemurica nikolasi* to *Turborotalita* because of the apparent presence of spine holes on illustrated specimens (whereas *Praemurica* is defined as a non-spinose genus), presence of the distinctive ampullate final chamber, and other morphologic features that are consistent with the emended concept of *Turborotalita*. Moreover, the type species of *Praemurica*, *Pr. taurica* (Morozova), has a very different general morphology and wall texture than *Tu. nikolasi*.

**Phylogenetic relationships.** Koutsoukos (2014) suggested that *Tu. nikolasi* is a descendant of *Muricohedbergella monmouthensis* since its lowest occurrence is just above the K/Pg boundary and it has a similar general morphology. This species may be directly ancestral to *Globorotalia imitata* Subbotina, which was tentatively assigned to *Turborotalita* by Pearson & Kučera (2018) and first occurs in Zone P1c according to Olsson et al. (1999; reported as *Globanomalina imitata*).

**Stratigraphic range.** The lowest occurrence of *Tu. nikolasi* is recorded immediately above the K/Pg boundary in the Campos Basin and at Maud Rise Site 690. The upper range is uncertain. In Hole 690C its highest occurrence is recorded in lowermost Zone AP1b, which is defined on

the lowest occurrence of *Subbotina triloculinoides* (Plummer) and is equivalent to the base of tropical/subtropical Zone P1b. Koutsoukos (2014) recorded *Tu. nikolasi* in Zone P1c in the Campos Basin, but its upper range was truncated at the top of the piston core.

**Geographic distribution.** Cosmopolitan.

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