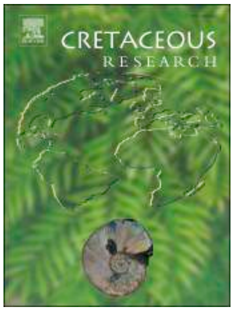

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PII: S0195-6671(20)30233-0

DOI: https://doi.org/10.1016/j.cretres.2020.104547

Reference: YCRES 104547

To appear in: *Cretaceous Research*

Received Date: 28 February 2020

Revised Date: 7 June 2020

Accepted Date: 10 June 2020

Please cite this article as: Petrizzo, M.R., Huber, B.T., Falzoni, F., MacLeod, K.G., Changes in biogeographic distribution patterns of southern mid-to high latitude planktonic foraminifera during the Late Cretaceous hot to cool greenhouse climate transition, *Cretaceous Research*, https://doi.org/10.1016/j.cretres.2020.104547.

Changes in biogeographic distribution patterns of southern mid- to high latitude planktonic foraminifera during the Late Cretaceous hot to cool greenhouse climate transition

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Abstract

The biogeographic distribution of planktonic foraminifera from southern mid- to high latitudes region are discussed to identify links between species distribution patterns and the changes in Late Cretaceous climate. We present relative abundance data for planktonic foraminifera spanning from the hot greenhouse climate of the Turonian to the cooler greenhouse of the Maastrichtian based on study of Ocean Drilling Program (ODP) holes 690C (Maud Rise), 700B (Northeast Georgia Rise), 1138A (Kerguelen Plateau) and 762C (Exmouth Plateau). These drill sites were located between 47° and 65°S paleolatitude in the southern South Atlantic and southern Indian Ocean where there is a good record of changes in vertical gradients and sea surface temperatures (SSTs) and shifts are well expressed due to amplification of global climatic variations in the circum-Antarctic region.

The stratigraphic distribution of planktonic foraminiferal marker species that consistently occur at all sites enables construction of a new biozonation scheme that is applicable to the southern mid- to high latitude region. Quantitative data from planktonic foraminifera are used to examine variation in assemblage composition, permitting interpretation of changes in the patterns of surface water stratification. In addition, temporal biogeographic patterns are documented from the stratigraphic record of endemic species of the Southern Ocean and of species displaying poleward or equatorward migration.

Results indicate that the broadest latitudinal expansion of the Tethyan tropical climatic belt coincided with the highest paleotemperatures of the Turonian–Santonian. The onset of significant sea surface temperature cooling in the late Santonian–early Campanian led to a progressive increase in the latitudinal temperature gradient and greater biogeographic differentiation among planktonic foraminiferal assemblages. These trends resulted in the establishment of a Transitional Bioprovince with Tethyan and Austral affinities in the southern latitudes that persisted through the Campanian and Maastrichtian and the development of a well-defined Austral Bioprovince that is observed by the early Maastrichtian at paleolatitudes south of 60°S.

Keywords: planktonic foraminifera; biozonation; paleoecology; biogeography; climate; circum-Antarctic; Late Cretaceous.

1. Introduction

The Late Cretaceous extreme greenhouse climate interval reached maximum warmth during the Turonian (Bice et al., 2003; Clarke and Jenkyns, 1999; Friedrich et al., 2012; Jenkyns et al., 1994; O'Brien et al., 2017; Voigt et al., 2004), with surface-ocean temperatures of about 36°C at low latitudes (Forster et al., 2007; MacLeod et al., 2013; Moriya et al., 2007), and equator-to-pole sea surface temperature gradients reduced to about 5°C (Huber et al., 2002; Linnert et al., 2014; O'Brien et al., 2017). This hot greenhouse phase ended in the late Santonian at the onset of prolonged cooling that persisted until the mid-Maastrichtian (Clarke and Jenkyns, 1999; Cramer et al., 2009; Falzoni et al., 2016; Friedrich et al., 2012; Huber et al., 2002, 2018; O'Brien et al., 2017). Regional warming and cooling episodes and regional differentiation in sea surface (Isaza-Londoño et al., 2006; MacLeod et al., 2005) and bottom water masses (Cramer et al., 2009) occurred during the late Campanian and late Maastrichtian (Abramovich et al., 2010; Falzoni et al., 2016; Friedrich et al., 2012; Haynes et al., 2020; Huber et al., 2018; Li and Keller, 1999; Linnert et al., 2014, 2018).

Planktonic foraminifera underwent major changes during the hot greenhouse interval with species diversification among oligotrophic taxa in the Turonian–Coniacian and appearance of additional oligotrophic and meso-eutrophic taxa in the Coniacian–Santonian (Premoli Silva and Sliter, 1999). The hot to warm greenhouse transition from the Santonian to the early Campanian coincides with faunal turnover among double keeled, meso-oligotrophic taxa characterized by the disappearance of marginotruncanids and radiation of globotruncanids (e.g., Petrizzo, 2000; Premoli Silva and Sliter, 1999). This assemblage change occurred globally, although the timing and magnitude of the planktonic foraminiferal biotic changes at higher latitudes are less understood since the assemblages are dominated by long-ranging, less ornate and more eutrophic taxa with few occurrences of Tethyan taxa.

Analysis of planktonic foraminiferal biogeographic distributions at southern mid- to high latitudes enhances understanding of the changes in the vertical structure of the water column and surface circulation patterns in the circum-Antarctic across the Late Cretaceous climatic transitions. Turonian–Maastrichtian planktonic foraminifera discussed in the present study are from four Ocean Drilling Program (ODP) sites drilled in the Southern Hemisphere (Fig. 1): Hole 690C (Maud Rise), Hole 700B (Northeast Georgia Rise), Hole 1138A (Kerguelen Plateau), and Hole 762C (Exmouth Plateau). In the Late Cretaceous these sites were located between 47°and 65°S paleolatitude in the southern South Atlantic and Indian Ocean (e.g., Hay et al., 1999; Müller et al., 2016; Scotese, 2016) (Fig. 1). Comparison and integration of planktonic foraminiferal stratigraphic ranges at the four holes studied here enables acquisition of the most complete record of foraminiferal distributions and changes in species composition at southern mid- to high latitudes during the Late Cretaceous yet assembled.

We present planktonic foraminiferal assemblage data based on quantitative analyses with the aim to understand the variation in the composition of the assemblages that are used to interpret changes in the patterns of stratification of the surface ocean waters. The taxonomic composition and species diversity of the deep-sea planktonic foraminiferal assemblages are compared among sites. Paleolatitudinal positions of the biogeographic boundaries are interpreted from observations of eco-morphogroup diversity (e.g., unkeeled/keeled/planispiral/serial and shallow/intermediate/deep dwellers), and current knowledge of species paleoecology inferred from latitudinal distributions and from stable isotope studies.

2. Materials and methods

2.1 Hole 690C Maud Rise

Hole 690C is located at 65°9’S; 1°12’E (present water depth 2914 m) on the southwestern flank of Maud Rise in the southern South Atlantic Ocean (Fig. 1). Cretaceous sediments were recovered from 252 mbsf (meters below sea floor) to 317 mbsf, and they rest on basaltic basement. The lithology from core 690C-16X to -22X is composed of laminated to strongly bioturbated, foraminifer-bearing muddy nannofossil chalk (Fig. 2) with and increasing proportion of terrigenous material down section (Barker, Kennett et al., 1988).

The pelagic carbonate sequence in Hole 690C is assigned to the late Campanian–Maastrichtian (Fig. 2) according to the primary magnetostratigraphic and planktonic foraminiferal studies of Hamilton et al. (1990) and Huber (1990), respectively, with age assignments updated by Huber et al. (2018) using the geological time scale of Gradstein et al. (2012). Ages and core depths for planktonic foraminiferal and magnetostratigraphic events are listed in Table 1. Planktonic foraminiferal distributions and abundances (Appendix A. Supplementary data) are from Huber

(1990). Paleogeographic reconstructions indicate that this site occupied nearly the same latitude as today during the Late Cretaceous (Hay et al., 1999; Müller et al., 2016; Scotese, 2016).

2.2 Hole 700B Northeast Georgia Rise

Hole 700B is located at 51°32'S, 30°17'W (present water depth 3601 m) and was drilled on the northeastern slope of the Northeast Georgia Rise (Fig. 1). The Cretaceous micritic limestone sequence cored in Hole 700B comprised most of lithostratigraphic Unit V (Fig. 2) and extends from 319 mbsf to the bottom of the hole at 489 mbsf. This unit was subdivided into three subunits based on the degree of lithologic homogeneity and differences in the amount and type of non biogenic constituents (Ciesielski and Kristoffersen, 1988).

The examined stratigraphic interval from core 700B-37R to -54R ranges in age from Maastrichtian to Coniacian (Fig. 2) based on magnetostratigraphy (Hailwood and Clement, 1991), calcareous nannofossil biostratigraphy (Cruz, 1991) and planktonic foraminiferal bioevents according to Huber (1991a) and this study. The topmost stratigraphic interval in core 37R contains planktonic foraminifera and calcareous nannofossils of Cretaceous age in agreement with paleomagnetic data that place the base of Chron C30N in core 37R-2. Age assignments using planktonic foraminifera and magnetic polarity chron boundaries are listed in Table 2. Planktonic foraminiferal stratigraphic distribution and abundance data (Appendix A. Supplementary data) are from Huber (1991a) and this study. According to plate reconstructions by Hay et al. (1999) and Scotese (2016) this site was located at about 58°S during the Late Cretaceous.

2.3 Hole 1138A Kerguelen Plateau

Hole 1138A (53°33’S, 75° 58’E; present water depth 1141 m) lies on central Kerguelen Plateau, approximately 150 km east-southeast of Heard Island (Fig. 1). In Hole 1138A Cretaceous sediments were recovered from 490.40 to 698.23 mbsf just above the basaltic basement. The lithology of the stratigraphic interval from core 1138A-52R to -69R (Fig. 2) varies from a foraminifer-bearing nannofossil chalk to a nannofossil claystone that overlies a glauconitic calcareous sandstone and shows a downward decrease in carbonate content (Coffin et al., 2000). Cores recovered range from Maastrichtian to latest Cenomanian in age according to the shipboard calcareous nannofossil (Coffin et al., 2000) and planktonic foraminifera (Petrizzo, 2001) data. Age assignments of the planktonic foraminiferal bioevents are listed in Table 3. The planktonic foraminiferal record (Appendix A. Supplementary data) discussed in this paper is based on the work of Petrizzo (2001) and this study. The paleolatitude of the hole was about 50°S in the Late Cretaceous according to the plate tectonic reconstructions of Hay et al. (1999) and Scotese (2016).

2.4 Hole 762C Exmouth Plateau

Hole 762C (19° 53’S, 112°15’E; present water depth 1360 m) was drilled during ODP Leg 122 on the western part of central Exmouth Plateau (Fig. 1). Located on the NW margin of Australia in the eastern Indian Ocean, Exmouth Plateau is the offshore extension of the northern Carnarvon Basin (Hocking et al., 1987). Exmouth Plateau is a thinned, subsided and sediment-starved continental block about 20 km thick, representing a passive continental margin with a wide continent/ocean transition (Haq et al., 1992; Wilcox and Exon, 1976). Hole 762C penetrated 770 m of sedimentary rocks above basement, which was reached at 940 mbsf. In this study we have examined the stratigraphic interval from core 762C-43X to -74X (Fig. 2), which consists mainly of pelagic calcareous clays and chalks (Haq et al., 1990) deposited above the carbonate compensation depth (Wonders, 1992). The Cretaceous interval ranges from Maastrichtian to Turonian in age according to magnetostratigraphy (Galbrun, 1992; Thibault et al., 2012), calcareous nannofossil biostratigraphy (Bralower and Siesser, 1992; Thibault et al., 2012), and planktonic foraminiferal observations of Wonders (1992), Zepeda (1998), Petrizzo (2000), and this study. Age assignments using planktonic foraminifera, calcareous nannofossils and magnetic polarity chron boundaries are listed in Table 4. Planktonic foraminiferal stratigraphic distributions and abundance data (Appendix A. Supplementary data) are from Zepeda (1998), Petrizzo (2000) and this study. Paleogeographic reconstructions indicate that this site was at about 47°S during the Late Cretaceous (Hay et al., 1999; Scotese, 2016).

Samples from Hole 690C are stored at the Department of Paleobiology, Smithsonian National Museum of Natural History (Washington, DC). Samples from holes 700B, 1138A and 762C are deposited at the Dipartimento di Scienze della Terra **“**A. Desio**”**, Università degli Studi di Milano (Milan, Italy) in the collection of Micropaleontology (Micro-Unimi). For all studied holes foraminiferal taxonomy follows 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). New foraminiferal stable-isotope ratio data were generated using a Thermo Finnegan^{TM} Delta Plus dual-inlet isotope-ratio mass spectrometer (IRMS) with Kiel III online automated carbonate reaction system at the University of Missouri. Results are reported in ‰ on the Vienna-PDB scale and have an external precision of +/- 0.03‰ and +/- 0.06‰ (1 standard deviation) for $\delta^{13}C$ and $\delta^{18}O$, respectively, based on long term monitoring of results for the NBS-19 standard. Dates used for the age models are based on the 2012 Geologic Time Scale (Gradstein et al., 2012).

3. Planktonic foraminiferal bioevents and biozonation

The most important planktonic foraminiferal bioevents identified at all localities are plotted in Fig. 3 using the age assignments included in Tables 1-4. The planktonic foraminiferal biozonation is based on identification of bioevents that consistently occur at all ODP holes discussed in this study. First and last occurrence events used to define the biozones are shown in bold in Figure 3. This new zonal scheme derives from the Transitional biozonation of Petrizzo (2001, 2003) applied at paleolatitudes between 58°S and 47°S (from Northeast Georgia Rise to Exmouth Plateau) in the Turonian to lower Campanian interval, and from the Austral biozonation of

Huber (1990, 1992) based on the middle Campanian to Maastrichtian record at Maud Rise and South Atlantic sites (paleolatitude > 60°S: Huber, 1992).

We observe a similar sequence of planktonic foraminiferal bioevents in the Turonian to lower Campanian interval at all sites (Fig. 3). The lower Turonian *Helvetoglobotruncana helvetica* Zone, defined on the total range of the nominal taxon, is observed only in holes 1138A and 762C because of lack of sediment recovery or presence of equivalent age sediments in holes 700B and 690C, respectively. The stratigraphic interval from the HO (highest occurrence) of *Falsotruncana maslakovae* in the upper Turonian to the LO (lowest occurrence) of the high latitude endemic species *"Globigerinelloides" impensus* in the Santonian–lowermost Campanian is equivalent to the *Marginotruncana marginata* (= *Marginotruncana pseudomarginata* Neagu 2012, see discussion in Petrizzo et al., 2017) and to the *Planoheterohelix papula* zones in the biozonation of Petrizzo (2003). To improve on the resolution of the planktonic foraminiferal biozonation we have further subdivided this interval using the LOs of *Planoheterohelix papula* and *Globotruncana linneiana*, as follows (Fig. 3): 1) the stratigraphic interval from the HO of *Falsotruncana maslakovae* to the LO of *Planoheterohelix papula* is assigned to the *Marginotruncana* spp. Zone defined here as an interval zone between the two bioevents, 2) the *Planoheterohelix papula* Zone is identified at the base by the LO of *Planoheterohelix papula* and at the top by the LO of *Globotruncana linneiana*, and 3) the stratigraphic interval from the LO of *Globotruncana linneiana* (base) to the LO of *"Globigerinelloides" impensus* (top) is assigned to the *Globotruncana linneiana* Zone (Fig. 3).

The HO of *Falsotruncana maslakovae* and the LO of *Planoheterohelix papula* in Hole 1138A are very close and spaced of about 4 meters (Appendix A. Supplementary data) to indicate the presence of a hiatus spanning the upper Turonian to upper Coniacian. Because of this and non-recovery of sediments between cores 66R and 67R (Fig. 2), the position of the lower and upper boundaries of the *Marginotruncana* spp. Zone in Hole 1138A are uncertain and dashed in Fig. 3.

Unlike the higher latitude sites, the Tethyan zonal marker species *Dicarinella asymetrica* and *Globotrucana neotricarinata* (= *Globotruncana* aff. *ventricosa* in Petrizzo, 2000) occur continuously in the Coniacian–Santonian interval in Hole 762C (Fig. 3, Appendix A. Supplementary data). The upper boundary of the *Globotruncana linneiana* Zone, which is used to approximate the base of the Campanian, is clearly identifiable using the LO of *“Globigerinelloides” impensus.* However, the overlying interval lacks bioevents suitable for correlation among sites (Fig. 3) from the base of the Campanian until the HO of *“Globigerinelloides” impensus*.

The HO of *“Globigerinelloides” impensus* defines the upper boundary of the *“Globigerinelloides” impensus* Total Range Zone in the Austral and Transitional zonations (Huber, 1992; Petrizzo, 2003) and is observed at correlative stratigraphic positions in the upper Campanian at all localities except Exmouth Plateau where it disappears earlier in the early Campanian. The top *“Globigerinelloides” impensus* Zone can be also identified in Hole 762C, though, as the HO of *“Globigerinelloides” impensus* is correlative with the LO of *Gublerina rajagopalani* based on the record displayed by the two species in Hole 1138A. Therefore, the top of the *“Globigerinelloides” impensus* Zone can be recognized by both the HO of “*Globigerinelloides*” *impensus* and the LO of *Gublerina rajagopalani* as the two bioevents are regarded to be interchangeable at 47° to 50° S (Fig. 3) although the latter species is absent at the southernmost localities (holes 700B and 690C). We are aware that the application of the *“Globigerinelloides” impensus* Zone could be misleading in Hole 762C being the nominal species absent in the upper part of the biozone, however, we feel this concern is outweighed by the benefit of applying the same scheme across all four sites using a zonal definition with two marker bioevents at the top. This definition is tentative pending further studies from coeval stratigraphic sections located at equivalent paleolatitudes.

The upper Campanian–lower Maastrichtian sequence previously assigned to the *Globotruncanella havanensis* Zone of the Austral zonation (Huber, 1992) is here replaced by the *Archaeoglobigerina australis* Zone, defined from the HO of *“Globigerinelloides” impensus/*LO of *Gublerina rajagopalani* at the base and by the LO of *Abathomphalus mayaroensis* at the top. *Archaeoglobigerina australis* was first described as an endemic species of the Southern Ocean

(Huber, 1990; 1992) and later documented in the lower Maastrichtian sediments of the North Russian Basin (Saratov Region) at 52°N paleolatitude (Alekseev et al., 1999). The species is very common in the assemblages at all localities (Appendix A. Supplementary data), although its appearance is recorded at different stratigraphic levels within the *“Globigerinelloides” impensus* Zone. Its lowest occurrence is at the base of the recovered sedimentary sequence at Maud Rise, in the lower Campanian of the Northeast Georgia Rise, and in the middle Campanian at Kerguelen and Exmouth plateaus (Fig. 3). The lowest occurrence of *Globotruncanella havanensis* consistently occurs within the *Archaeoglobigerina australis* Zone in the upper Campanian at all holes (Fig. 3), but the species is quite rare, has a scattered stratigraphic record, and is sometimes difficult to detect.

The *Abathomphalus mayaroensis* Zone spans the interval between the LO of the nominate species and the extinction of Cretaceous taxa at the Cretaceous–Paleogene boundary. Although a slightly later appearance is observed in Hole 762C than at other sites, *Abathomphalus mayaroensis* commonly occurs at all localities starting in the lower Maastrichtian record (Fig. 3).

A number of species are found to have considerable variability in their distributions among and within sites. *Muricohedbergella sliteri,* a species interpreted to be restricted to the Southern Ocean (Huber 1992), shows a discontinuous record among sites as it first appears in the Santonian within the *Globotruncana linneiana* Zone at Exmouth Plateau, at the base of the Campanian in the same sample as *“Globigerinelloides” impensus* at Kerguelen Plateau and Northeast Georgia Rise, and in the upper Campanian *Archaeoglobigerina australis* Zone at Maud Rise (Fig. 3). *Rugotruncana circumnodifer,* regarded to be a common species in the Southern Ocean record (Huber, 1992), shows lowest occurrences ranging from the *Archaeoglobigerina australis* Zone to the lower part of the *Abathomphalus mayaroensis* Zone and is absent in Hole 762C. *Archaeoglobigerina mateola*, an endemic species of the Southern Oceans (Huber, 1992) is recorded at Maud Rise where it was first described (Huber, 1990) and in one sample co-occurring with *Rugotruncana circumnodifer* at Northeast Georgia Rise (Appendix A. Supplementary data). It does not occur in holes 1138A and 762C although rare specimens were reported in the *Abathomphalus* *mayaroensis* Zone in Hole 738C drilled on the Kerguelen Plateau (Huber, 1991b). *Praegublerina acuta* occurs at different stratigraphic levels in the studied holes: in the middle Campanian *"Globigerinelloides" impensus* Zone at Exmouth Plateau, in the upper Campanian *Archaeoglobigerina australis* Zone at Kerguelen Plateau, and in the Maastrichtian *Abathomphalus mayaroensis* Zone at Northeast Georgia Rise and Maud Rise (Fig. 3). Similarly, *"Globigerinelloides" subcarinatus* shows a much earlier appearance at Exmouth Plateau (middle Campanian *"Globigerinelloides" impensus* Zone in the same sample having the LO of *Praegublerina acuta*) than it does at other localities whereas it first occurs in the Maastrichtian *Abathomphalus mayaroensis* Zone (Fig. 3). Interestingly, the Maastrichtian Tethyan marker species *Racemiguembelina fructicosa* occurs at the Kerguelen and Exmouth Plateau close to the LO of *Abathomphalus mayaroensis*, whereas *Contusotruncana contusa* and the Campanian-Maastrichtian *Contusotruncana plummerae* are only observed in the assemblages of the Exmouth Plateau. The LO of *Contusotruncana plummerae* defines the base of the *Contusotruncana plummerae* Zone at low latitudes (Gradstein et al., 2012; Petrizzo et al., 2011) and its presence in Hole 762C, thus, is a useful observation allowing correlation between Austral and Tethyan biozonations.

4. Remarks on planktonic foraminiferal stratigraphic distribution across mid- to high latitudes

The stratigraphic ranges of cosmopolitan taxa (*Helvetoglobotruncana helvetica*, *Falsotruncana maslakovae*, *Planoheterohelix papula*, *Globotruncana linneiana*, *"Globigerinelloides" subcarinatus*, *Praegublerina acuta* and *Abathomphalus mayaroensis*) and taxa endemic or common to the Southern Ocean (*Muricohedbergella sliteri*, "*Globigerinelloides*" *impensus* and *Archaeoglobigerina australis*) at the localities examined are compared in Fig. 4. Some taxa show the same stratigraphic and temporal distribution at all latitudes, some taxa migrate towards higher latitudes, and some others migrate from higher to lower latitudes, as discussed below.

The total stratigraphic range of *Helvetoglobotruncana helvetica* is only recorded in holes 1138A and 762C while no information is available on its occurrence in holes 700B and 690C (Fig. 4) because lower Turonian sediments were not recovered there (Fig. 2). In Hole 762C the absence of *Helvetoglobotruncana helvetica* from lower Turonian samples just below its recorded lowest occurrence (Fig. 4) is probably an artifact of poor preservation or uncomplete sediments recovery (Falzoni et al., 2016) although the LO of *Helvetoglobotruncana helvetica* has been inconsistently recorded at some locations because it tends to be rare in its lower stratigraphic range (e.g., Caron et al., 2006; Falzoni et al., 2018; Huber and Petrizzo, 2014). Nonetheless, correlation of calcareous plankton events in Italian and Tunisian sections (Coccioni and Premoli Silva, 2015; Premoli Silva and Sliter, 1995; Robaszynski et al., 2000) and the age model applied in this study indicate that the timing of its LO and HO at most low latitude sites is nearly synchronous.

In holes 762C, 1138A and 700B *Falsotruncana maslakovae* shows a consistent stratigraphic range (Fig. 4), although its highest occurrence is not observed in Hole 1138A because of a stratigraphic gap (Figs. 2, 3) and its lowest occurrence could not be identified in Hole 700B because lower Turonian sediments were not recovered (Fig. 2). Its lowest occurrence is coincident with or falls immediately above the extinction of *Helvetoglobotruncana helvetica* in the middle Turonian at Exmouth and Kerguelen plateaus, in Tanzania (35°S paleolatitude; Huber et al., 2017), and at the Pont du Fahs type region in Tunisia (about 20°N paleolatitude) where the species was first described (Caron, 1981). In the studied holes, *Falsotruncana maslakovae* likely has a simultaneous level of highest occurrence (Fig. 4). Correlation of this level with nannofossil distributions in holes 1138A and 762C indicates that its extinction occurs near the LO of *Micula staurophora* (Bralower and Siesser, 1992; Crux, 1991; base of the UC10a Nannofossil Subzone, Burnett, 1998). On the other hand, all *Falsotruncana* species disappear well below the lowest occurrence of *Micula staurophora* in Tanzania (Huber et al., 2017). At low latitudes in the Tethyan region, the highest occurrence of *Falsotruncana maslakovae* is not well documented as the taxon becomes very rare at the end of its stratigraphic range (Robaszynski et al., 2000). Further study of well-preserved material from the Tethyan region is needed to verify the range of *Falsotruncana* at low latitudes and evaluate possible diachronism of its extinction level.

Planoheterohelix papula displays the same stratigraphic distribution at holes 762C, 1138A and 700B, although the base of its range is not registered at Hole 1138A because of a stratigraphic gap (Figs. 3, 4). Based on correlation with calcareous nannofossil bioevents, the lowest occurrence of *Planoheterohelix papula* at Exmouth Plateau (holes 762C and 763B) occurs slightly below the appearance of *Lithastrinus grillii* (Bralower and Siesser, 1992; Petrizzo, 2000) in the upper Coniacian. On the contrary in the Ten Mile Creek section Texas (30°N paleolatitude) and in Tanzania (35°S paleolatitude; Petrizzo, 2019; Petrizzo et al., 2017) the LO of *Planoheterohelix papula* is slightly above the LO of *Lithastrinus grillii* and below the LO of *Globotruncana linneiana*, which is used to approximate the Coniacian/Santonian boundary (Lamolda et al., 2014; Petrizzo, 2019; Petrizzo et al., 2017).

Muricohedbergella sliteri, a species described from the planktonic foraminiferal assemblages of Maud Rise (Huber, 1990) is the only endemic species in the circum-Antarctic region (Huber, 1992) that shows a distinct poleward migration indicated by its progressively delayed appearance at higher latitudes. Its lowest occurrence falls within Chron C34N at 762C, slightly below and above the base of Chron C33R in holes 1138A and 700B, respectively, whereas in Hole 690C it is first recorded within Chron C32R.

"Globigerinelloides" impensus was first described from the Campanian at the Falkland Plateau (DSDP Site 71: Sliter, 1977) and was later regarded as a species endemic to the circum-Antarctic region (Huber, 1992). It first occurs at about the same stratigraphic level in holes 762C and 1138A. While its LO shows a delay of about 0.5 ky at Hole 700B, which is probably an artifact of poor preservation or rarity of the species at the beginning of its stratigraphic range. The oldest occurrence of *"Globigerinelloides" impensus* is not recorded at Maud Rise because of lack of sediment recovery. The highest occurrence is registered within Chron C33N in holes 690C, 700B, and 1138A at about the same age, although the HO is slightly delayed (about 0.2 ky) in Hole 690C

according to the age model adopted in this study. In Hole 762C *“Globigerinelloides” impensus* shows a shorter stratigraphic range and disappears at 79.2 Ma indicating a poleward contraction of its biogeographic distribution (Fig. 4).

Praegublerina acuta is a Tethyan species that clearly shows a poleward migration from the southern mid- to high latitudes (Exmouth Plateau to Maud Rise; Fig. 4). In holes 762C and 1138A its lowest occurrence is recorded within Chron C33N, whereas it only occurs in the upper part of Chron C31R in holes 700B and 690C. Moreover, in the latter locality *Praegublerina acuta* shows a shorter stratigraphic range and disappears in the late Maastrichtian within Chron C30N (Fig. 4). The species may be regarded as cosmopolitan at least in the middle Maastrichtian being identified at low latitudes from Cuba to the El Kef section in Tunisia, in the Pacific, Atlantic and Indian Ocean (Georgescu et al., 2008).

“Globigerinelloides” subcarinatus is a cosmopolitan species with a diachronous stratigraphic range from low to high latitudes from the Campanian to the Maastrichtian. Its lowest occurrence in the Tethyan Realm has been observed within the Santonian *Dicarinella asymetrica* Zone (Coccioni and Premoli Silva, 2015; Premoli Silva and Sliter, 1995). The present study reveals *“Globigerinelloides” subcarinatus* migrated poleward from the southern mid- to high latitudes (Exmouth Plateau to Maud Rise; Fig. 4). In Hole 762C its LO is in the Campanian within Chron C33N, whereas it is recorded only in Maastrichtian sediments at holes 1138A, 700B and 690C, first occurring at slightly different ages within Chron C31R (Fig. 4; Tables 1-4).

Archaeoglobigerina australis is a species first described from Campanian-Maastrichtian assemblages of the Maud Rise (Huber, 1990) and it occurs in high abundance in the Southern Ocean (Huber, 1992). Its stratigraphic record reveals a distinct equatorward migration from Maud Rise to Exmouth Plateau, although its oldest occurrence is not observed in Hole 690C because of a lack of sediment recovery. In Hole 700B *Archaeoglobigerina australis* first appears within Chron C33R, and in holes 1138A and 762C it first appears at a slightly younger stratigraphic interval (lower part of Chron C33N; Fig. 4; Tables 1-4).

Abathomphalus mayaroensis is a cosmopolitan species characterized by a clear equatorward migration for its lowest occurrence (Huber and Watkins, 1992). In fact, *Abathomphalus mayaroensis* first occurs in Hole 690C in lower Chron C31R (Huber, 1992). A slightly younger age within Chron C31R is registered in holes 700B and 1138A (Petrizzo, 2001) and in the Exmouth Plateau (Fig. 4), which are all earlier compared to the Tethyan sections where *Abathomphalus mayaroensis* first appears at the base of Chron C31N (Coccioni and Premoli Silva, 2015; Robaszynski and Caron, 1995).

Globotruncana linneiana occurs at all localities examined in this study except Maud Rise (Appendix A. Supplementary data). The LO of this species is a secondary marker for the identification of the Santonian GSSP (Lamolda et al., 2014) and has been used to approximate the base of the Santonian Stage at low to mid latitudes (Spain, Texas, Tanzania: see Petrizzo 2019; Petrizzo et al., 2017). According to the age model used in this study the lowest occurrence of *Globotruncana linneiana* is almost synchronous at the three localities, confirming the cosmopolitan appearance of the species from low to high latitudes. However, *Globotruncana linneiana* shows a poleward contraction of its stratigraphic range and diachronism of its extinction level. It disappears in the Campanian within Chron C33N in Hole 700B and in the Maastrichtian above the base of Chron C31R in Hole 1138A and within Chron C30N in Hole 762C (Fig. 4).

5. Planktonic foraminiferal morphogroups abundance

Planktonic foraminiferal assemblages in Hole 690C (Fig. 5, Appendix A. Supplementary data) are characterized by dominance of unkeeled trochospiral taxa (from 20 to 62%) with *Archaeoglobigerina australis*, *Rugotruncana circumnodifer*, *Muricohedbergella monmouthensis* and *Muricohedbergella sliteri* being the most abundant species. Keeled taxa are rare throughout the stratigraphic section, never exceeding 4% of the total assemblages, with *Abathomphalus mayaroensis* being the most common keeled species. Planispiral taxa are most abundant (up to 70%) in the lowermost part of the upper Campanian, they decrease and fluctuate in abundance (average values 25%) in the uppermost Campanian and slightly increase in abundance through the upper Maastrichtian. The biapertural *"Globigerinelloides" multispinus* is the most common species throughout. Biserial taxa are mainly represented by the species *Planoheterohelix globulosa* and *Planoheterohelix planata*.

Assemblages in Hole 700B (Fig. 5, Appendix A. Supplementary data) show a change in species composition in the lower Campanian. Trochospiral unkeeled taxa are common (from 25% to 74%) throughout the section and are dominated by *Muricohedbergella planispira* in the Turonian to Santonian interval, and by *Archaeoglobigerina australis* in the Campanian until the top of the studied section. Keeled taxa occur from the Turonian to lower Campanian and are mainly represented by marginotruncanids ranging from 20% to 35%. This group then becames rare to absent and is represented by only few specimens of *Globotruncana linneiana* in the lower Campanian and of *Abathomphalus mayaroensis* in the Maastrichtian. Planispiral taxa, mainly *"Globigerinelloides" bollii* and *"Globigerinelloides" prairiehillensis*, show a progressive increase in abundance from the base of the section and became common in the lower Campanian and reach 80% of the assemblages in the middle Campanian. From the upper Campanian through Maastrichtian the total abundance of planispiral taxa decreases to an average of 30%, and *"Globigerinelloides" multispinus* is the most common planispiral species. Biserial taxa are always present (averaging 30%) with *Planoheterohelix globulosa* and *Planoheterohelix planata* being the most common species. Planispiral taxa increase in abundance to an average of 45% from the middle Campanian upward.

Assemblages in Hole 1138A show three compositional changes (Fig. 5, Appendix A. Supplementary data). The oldest shift is recorded in the upper Santonian to lower Campanian when the keeled *Marginotruncana* species became very rare and the planispiral *"Globigerinelloides" ultramicrus* and the biserial *Planoheterohelix globulosa* increase in abundance. Through the uppermost Campanian, planispiral and biserial taxa remain relatively abundant representing 40 to 60% of the assemblage, respectively, in many samples. Unkeeled trochospiral *Muricohedbergella* *planispira* and *Muricohedbergella monmouthensis* are common (from 25% to 60%) throughout the section. A second assemblage change is registered in the lowermost Maastrichtian and coincides with the progressive increase in abundance of the keeled *Abathomphalus mayaroensis* coupled with the decrease of biserial and planispiral taxa and increase in the unkeeled *Archaeoglobigerina australis* and *Rugoglobigerina rugosa*. The third assemblage change occurs in the uppermost Maastrichtian when keeled taxa became rare again, planispiral and unkeeled taxa also decrease in abundance slightly, and the biserial group (dominated by *Gublerina rajagopalani* and *Praegublerina acuta*) reach the 60% of the assemblage (Appendix A. Supplementary data).

Assemblages in Hole 762C (Fig. 5, Appendix A. Supplementary data) show two faunal changes. Assemblages from the Turonian to the Coniacian interval are characterized by common keeled *Marginotruncana* and *Dicarinella* species and unkeeled *Whiteinella* and *Muricohedbergella* (mean abundance values from 30 to 40% for both groups). Planispiral taxa are less than 20% in abundance and biserial taxa (*Planoheterohelix globulosa* and *Laeviheterohelix pulchra*) show a progressive increase in relative abundance upsection from 10% to about 40%. The first assemblage change occurred in the Santonian–lower Campanian stratigraphic interval where we observed a decrease of the unkeeled taxa to mean values of about 20%, mainly because of the progressive disappearance of whiteinellids, and a slight increase of planispiral (*"Globigerinelloides" prairiehillensis* and *"Globigerinelloides" bollii*) and biserial (*Planoheterohelix planata*, *Pseudotextularia nuttalli*) taxa. The abundance of keeled taxa fluctuates but does not show long term changes, although the *Marginotruncana* species decrease and then disappear being replaced by *Globotruncana* species in the uppermost Santonian. There is a second variation in the composition of assemblages identified in the middle Campanian. From this stratigraphic interval to the top of the Maastrichtian, the keeled trochospiral (*Globotruncana*, *Contusotruncana*) decrease in relative abundance and, with the planispiral (*"Globigerinelloides" prairiehillensis*, *"Globigerinelloides" multispinus*) taxa, represent a minor component of the assemblages. On the other hand, the unkeeled *Archaeoglobigerina* and *Rugoglobigerina*, the biserial taxa *Planoheterohelix globulosa* and

Planoheterohelix striata and some multiserial taxa (*Planoglobulina*, *Racemiguembelina*) dominate the assemblage, constituting 80% of the specimens counted in some samples.

6. Planktonic foraminiferal depth ecology and trophic groups abundance

Changes in assemblages combined with published planktonic foraminiferal paleoecological preferences are used to interpret variations in the vertical structure of the water column at the four localities analyzed in this study. Current knowledge of planktonic foraminiferal paleoecology is inferred from latitudinal distributions (e.g. Hart, 1980, 1999; Leckie, 1987; MacLeod et al., 2001; Premoli Silva and Sliter, 1999) and from interspecific patterns of offsets in oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) stable isotopes from well preserved foraminiferal shells, suggesting depth stratification. The latter is proposed to be a more reliable paleoecological indicator than morphotype due to the high number of exceptions to the morphology-based assignment of species-specific depth habitat that have been documented as isotopic data for Cretaceous taxa have become more numerous (e.g. Abramovich et al. , 2003; Ando et al., 2010; Bornemann and Norris, 2007; D'Hondt and Arthur, 1995; Falzoni et al., 2013, 2014, 2016; Huber et al., 1995, 1999; MacLeod et al., 2013; Pearson et al., 2001; Petrizzo et al., 2008; Wendler et al., 2013; Wilson et al., 2002).

Planktonic foraminiferal species are subdivided in three categories: thermocline, intermediate and mixed layer dwellers (Tables 5a, 5b, 5c) based on available stable isotope data or, in the absence of stable isotope-based paleoecological information taxa present, according to these species biogeographic distribution and/or analogy to phylogenetically-related species with known paleoecological preferences. The species-specific isotope dataset compiled from the literature is here supplemented by new isotope measurements performed on species for which no data were previously available. This includes *Archaeoglobigerina cretacea*, *Falsotruncana maslakovae*, *Planoheterohelix papula*, and *Whiteinella brittonensis* (Fig. 6; Appendix A. Supplementary data). These new data are particularly enlightening because they were obtained from IODP Exp. 369 in the Mentelle Basin (Hobbs et al., 2019) located at 60°S paleolatitude in the southeast Indian Ocean during the Late Cretaceous.

Thermocline dwellers (Table 5a) include most keeled taxa (*Abathomphalus, Globotruncana, Globotruncanella, Globotruncanita, Falsotruncana, Marginotruncana, Rugotruncana*) and some biserial-multiserial taxa (*Gublerina rajagopalani*, *Planoheterohelix papula*) that are interpreted as specialized to more oligotrophic regimes and thus abundant in the low latitude settings (e.g. Abramovich et al., 2003; Bornemann and Norris, 2007; Caron and Homewood, 1983; D'Hondt and Arthur, 1995; Falzoni et al., 2013, 2016; Hart, 1980, 1999; Leary and Hart, 1989; Leckie, 1987; MacLeod and Huber, 1996; Premoli Silva and Sliter, 1999; Wilson et al., 2002).

Intermediate dwellers (Table 5b) include the trochospiral smooth and muricate *Muricohedbergella*, the planispiral *"Globigerinelloides"*, the keeled *Contusotruncana* and *Praeglobotruncana*, and the biserial-multiserial *Planoheterohelix* and *Planoglobulina*. These taxa show a high degree of adaptation to different trophic regimes from the mixed layer during the cooler seasons or growth in the seasonal thermocline (Bornemann and Norris, 2007; Huber et al., 1995; Norris et al., 2002; Wilson et al., 2002) or the permanent thermocline (Ando et al., 2010; Norris and Wilson, 1998; Petrizzo et al., 2008). Some species show a broad depth-distribution overlapping with deeper and/or shallower dwelling taxa (Abramovich et al., 2003, 2010; Falzoni et al., 2016; Isaza-Londoño et al., 2006; Price et al., 1998).

An intermediate trophic strategy is also documented for the double-keeled *Globotruncana linneiana* and *Marginotruncana pseudolinneiana* and single-keeled *Helvetoglobotruncana helvetica* (Table 5b) according to the stable isotope presented in this study (Fig. 6; Appendix A. Supplementary data) and previous studies (Abramovich et al., 2003; Falzoni et al., 2013, 2016; Huber et al., 1995). The double-keeled and umbilico-convex *Dicarinella* (*Dicarinella asymetrica*, *Dicarinella concavata*), only observed at Exmouth Plateau (Appendix A. Supplementary data), are better interpreted as mixed layer rather than thermocline dwellers (Falzoni et al., 2016) and thus are included in the intermediate trophic group (Table 5b). The double-keeled and biconvex *Dicarinella*

(*Dicarinella hagni*, *Dicarinella imbricata*) were previously regarded to be deeper/cooler dwellers in the Exmouth Plateau record (Falzoni et al., 2016), whereas according to isotope data (Fig. 6; Appendix A. Supplementary data) from IODP Exp. 369 in the Mentelle Basin they show $\delta^{18}O$ values between the shallower *Whiteinella brittonensis* and the deeper *Falsotruncana maslakovae*. We infer the biconvex *Dicarinella* inhabited the thermocline at low to mid latitudes till 47°S and shallower depths in colder waters at higher latitudes. Hence, they are interpreted as intermediate dwellers in holes 700B and 1138A and as thermocline dwellers in Hole 762C (Table 5b).

The multiserial species *Racemiguembelina fructicosa* was regarded either as a surface mixed-layer dweller, possibly harboring photoautotrophic algae due to its ontogenetic enrichment in $\delta^{13}C$, based on its record at Site 1049 Blake Nose (Fig. 6) in the northwest Atlantic Ocean (Houston and Huber, 1998; Houston et al., 1999; Isaza- Londoño et al., 2006; Norris et al., 1998). It has also been considered as a thermocline dweller because of relatively high $\delta^{18}O$ values recorded in the South Atlantic (Site 525A) and Equatorial Pacific (Site 577A) Oceans (Abramovich et al., 2003), or as an intermediate dweller at Shatsky Rise in the Central Pacific Ocean (Abramovich et al., 2010). *Racemiguembelina fructicosa* is regarded as an intermediate dweller at southern mid-latitudes as its $\delta^{18}O$ values are lower than values in the deep/cool dwellers (e.g., *Gublerina* spp.) and higher than values for shallow/warm dwellers (e.g., *Rugoglobigerina* spp.) at Exmouth Plateau (Falzoni et al., 2016).

The planispiral *“Globigerinelloides”* shows isotopic signatures indicating a wide range of habitats from the mixed layer to the summer thermocline for the various species analyzed from IODP Exp. 369 sites in the Mentelle Basin, at Blake Nose in the northwest Atlantic Ocean and at Kerguelen Plateau in the southern Indian Ocean (Fig. 6, Appendix A. Supplementary data). Similar variation in isotopic data are reported in the literature (Abramovich et al., 2003, 2010; MacLeod et al., 2001; Petrizzo et al., 2008). Pending further studies, we interpret the *“Globigerinelloides”* species primarily as intermediate dwellers, but more detailed species-specific isotope data are needed for a more precise characterization of their depth ecology.

Mixed layer dwellers (Table 5c) mainly include trochospiral muricate (*Archaeoglobigerina*), trochospiral pustulose (*Whiteinella*), and costellate (*Costellagerina*, *Rugoglobigerina*) taxa that may have had a higher reproductive potential in shallow and relatively nutrient-rich waters close to the mesotrophic part of the resource spectrum relative to most larger-sized keeled morphotypes (Abramovich et al., 2003, 2010; Bornemann and Norris, 2007; D'Hondt and Zachos, 1998; Falzoni et al., 2013, 2014, 2016; Hart, 1999; Huber et al., 1995, 1999; Isaza-Londoño et al., 2006; Leckie, 1987; MacLeod and Huber, 1996; Nederbragt et al., 1998; Pearson et al., 2001; Petrizzo et al., 2008; Premoli Silva and Sliter, 1999). However, some double keeled (*Globotruncana bulloides, Contusotruncana fornicata*, *Contusotruncana plummerae*, *Marginotruncana coronata*, *Marginotruncana pseudomarginata*) and serial-multiserial (*Pseudoguembelina palpebra, Heterohelix sphenoides, Praegublerina acuta*) taxa are included in this category (Table 5c) based on their consistent stable isotope signal suggesting growth in the upper mixed layer during summer or spring/autumn (Abramovich et al., 2003; Bice et al., 2003; Falzoni et al., 2013; Houston and Huber, 1998; Huber et al., 1995).

Assemblages from the base of the Turonian to the lowermost Campanian at all southern mid- and high latitude localities are quite diverse, with species richness varying from about 14 species in Hole 700B to about 32 species in Hole 762C (Fig. 7). No endemic species are recorded within this time interval, and the assemblages at these sites are similar to those from the Tethyan Realm (Premoli Silva and Sliter, 1995, 1999; Robaszynski and Caron, 1995; Robaszynski et al., 2000) and at low latitudes in the U.S. Western Interior (e.g., Douglas, 1969; Pessagno, 1967; Puckett, 2005) including the presence of Tethyan marker species (e.g., *Helvetoglobotruncana helvetica* and abundant low latitude marginotruncanids and dicarinellids). The Tethyan affinity of the assemblages is most evident in the Exmouth Plateau record. A slight decline in species richness in the lower-middle Campanian is followed by an increase in diversity from the middle Campanian to the Maastrichtian with an equivalent number of species at all localities. Campanian–Maastrichtian assemblages at Exmouth Plateau continue to show a Tethyan affinity, whereas at higher latitude localities the assemblages are dominated by long-ranging and cosmopolitan taxa and species that are endemic to the Austral Bioprovince (e.g., *"Globigerinelloides" impensus, Muricohedbergella sliteri*).

Comparison of the species richness and relative abundance curve for the three depth-ecology groups highlights changes in assemblage compositions and clues to variations in the properties of the surface water column. Thermocline dwellers are present throughout the Turonian to the Santonian at all sites where the sediments were recovered (Fig. 7). In holes 700B and 1138A thermocline taxa are conspicuously absent or very rare from the near the Santonian/Campanian boundary through the upper Campanian, while at the Exmouth Plateau they decline in abundance only from the middle Campanian upward. Thermocline dwellers are also rare or absent from the upper Campanian in Hole 690C. This deep-dwelling group reappears, although in low numbers, in the lower Maastrichtian at the southernmost localities, they persist into the upper Maastrichtian (Fig. 7), and they are represented by *Abathomphalus mayaroensis, Rugotruncana circumnodifer* and *Globotruncanella*. In the same time interval thermocline species in Hole 762 are more diverse due to the additional presence of several Tethyan species of *Globotruncana*. The topmost Maastrichtian record contains only rare thermocline taxa at the southernmost localities while no change in the composition of the assemblages and distribution of the depth-ecology groups is observed in Hole 762C.

The intermediate dwellers are always the major components of the Austral assemblages ranging from 60% to 100% at all localities. The slight decrease in abundance observed in the upper Campanian to lower Maastrichtian at Maud Rise and in the Maastrichtian assemblages at Kerguelen Plateau corresponds to an increase of surface dwellers, although intermediate dwellers are still the dominant taxa (Fig. 7). On the contrary the decline of intermediate dwellers in the Maastrichtian record at Exmouth Plateau is more pronounced and coincides with a quite dramatic increase in the relative abundance of surface dwellers (Fig. 7). Among the intermediate taxa the planispiral taxa are always common, varying from 25 to 60% of the total assemblages (Fig. 7).

In holes 700B and 1138A surface dwellers show an abundance trend similar to the thermocline taxa, with an abundance decrease in the lower to middle Campanian where intermediate dwellers range from 80% to 100% of the total assemblage. Surface dwellers are quite common at Maud Rise from the upper Campanian to the lower Maastrichtian ranging from 20% to 50% where *Archaeoglobigerina australis* is the dominant taxon. This species is also recorded in Hole 700B, although in low numbers reflecting the general low abundance (<20%) of surface dwellers at Northeast Georgia Rise compared to the other localities. Among the surface dwellers at Kerguelen Plateau *Rugoglobigerina* species, *Pseudoguembelina palpebra* and *Archaeoglobigerina australis* are equally distributed in abundance (Fig. 7, Appendix A. Supplementary data), whereas at Exmouth Plateau the mixed layer group is dominated by a diversifying group of rugoglobigerinids (Fig. 7, Appendix A. Supplementary data). This difference may indicate an ecological separation within the upper and lower mixed layer at 47°S paleolatitude.

The quantitative distribution of thermocline taxa reflects the presence of a well-defined thermocline and of a thick mixed layer that accommodated a high number of ecological niches during the Turonian to Santonian. The absence and rarity of thermocline dwellers in most of the Campanian record in holes 690C, 700B and 1138A, coupled with the high abundance of intermediate dwellers and the presence of surface dweller taxa at those sites, may indicate poorly defined surface water stratification, a dominantly eutrophic regime, the presence of a thick lower mixed layer and/or a reduced seasonal thermocline, and a thin upper mixed layer. The reappearance of thermocline taxa and variation in abundance of intermediate and surface water dwellers in the upper Campanian–Maastrichtian in holes 690C, 700B and 1138A may reflect fluctuation of the water mass stratification and possibly cyclic onset and disruption of the thermocline with concomitant variation in the thickness of the lower mixed layer. At the same time, the distribution of the depth-ecology groups at Exmouth Plateau might indicate the presence of a reduced, but stable thermocline, and a likely well-defined thick upper mixed layer suitable to accommodate the numerous *Rugoglobigerina* species.

In summary, the composition of the upper Campanian–Maastrichtian assemblages (Appendix A. Supplementary data) and the stratigraphic distribution of the depth-ecology groups reveal that sites located from 50°S to 65°S paleolatitude yielded similar assemblages that lost their Tethyan affinity. These assemblages still contained some Tethyan marker taxa, although the typical tropical species are absent and the diversity is low compared to Exmouth Plateau's assemblages which have more of a lower latitude aspect.

7. Discussion

The planktonic foraminiferal assemblage data from the localities analyzed in this study are correlated with recent sea surface and bottom waters paleotemperature compilations by Huber et al. (2018) and Falzoni et al. (2016) from southern mid- to high latitudes. Data by Huber et al. (2018) are based on foraminiferal stable isotope measurements from DSDP and ODP sites located in the southern South Atlantic (Sites 511, 327, 689, 690) and southern Indian Ocean (Site 258) at paleolatitudes higher than 60°S, whereas data by Falzoni et al. (2016) are from Hole 762C at 47°S paleolatitude. These compilations nicely document the extreme warmth during the early-mid-Turonian through the late Santonian, and the beginning of the long-term cooling trend in the latest Santonian–early Campanian that culminated in Cretaceous temperature minima during the Maastrichtian (Fig. 8).

The patterns of Late Cretaceous foraminiferal assemblage composition in terms of morphogroups, depth life strategies and diversity (Figs. 7, 8) allow identification of the Austral, Transitional and Tethyan biogeographic provinces (Fig. 9). The Austral and Transitional foraminiferal provinces were first recognized by Scheibnerova (1971, 1973) and later applied by Herb (1974), Sliter (1977), Krasheninnikov and Basov (1983, 1986), Rexilius (1984), Huber

(1992), Huber and Watkins (1992), Howe et al. (2000), Petrizzo (2000, 2003), Campbell et al. (2004). The definition of the Austral Bioprovince was originally based on the dominance of cool water agglutinated and calcareous benthic foraminiferal assemblages, low taxonomic diversity of planktonic foraminiferal assemblages, absence of typical Tethyan marker taxa and presence of endemic planktonic foraminiferal species, whereas the Transitional Bioprovince was defined as being intermediate in species composition between the Austral and Tethyan Bioprovinces.

Presence of diverse ecological niches distributed in the thermocline and mixed layer during the Turonian–Santonian in holes 700B, 1138A and 762C parallels the $\delta^{18}O$ paleotemperature trend for that time of the surface waters (Fig. 8). The Tethyan affinity in this time interval for sites located from 58° to 47° S is demonstrated by the occurrence of typical Tethyan marker taxa such as *Helvetoglobotruncana helvetica* and common *Marginotruncana* and *Dicarinella* species. In addition, the occurrence of *Dicarinella concavata* and *Dicarinella asymetrica* at Exmouth Plateau and their absence at the other localities suggests that the maximum poleward expansion of these Tethyan marker species was between 47° and 50° S of paleolatitude (Fig. 9). The Turonian–Santonian planktonic foraminiferal distributions at Northeast Georgia Rise correlates with the broadest expansion of the tropical climatic belt and the highest paleotemperatures. Moreover, no planktonic foraminifera are known to be endemic to the southern high latitude region in this time interval, and latitudinal gradients of species diversity were quite low, allowing the application of the Tethyan biozonation at least up to 58°S of paleolatitude (Fig. 3).

The Tethyan affinity of planktonic foraminifera at the localities analyzed in this study reveals a tropical-subtropical gyre that penetrated higher latitudes during the Turonian–Santonian. The southern limit of the subtropical gyre is inferred to pass along the southern edge of India, the northern edge of Falkland Plateau and eastward to the northwestern edge of Australia, while a subantarctic gyre is inferred to flow northward along the Antarctic Peninsula to the Falkland Plateau and then eastward into the southern Indian Ocean (e.g., Huber, 1992; Pucéat et al., 2005). The presence of warmer water currents along the northwestern Australian margin is suggested by the planktonic foraminifera assemblage data presented in this study and by those from the literature (Belford, 1960; Campbell et al., 2004; Edgell, 1957; Falzoni et al., 2013; Herb, 1974; Howe et al., 2003; Petrizzo, 2000; Wonders, 1992; Wright and Apthorpe, 1976), which report moderate to high abundance of keeled and of thermocline dwellers with Tethyan affinities.

A tropical-subtropical gyre surrounded Madagascar according to inferred surface circulation patterns (Huber, 1992; Pucèat et al., 2005). This interpretation is supported by land-based studies (e.g., Madagascar: Ujiiè and Randrianasolo, 1977; Tanzania: Falzoni and Petrizzo, 2011; Petrizzo et al., 2017; South India: Govindan and Narayanan, 1980; Govindan et al., 1996) and deep-sea sites (DSDP Leg 25: Simpson et al., 1974) that document the occurrence of Tethyan and thermocline species in the Cenomanian and Campanian.

An increase of the temperature gradient between low and high latitudes in the latest Santonian–early Campanian (Huber et al., 1995, 2002; Linnert et al., 2014; O'Brien et al., 2017) marks the beginning of the long term cooling, which is well-documented from low to high latitudes based on foraminiferal $\delta^{18}O$ values and TEX_{86} paleothermometry (e.g., Ando et al., 2013; Falzoni et al., 2016; Friedrich et al., 2012; Huber et al., 2018; Li and Keller, 1999; Linnert et al., 2014). The onset of sea-surface cooling is correlative with the abrupt decline and disappearance of thermocline dwellers and increase in abundance of the intermediate dweller taxa at the Northeast Georgia Rise and Kerguelen Plateau (Fig. 8).

In the lower to middle Campanian the assemblages change and the occurrence of common endemic species of the Southern Ocean at the Northeast Georgia Rise demonstrate the presence of the Austral Bioprovince and marks the location of the boundary between it and the Tethyan Bioprovince at about 60°S. This conclusion is supported by the inferred boundary between the Tethyan and Austral Bioprovinces in the South Atlantic Ocean to the north of deep-sea sites 327 and 511 on Falkland Plateau (Huber et al., 1995, 2018), although challenges of mapping this boundary in the South Atlantic due to an incomplete stratigraphic record and absence of planktonic foraminifera because of shallowing of the foraminiferal lysocline (Basov and Krasheninnikov, 1983; Huber et al., 1995) is acknowledged. The assemblage change within the Campanian is consistent with a decrease in the vertical density stratification of the water column due to a reduced thermal gradient between sea-surface and deeper waters (Fig. 8) and may indicate the development of a thick and strongly seasonal mixed layer and a weak/unstable thermocline. Thermocline dwellers are consistently present and compose about the 20% of the assemblages (Fig. 8) only at the lower latitude location examined, Exmouth Plateau, suggesting that sea-surface waters at 47°S were sufficiently well-stratified to sustain a relatively diversified thermocline assemblage.

Importantly, planktonic foraminifera underwent an ~3 m.y.-long major turnover during the mid-Coniacian–mid-Santonian (e.g., Hart, 1999; Premoli Silva and Sliter, 1999), followed by the disappearance of all pre-Campanian double-keeled taxa (*Marginotruncana* and *Dicarinella*) within the latest Santonian–earliest Campanian. This assemblage change is documented at low to high latitude sites, although not simultaneously at all localities (e.g., Caron and Homewood, 1983; Hart, 1999; Hart and Bailey, 1979; Petrizzo et al., 2017; Premoli Silva and Sliter, 1999; Wonders, 1980, 1992). It is well documented from the Northeast Georgia Rise to Exmouth Plateau where we clearly record taxonomic replacement in the assemblages with the disappearance of *Marginotruncana* species and the progressive appearance of *Contusotruncana fornicata* followed by *Globotruncana* species such as *Globotruncana linneiana*, *Globotruncana ventricosa* and *Globotruncana neotricarinata*, although the total number of specimens of the latter species is very low in the southernmost localities. According to the age model applied in this study the appearance of the first species included in the Globotruncanidae, *Contusotruncana fornicata,* occurs earlier (88.2 Ma) at Exmouth Plateau than at Kerguelen Plateau and Northeast Georgia Rise (86.2 Ma), and the disappearance of marginotruncanids occurs between 83.3-84.0 Ma. The extinction of all pre-Campanian double-keeled taxa was ascribed to the onset of surface-ocean cooling during the late Santonian (Fig. 8) leading to expansion of deep/cold ecological niches, which favored proliferation of cooler/deeper dwelling globotruncanids, and negatively affecting all warmer/shallower dwelling

Marginotruncana and umbilico-convex *Dicarinella* species that had evolved during the Turonian–Coniacian hot greenhouse interval (Falzoni et al., 2016).

Therefore, the onset of sea-surface cooling in the late Santonian had two important outcomes: 1) a faunal turnover within double-keeled planktonic foraminiferal taxa that is observed on a global scale, and 2) the development of the Transitional Bioprovince at mid-high latitudes (Fig. 9), which is characterized by the loss of many Tethyan taxa particularly at the southern localities examined in this study (Northeast Georgia Rise and Kerguelen Plateau). Moreover, in the early Campanian the boundary between the Transitional and Tethyan Bioprovinces was well defined in the southern Indian Ocean and likely located north of Exmouth Plateau and south of Madagascar and India at about 45°S of paleolatitude (Fig. 9). This inference is based on the distribution and assemblage composition of planktonic foraminifera and on the stratigraphic occurrence of endemic Austral species which were confined to latitudes higher than 50°S by the middle Campanian (Fig. 4).

The development of a major water mass boundary between cool surface waters south of Kerguelen Plateau at about 50°S paleolatitude and warmer surface waters to the north in the South Atlantic and Indian Ocean may have caused biogeographic isolation of the Austral Bioprovince assemblages during the latest Campanian and Maastrichtian and development of a well-defined Transitional Bioprovince. The boundary between the Transitional and Austral Bioprovinces was located at 58°- 60°S paleolatitude in the latest Campanian–Maastrichtian according to the patterns of planktonic foraminiferal distributions and abundances (Figs. 8, 9). Maastrichtian thermocline taxa are mainly represented by species preferring cooler water (e.g., *Abathomphalus mayaroensis* and *Rugotruncana circumnodifer*). The former species is rare at Maud Rise and Northeast Georgia Rise, occurs discontinuously and in low percentage (5 to 20%) in the early Maastrichtian at Kerguelen Plateau and is continuously present at Exmouth Plateau. It also showed an equatorward migration (Huber and Watkins, 1992) from Maud Rise to Exmouth Plateau that took about 1 m.y. (Fig. 4). The latter species occurs in low abundance from 65° to 50°S and is absent from Hole

762C. Moreover, in the Maastrichtian record at Maud Rise and Kerguelen Plateau some of the biserial taxa and the trochospiral *Archaeoglobigerina* are the most abundant surface dwellers, whereas the trochospiral *Muricohedbergella* and the planispiral *"Globigerinelloides"* equally compose the majority of the intermediate dwellers. The surface dweller and cosmopolitan species *Praegublerina acuta*, first recorded at the Exmouth Plateau in the mid Campanian (lower part of Chron C33N), only occurs in the Maastrichtian at Northeast Georgia Rise and Maud Rise (Fig. 4). The surface dweller *Archaeoglobigerina australis* is very common at Maud Rise and occurs in low numbers at the other localities, confirming the presence of a well-defined Austral Bioprovince at Maud Rise.

At Exmouth Plateau the assemblages are quite diverse with a clear separation of the different depth-ecology groups, and they are characterized by the occurrence of many typical Tethyan species (Appendix A. Supplementary data). However, these late Campanian–Maastrichtian depth ecology groups are unequally distributed as thermocline and intermediate dwelling species, which together represent about the 50% of the assemblages, and the surface dwellers constitute the remaining 50%. The high abundance of surface dwellers in Hole 762C (Figs. 7 and 8) coincides with the species diversification of multiserial-biserial taxa (*Pseudoguembelina*, *Planoheterohelix*, *Racemiguembelina*) and diversification and high abundance of *Rugoglobigerina* species, which are not recorded at the other localities.

We assume that species assigned to the same genus have similar trophic preferences, although we are aware that biserial taxa with thin to thick costae and *Rugoglobigerina* with less or more meridionally ornamented test may not share the same ecological niches (Falzoni et al., 2014; Haynes et al., 2015). High abundances and diversification of biserial taxa previously assigned to the genus *Heterohelix* are traditionally interpreted as reflecting high productivity in the surface water and may indicate the presence of a thick upper mixed layer characterized by strong water mass mixing or influence from frequent episodes of coastal upwelling. Stable isotope analyses suggest that *Rugoglobigerina* was among the shallowest and warmest water dwelling taxa (Fig. 6) among

Campanian–Maastrichtian planktonic foraminiferal assemblages (Falzoni et al., 2013, 2014, 2016; Isaza-Londoño et al., 2006; Pearson et al., 2001) and is regarded either to have been symbiont-bearing (Abramovich et al., 2003) or asymbiotic (Isaza-Londoño et al., 2006), or hosting facultative symbionts (D'Hondt and Zachos, 1998). At Exmouth Plateau the increase in abundance of *Rugoglobigerina* in the Campanian–Maastrichtian (Figs. 7, 8) coincides with the paleotemperature decline in the late Campanian (Falzoni et al., 2016).

There are no modern species with meridionally ornamentation that resemble *Rugoglobigerina* making determination of the paleobiological importance, if any, of these features. However, in the modern oceans some non-keeled, trochospiral surface dwellers species such as *Globigerina bulloides* are very abundant either in environments characterized by enhanced production of algal prey at temperate to high latitudes during the Spring (e.g., Bé and Tolderlund, 1971; Chapman, 2010; Schiebel and Hemleben, 2000) or in upwelling conditions at low to mid latitudes (e.g., Conan and Brummer, 2000; Naidu and Malmgren, 1996). Although we have no supporting data, we infer that rugoglobigerinids may have had a similar behavior in the Cretaceous and their high diversity and abundance at Exmouth Plateau may be linked to episodes of increased productivity. The lower $\delta^{18}O$ and high $\delta^{13}C$ values measured from Exmouth Plateau *Rugoglobigerina* specimens (Falzoni et a., 2014) was interpreted as an adaptation to low salinity waters created by fresh water input from land. This inferences is consistent with the paleogeographic location of the Exmouth Plateau at the Australian shelf edge (Haq et al., 1990; Wilcox and Exon, 1976) and with the cyclic sedimentation characterized by alternation of dark and more clayey sediments and light nannofossils oozes observed in the Late Cretaceous sediments (Huang et al., 1992). An alternative hypothesis is that episodes of increased productivity may have occurred in a coastal upwelling system over Exmouth Plateau and favored proliferation of *Rugoglobigerina*. The assumption of episodic upwelling along the western Australia margin in the late Campanian–Maastrichtian agrees with the atmospheric general circulation model (AGCM) of

Barron and Washington (1984) and models by Kruijs and Barron (1990), which suggest possibility of upwelling along the western margin of Australia.

Progressive changes in assemblages at Exmouth Plateau from the early Campanian to the Maastrichtian and increasing similarity between Exmouth Plateau and Tethyan assemblages indicate that by the late Maastrichtian Exmouth Plateau was located near the southern margin of the Tethyan Bioprovince (Fig. 9). In addition, the late Campanian paleotemperature record at Exmouth Plateau (Fig. 8) shows short-term warming episodes (Falzoni et al., 2016) that can be linked to coeval warming events at low to middle latitudes localities in the Pacific Ocean (Site 463, Li and Keller, 1999; sites 305 and 463, Ando et al., 2013; Friedrich et al., 2012), and subtropical South Atlantic Ocean (Site 525, Friedrich et al., 2012 and references herein).

8. Conclusions

Planktonic foraminiferal biogeographic distribution patterns reveal that the poleward expansion of the Tethyan Bioprovince reached about 60°S paleolatitude at time of the highest Cretaceous paleotemperatures during the Turonian–Santonian hot greenhouse climate. Within this time interval, Tethyan biozones can be recognized at least to 58°S paleolatitude (Figs. 4, 9). The distribution of morphological and ecological groups reveals the presence of a well-established surface water stratification and a separation between deep and surface waters as indicated by the occurrence of cosmopolitan thermocline dwelling taxa.

The increase of the latitudinal gradient and the onset of surface water cooling in the late Santonian–early Campanian led to a change in composition of the southern high latitude planktonic foraminiferal assemblages, marking the transition away from a dominantly Tethyan influenced population and the development of a Transitional Bioprovince from 60°S to about 45°S paleolatitude throughout the Campanian (Fig. 9). The transition coincides with changes in surface water stratification as interpreted by the occurrence and distribution of the depth ecology groups, which indicate a reduction of ecological niches at deeper levels of the surface waters. This scenario may coincide with a dominantly eutrophic regime and presence of a deepened lower mixed layer, as demonstrated by absence of thermocline dwellers in the Campanian record of the southernmost localities (Figs. 7, 8). Increased provincialism and the occurrence of endemic species among the circum-Antarctic assemblages parallels a paleoclimate shift at the Santonian–Campanian boundary interval, although we cannot exclude the possibilities that these species appeared earlier at paleolatitudes south of 60°S where we do not have a sediment record.

Further high latitude cooling starting in the early Campanian led to the development of a well-defined Austral Bioprovince at paleolatitudes south of 60°S in the Maastrichtian (Fig. 9). The circum-Antarctic assemblages are characterized by a low species diversity, presence of abundant endemic Austral species, and occurrence of opportunistic cosmopolitan and cold-water species. Locations at paleolatitudes north of 60°S yield planktonic foraminifera whose depth ecology preferences indicate the presence of a defined, but thin, thermocline and of a thick mixed layer that progressively increased in thickness equatorward to accommodate a higher number of ecological niches.

Acknowledgements

We warmly thank the editor Eduardo Koutsoukos and two anonymous reviewers for their helpful comments and suggestions. This study was supported by the Italian Ministry of Education, University and Research (Ministero dell’Istruzione, dell’Università e della Ricerca – MIUR), grant FFABR 2017 to M.R. Petrizzo. Financial support to B.T. Huber was provided by the Smithsonian Institution’s Department of Paleobiology. The Ocean Drilling Program (ODP) and the International Ocean Discovery Program (IODP) are thanked for providing samples analyzed in this study.

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Captions

Fig. 1. Location of the deep-sea sites discussed in the present study today and plotted on a paleogeographic reconstruction for the Campanian (80 Ma) according to Scotese (2016).

Fig. 2. Core recovery, lithologic description and age of the sediments of ODP Hole 690C (Maud Rise), Hole 700B (Northeast Georgia Rise), Hole 1138A (Kerguelen Plateau), and Hole 762C (Exmouth Plateau).

Fig. 3. Late Cretaceous planktonic foraminifera biozonation scheme for the southern mid- to high latitude with shown the lowest and highest occurrences of the most important species at the four localities discussed in this study. The biozonal markers defining the biozones introduced in this study are in bold. The Austral biozonation (Huber, 1992) and the Transitional biozonation (Petrizzo, 2003) are shown for comparison.

Fig. 4. Stratigraphic distribution of the planktonic foraminiferal species that show poleward or equatorward migration recorded at all localities analyzed in this study. Paleolatitude for each location is shown. Question marks indicate uncertain stratigraphic range because of lack of sediment recovery.

Fig. 5. Planktonic foraminiferal morphogroups relative abundance data at the four ODP holes discussed in this study. See text for further explanations.

Fig. 6. $\delta^{18}O$ vs. $\delta^{13}C$ cross-plots calculated for well-preserved specimens from four deep sea sites drilled in three different paleogeographic locations: a) ODP Leg 120, Site 750 Kerguelen Plateau, southern Indian Ocean (Schlich et al., 1989), paleolatitude 50°S, isotope data after MacLeod and Huber, 1996; b) ODP Leg 171B, Site 1049 Blake Nose, northwest Atlantic (Norris et al., 1998),

paleolatitude 30°N, isotope data this study; c) IODP Exp. 369, Sites U1513 and U1516 Mentelle Basin, southeast Indian Ocean (Hobbs et al., 2019), paleolatitude 60°S, isotope data this study. Species showing the lowest δ^{18}O and the highest δ^{13}C values cluster are in the upper right of the graph and are interpreted as surface dwellers, species displaying the highest δ^{18}O values and the lowest δ^{13}C values are interpreted as thermocline dwellers and plot in the bottom left (Pearson, 1998; Pearson et al., 2001). Benthic foraminifera (*Gavelinella beccariformis*, *Nuttallides* sp. and *Gavelinellinae*) are plotted for comparison with the planktonic species.

Fig. 7. Planktonic foraminifera species diversity and relative abundance of the thermocline, intermediate and surface dwellers at the studied localities. See text for explanations of the changes in assemblage composition and comparison among sites.

Fig. 8. Planktonic foraminiferal abundance data of the three depth ecology groups and of *Rugoglobigerina* plotted relative to the Late Cretaceous paleotemperature record from DSDP and ODP sites 690, 327, 689, 511 and 258 by Huber et al. (2018) and from ODP Hole 762C by Falzoni et al. (2016).

Fig. 9. Paleogeographic maps (Scotese, 2016) showing the position of the paleogeographic boundaries of the Austral, Transitional and Tethyan Bioprovinces in the Turonian, Campanian and Maastrichtian.

Table 1. Ages and depths for planktonic foraminiferal species and base magnetic polarity chron boundaries from ODP Hole 690C. FAD = first appearance datum. LAD = last appearance datum.

Table 2. Ages and depths for planktonic foraminiferal species and base magnetic polarity chron boundaries from ODP Hole 700B. FAD = first appearance datum. LAD = last appearance datum.

Table 3. Ages and depths for planktonic foraminiferal species from ODP Hole 1138A. FAD = first appearance datum. LAD = last appearance datum.

Table 4. Ages and depths for planktonic foraminiferal species, calcareous nannofossils and base and top of magnetic polarity chron boundaries from ODP Hole 762C. FAD = first appearance datum. LAD = last appearance datum.

Tables 5a, 5b, 5c. Depth ecologies of Late Cretaceous genera and species identified in the four deep sea sites analyzed in this study. Paleoecological inferences of the taxa are based on stable isotope measurements and interpretations available in the literature, and on data obtained in this study (Fig. 6, Appendix A. Supplementary data). The trophic strategy of species for which no stable isotopes information are available is inferred based on their geographic and latitudinal distributions and on similarities with phylogenetically related species. Asterisk = species interpreted as intermediate dwellers in holes 700B and 1138A and as thermocline dwellers in Hole 762C, see discussion in the text.

Events	Depth (mbsf)	Age (m.y.)	References
base C29R	252.28	66.40	Huber et al. 2018
base C31N	272.25	69.27	Huber et al. 2018
FAD "*G.*" *subcarinatus*	273.24	69.66	This study
FAD *P. acuta*	277.35	70.32	This study
FAD *A. mayaroensis*	283.04	71.23	This study
base C31R	283.39	71.45	Huber et al. 2018
FAD *R. circumnodifer*	291.33	72.56	This study
base C32R.2N	302.78	73.65	Huber et al. 2018
FAD *M. sliteri*	306.83	74.09	This study
FAD *G. havanensis*	307.84	74.28	This study
base C32R.2R	308.02	74.31	Huber et al. 2018
LAD "*G.*" *impensus*	313.48	75.36	Huber et al. 2018
occurrence *A. australis*	315.78	75.81	This study

Events	Top depth (mbsf)	Bottom depth (mbsf)	Mean depth (mbsf)	Age (m.y.)	References
base C29N	333.26	333.33	333.29	65.69	Gradstein et al. 2012
base C31N	342.30	346.14	344.22	69.27	Huber et al. 2018
FAD *"G." subcarinatus*	347.22	348.72	347.97	69.48	This study
FAD *R. circumnodifer*	348.72	350.22	349.47	69.83	This study
FAD *P. acuta*	348.72	350.22	349.47	69.83	This study
FAD *A. mayaroensis*	350.22	355.18	352.70	70.58	This study
base C31R	357.65	357.85	357.75	71.45	Gradstein et al. 2012
FAD *G. havanensis*	365.90	367.40	366.65	73.82	This study
base C32R	384.66	384.96	384.82	74.31	Huber et al. 2018
LAD *"G." impensus*	385.87	387.40	386.64	75.66	This study
LAD *G. linneiana*	405.99	407.74	406.87	79.04	This study
base C33N	407.35	407.55	407.45	79.90	Gradstein et al. 2012
FAD *A. australis*	419.12	423.10	421.11	82.01	This study
FAD *M. sliteri*	428.44	429.07	428.76	83.23	This study
FAD *"G." impensus*	428.44	429.07	428.76	83.23	This study
base C33R	430.85	431.05	430.95	83.64	Gradstein et al. 2012
LAD *P. papula*	453.41	454.91	454.16	85.61	This study
FAD *G. linneiana*	456.41	457.91	457.16	86.26	Gradstein et al. 2012
FAD *P. papula*	471.11	474.12	472.62	87.77	This study
LAD *F. maslakovae*	482.91	488.78	485.85	90.26	This study

Events	Top depth (mbsf)	Bottom depth (mbsf)	Mean depth (mbsf)	Age (m.y.)	References
LAD Cretaceous taxa	489.14	490.40	489.77	66.02	Gradstein et al. 2012
FAD *R. fructicosa*	503.15	503.57	503.36	70.03	This study
FAD *"G." subcarinatus*	506.35	507.85	507.10	71.14	This study
LAD *G. linneiana*	506.35	507.85	507.10	71.14	This study
FAD *A. mayaroensis*	506.35	507.85	507.10	71.14	This study
FAD *R. circumnodifer*	509.05	516.05	512.55	75.24	This study
FAD *G. havanensis*	509.05	516.05	512.55	75.24	This study
FAD *P. acuta*	509.05	516.05	512.55	75.24	This study
LAD *"G." impensus*	509.05	516.05	512.55	75.36	Huber et al. 2018
FAD *G. rajagopalani*	516.05	518.06	517.06	75.55	Petrizzo et al. 2011
FAD *A. australis*	545.00	554.37	549.69	78.75	This study
FAD *M. sliteri*	602.52	603.00	602.76	83.94	This study
FAD *"G." impensus*	602.52	603.00	602.76	83.94	This study
LAD *P. papula*	621.86	612.25	617.06	85.34	This study
FAD *G. linneiana*	626.32	626.59	626.46	86.26	Gradstein et al. 2012
FAD *P. papula*	626.59	631.38	628.99	86.51	This study
LAD *F. maslakovae*	631.38	626.59	628.99	88.59	This study
FAD *F. maslakovae*	631.46	632.79	632.13	91.49	This study
LAD *H. helvetica*	631.46	632.79	632.13	91.51	Huber and Petrizzo 2014
FAD *H. helvetica*	645.46	645.50	645.48	93.52	Huber and Petrizzo 2014
LAD *"G." bentonensis*	653.80	654.35	654.08	94.41	Falzoni et al. 2018

Events	Top depth (mbsf)	Bottom depth (mbsf)	Mean depth (mbsf)	Age (m.y.)	References
FAD *M. prinsii*	560.46	561.40	560.93	66.39	Gradstein et al. 2012
base C29R	565.32	566.02	565.67	66.40	Gradstein et al. 2012
LAD *G. linneiana*	586.25	579.75	583.00	68.12	This study
top C30R	588.64	592.94	590.79	68.20	Gradstein et al. 2012
FAD *R. fructicosa*	594.85	600.64	597.75	69.70	This study
top C31N	593.51	595.93	594.72	68.37	Gradstein et al. 2012
top C31R	598.12	598.20	598.16	69.27	Gradstein et al. 2012
FAD *A. mayaroensis*	600.64	606.17	603.41	70.30	This study
FAD *A. mayaroensis*	600.64	606.17	603.41	70.30	Huber et al. 2018
top C32n1n	611.40	611.52	611.46	71.17	This study
top C32n1r	612.28	612.46	612.37	71.26	This study
top C32N.n2	612.92	613.03	612.98	71.94	Gradstein et al. 2012
LAD *U. trifidus*	614.00	614.12	614.06	72.03	This study
top C32R	631.08	631.87	631.48	73.65	Gradstein et al. 2012
LAD *E. eximius*	635.12	636.60	635.86	73.97	Thibault et al. 2012
base C32R	638.43	639.13	638.78	74.31	Gradstein et al. 2012
FAD *G. havanensis*	637.21	642.65	639.93	74.35	This study
FAD *G. rajagopalani*	669.00	669.36	669.18	75.55	Petrizzo et al. 2011
FAD *"G." subcarinatus*	680.73	684.60	682.67	78.16	This study
FAD *P. acuta*	684.60	687.10	685.85	78.44	This study
FAD *A. australis*	687.10	687.10	687.10	78.55	This study
FAD *C. plummerae*	691.07	697.76	694.42	78.82	Petrizzo et al. 2011
base C33N	704.72	707.15	705.94	79.90	Gradstein et al. 2012
LAD *"G." impensus*	697.76	691.07	694.42	79.21	This study
LAD *H. carinatus*	712.14	712.55	712.35	80.81	Petrizzo et al. 2011
base C33R	741.10	742.07	741.59	83.64	Gradstein et al. 2012
FAD *B. parca*	744.74	744.74	744.74	83.83	Bralower and Siesser 1992
FAD *D. asymetrica*	741.09	740.50	740.80	83.56	This study
FAD *"G." impensus*	744.59	744.59	745.22	83.86	This study
FAD *L. cayeuxii*	771.96	771.96	771.96	86.38	Gradstein et al. 2012
FAD *M. sliteri*	771.60	772.75	772.18	85.66	This study
FAD *G. arca*	771.74	775.14	773.44	85.75	This study
LAD *P. papula*	775.14	771.74	773.44	85.75	This study
FAD *G. linneiana*	780.42	780.92	780.67	86.26	Gradstein et al. 2012
FAD *G. neotricarinata*	775.14	775.73	775.44	86.16	This study
FAD *D. asymetrica*	780.09	780.42	780.26	87.18	This study
FAD *D. concavata*	782.18	783.18	782.68	87.69	This study

FAD *P. papula*	783.18	785.13	784.16	88.01	This study
FAD *G. stuartiformis*	785.45	785.64	785.55	88.30	This study
FAD *C. fornicata*	785.13	785.45	785.29	88.25	This study
FAD *M. staurophora*	786.20	786.20	786.20	88.44	Gradstein et al. 2012
LAD *F. maslakovae*	799.50	790.10	794.80	90.26	This study
FAD *F. maslakovae*	802.55	802.55	802.94	91.51	This study
LAD *H. helvetica*	802.25	802.55	802.40	91.51	Huber and Petrizzo 2014
FAD *H. helvetica*	807.00	807.00	807.00	93.52	Huber and Petrizzo 2014

THERMOCLINE DWELLERS	References
Abathomphalus intermedius	
Abathomphalus mayaroensis	Abramovich et al. 2003; this study
Dicarinella canaliculata *	
Dicarinella hagni *	Huber et al. 1999; Wendler et al. 2013; Falzoni et al. 2016; this study
Dicarinella imbricata *	Falzoni et al. 2016; this study
Dicarinella primitiva *	Falzoni et al. 2016
Falsotruncana douglasi	
Falsotruncana loeblichae	
Falsotruncana maslakovae	this study
Falsotruncana spp.	Falzoni et al. 2016
Globotruncana aegyptiaca	Abramovich et al. 2003
Globotruncana angulata	Abramovich et al. 2003
Globotruncana angusticarenata	
Globotruncana arca	Abramovich et al. 200; Falzoni et al. 2014
Globotruncana dupeublei	Abramovich et al. 2003
Globotruncana duwi	
Globotruncana falsostuarti	Pearson et al. 2001; Abramovich et al. 2003
Globotruncana hilli	
Globotruncana insignis	Abramovich et al. 2003
Globotruncana mariei	Abramovich et al. 2003; Falzoni et al. 2013
Globotruncana morozovae	
Globotruncana neotricarinata	Falzoni et al. 2013; this study
Globotruncana orientalis	Falzoni et al. 2013
Globotruncanita pettersi	Abramovich et al. 2003
Globotruncana rosetta	Abramovich et al. 2003
Globotruncana spp.	Falzoni et al. 2016
Globotruncana stuarti	Abramovich et al. 2003
Globotruncana ventricosa	Falzoni et al. 2013; this study
Globotruncanella citae	
Globotruncanella havanensis	D'Hondt and Arthur 1995; Abramovich et al. 2003
Globotruncanella petaloidea	
Globotruncanita elevata	Falzoni et al. 2013
Globotruncanita spp.	Falzoni et al. 2016
Globotruncanita stuartiformis	Abramovich et al. 2003; Falzoni et al. 2013
Gublerina cuvillieri	Abramovich et al. 2003
Gublerina rajagopalani	D'Hondt and Arthur 1995; Abramovich et al. 2003; Falzoni et al. 2014
Marginotruncana marianosi	
Marginotruncana paraconcavata	
Marginotruncana renzi	
Marginotruncana schneegansi	Wilson et al. 2002; Bornemann and Norris 2007
Marginotruncana sigali	
Marginotruncana sinuosa	
Marginotruncana tarfayensis	
Planoheterohelix papula	this study
Rugotruncana circumnodifer	MacLeod and Huber 1996

Rugotruncana subcircumnodifer	

TERMEDIATE DWELLERS (seasonal thermocline or inter mixed layer dwellers)	References
eoglobigerina blowi	
eoglobigerina cretacea	this study
ella punctulata	Abramovich et al. 2003
sotruncana contusa	Isaza Londoño et al. 2006; Abramovich et al. 2010
sotruncana spp.	Falzoni et al. 2016
sotruncana walfishensis	
ella asymetrica	Falzoni et al. 2016
ella canaliculata *	
ella concavata	Falzoni et al. 2016
ella elata	
ella hagni *	Huber et al. 1999; Wendler et al. 2013; Falzoni et al. 2016; this study
ella imbricata *	Falzoni et al. 2016; this study
ella primitiva *	Falzoni et al. 2016
gerinelloides" bentonensis	Petrizzo et al. 2008
gerinelloides" bollii	
gerinelloides" impensus	
gerinelloides" messinae	
gerinelloides" multispinus	
gerinelloides" prairiehillensis	
gerinelloides" spp.	Abramovich et al. 2003; this study
gerinelloides" subcarinatus	Abramovich et al. 2003; this study
gerinelloides" ultramicrus	Abramovich et al. 2003
truncana linneiana	Huber et al. 1995; Abramovich et al. 2003; Falzoni et al. 2013; this study
oglobotruncana helvetica	Huber et al. 1999; Wendler et al. 2013; Falzoni et al. 2016
oglobotruncana praehelvetica	Wendler et al. 2013
rsonites carinatus	
eterohelix dentata	
otruncana caronae	
otruncana coldreriensis	
otruncana pseudolinneiana	Falzoni et al. 2013; this study
hedbergella delrioensis	Norris and Wilson, 1998; Price et al. 1998; Wilson et al. 2002; Ando et al. 2010
hedbergella flandrini	
hedbergella hoelzli	
hedbergella holmdelensis	
hedbergella mounmouthensis	
hedbergella planispira	Petrizzo et al. 2008
hedbergella simplex	Petrizzo et al. 2008
hedbergella sliteri	
hedbergella spp.	Huber et al. 1995; Price et al. 1998; Falzoni et al. 2016; this study
globulina acervulinoides	Abramovich et al. 2003
globulina carseyi	Abramovich et al. 2003
globulina riograndensis	
eterohelix globulosa	Huber et al. 1995, 1999; Abramovich et al. 2003, 2010; Bornemann and Norris 2007; this stu
eterohelix moremani	Huber et al. 1999
eterohelix planata	Huber et al. 1995
eterohelix reussi	
obotruncana algeriana	
obotruncana gibba	Huber et al., 1999; Petrizzo et al. 2008
obotruncana hilalensis	
obotruncana stephani	Huber et al. 1995; Petrizzo et al. 2008; Ando et al. 2010; Wendler et al. 2013; this study
otextularia elegans	Pearson et al. 2001; Abramovich et al. 2003

otextularia intermedia	
otextularia nuttallii	Abramovich et al. 2010; Falzoni et al. 2016; this study
niguembelina fructicosa	Houston and Huber 1998; Isaza-Londoño et al. 2006; Falzoni et al. 2016; this study
lla scotti	Abramovich et al. 2003
abrella eggeri	
nella baltica	Huber et al. 1995; Bornemann and Norris 2007; this study

MIXED LAYER DWELLERS (summer or spring/autums)	References
aeoglobigerina australis	Huber et al. 1995; Macleod and Huber 1996; this study
aeoglobigerina bosquensis	Huber et al. 1995; Bice et al. 2003; Falzoni et al. 2013
aeoglobigerina mateola	
usotruncana fornicata	Falzoni et al. 2013
usotruncana plummerae	Abramovich et al. 2003; Falzoni et al. 2013
ellagerina bulbosa	Petrizzo et al. 2008
ellagerina pilula	Petrizzo et al. 2008
otruncana bulloides	Huber et al. 1995; Falzoni et al. 2013
mbelitria cretacea	
rohelix sphenoides	Falzoni et al. 2013
erina rotundata	
inotruncana coronata	Falzoni et al. 2013
inotruncana pseudomarginata	Bice et al. 2003; Falzoni et al. 2013
gublerina acuta	Abramovich et al. 2003
udoguembelina costulata	Abramovich et al. 2003
udoguembelina excolata	Abramovich et al. 2003
udoguembelina palpebra	Abramovich et al. 2003
oglobigerina hexacamerata	Abramovich et al. 2003; Falzoni et al. 2014
oglobigerina macrocephala	Abramovich et al. 2003
oglobigerina milamensis	Abramovich et al. 2003; Falzoni et al. 2014
oglobigerina pennyi	Abramovich et al. 2003; Falzoni et al. 2014
oglobigerina rugosa	Pearson et al. 2001; Abramovich et al. 2003; Isaza-Londoño et al. 2006; Falzoni et al. 201
oglobigerina spp.	D'Hondt and Arthur 1995; Abramovich et al. 2003; this study
ackoina cenomana	
ackoina multispinata	
einella aprica	
einella archaeocretacea	
einella aumalensis	
einella brittonensis	this study
einella inornata	
einella paradubia	
einella spp.	Huber et al. 1999; Falzoni et al. 2016

Fig. 1

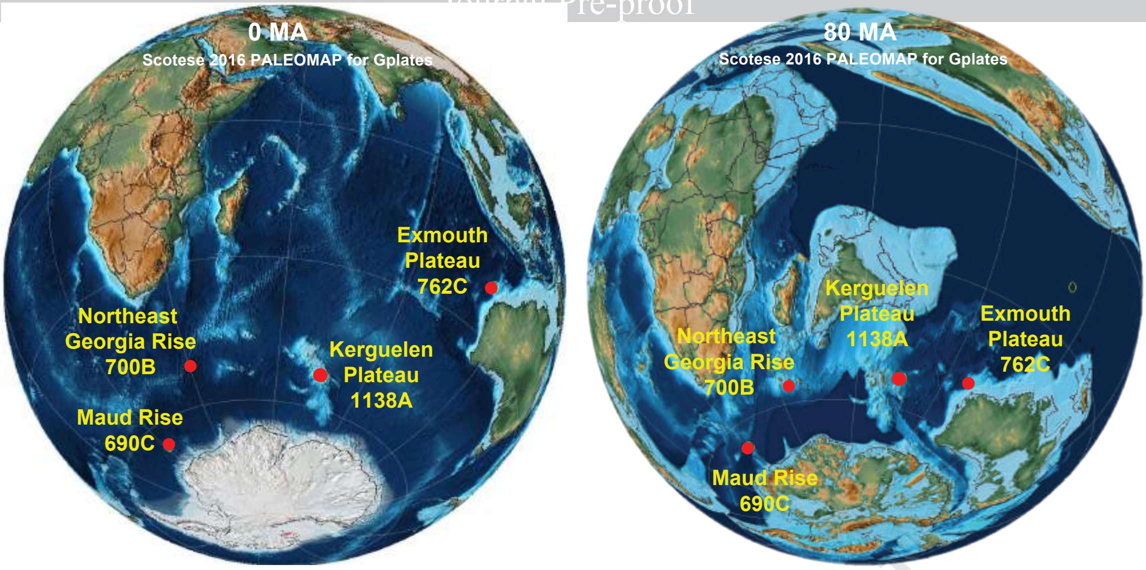

0 MA
Scotese 2016 PALEOMAP for Gplates
Exmouth Plateau 762C
Northeast Georgia Rise 700B
Kerguelen Plateau 1138A
Maud Rise 690C
80 MA
Scotese 2016 PALEOMAP for Gplates
Kerguelen Plateau 1138A
Exmouth Plateau 762C
Northeast Georgia Rise 700B
Maud Rise 690C

Fig. 2

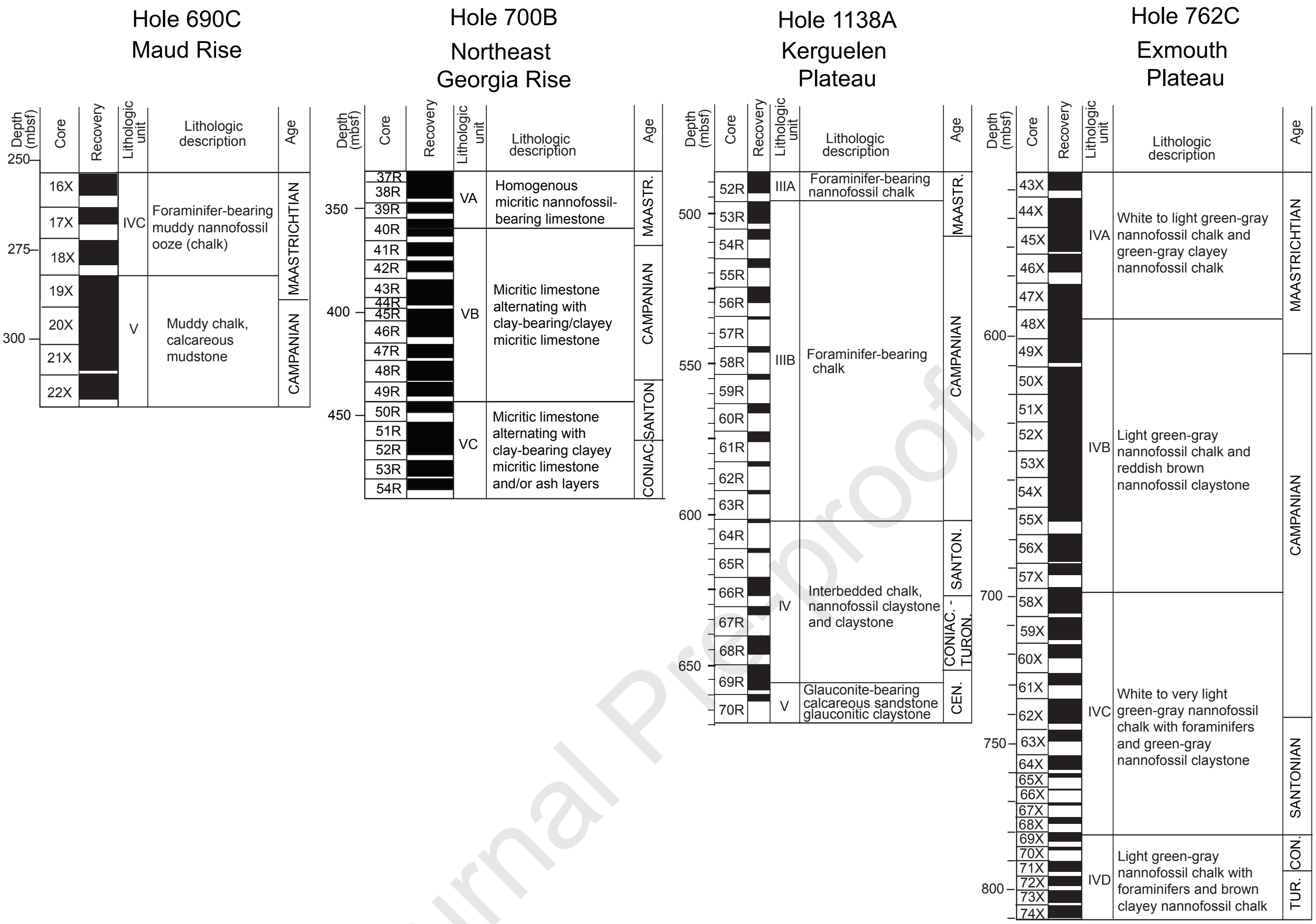
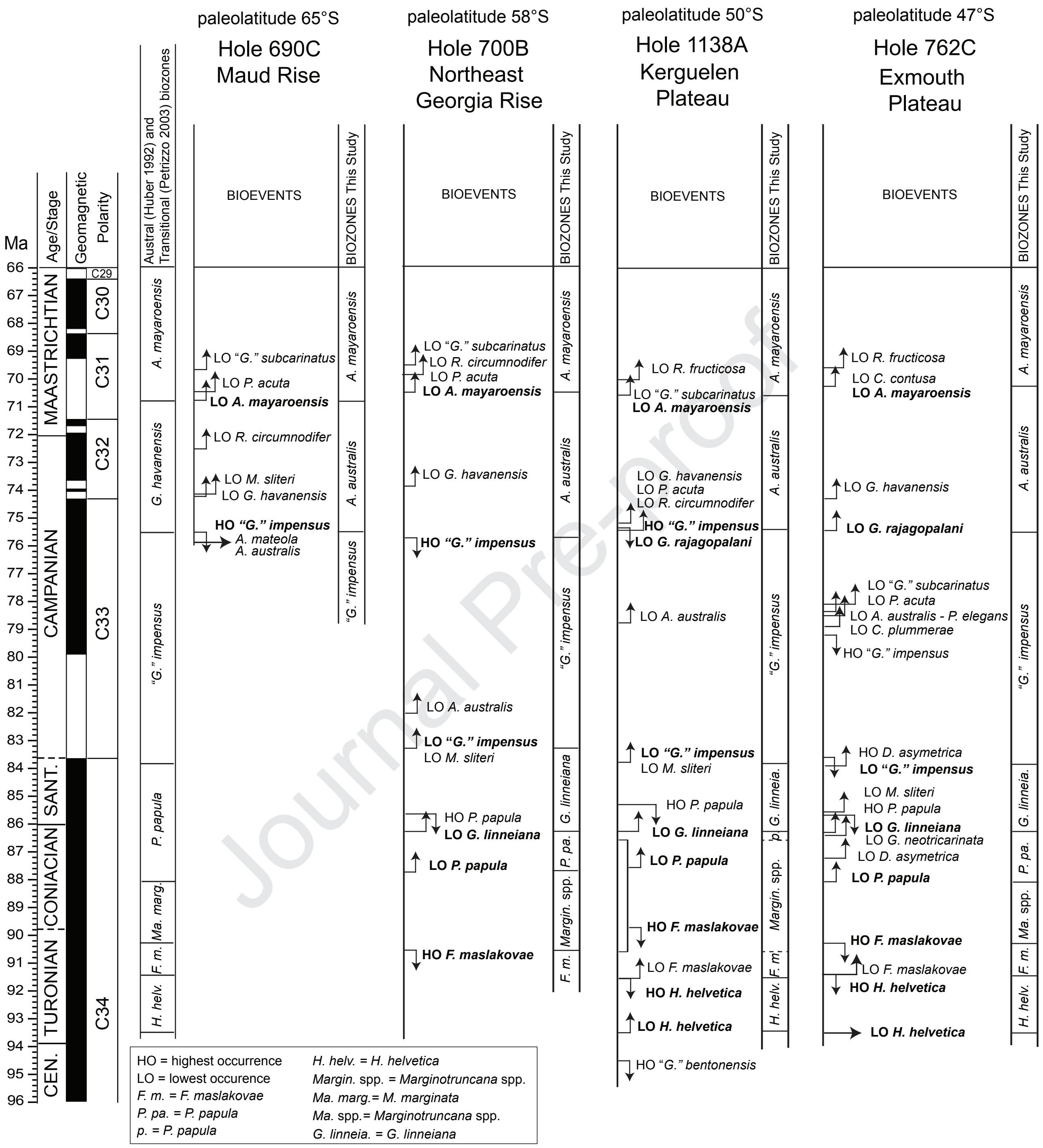

Hole 690C
Maud Rise
Depth (mbsf)
Core
Recovery
Lithologic unit
Lithologic description
Age
250
275
300
16X
17X
18X
19X
20X
21X
22X
IVC
Foraminifer-bearing muddy nannofossil ooze (chalk)
V
Muddy chalk, calcareous mudstone
MAASTRICHTIAN
CAMPANIAN
Hole 700B
Northeast Georgia Rise
350
400
450
37R
38R
39R
40R
41R
42R
43R
44R
45R
46R
47R
48R
49R
50R
51R
52R
53R
54R
VA
Homogenous micritic nannofossil-bearing limestone
VB
Micritic limestone alternating with clay-bearing/clayey micritic limestone
VC
Micritic limestone alternating with clay-bearing clayey micritic limestone and/or ash layers
MAASTR.
CAMPANIAN
SANTON
CONIAC.
Hole 1138A
Kerguelen Plateau
500
550
600
650
52R
53R
54R
55R
56R
57R
58R
59R
60R
61R
62R
63R
64R
65R
66R
67R
68R
69R
70R
IIIA
Foraminifer-bearing nannofossil chalk
IIIB
Foraminifer-bearing chalk
IV
Interbedded chalk, nannofossil claystone and claystone
V
Glauconite-bearing calcareous sandstone glauconitic claystone
MAASTR.
CAMPANIAN
SANTON.
CONIAC. - TURON.
CEN.
Hole 762C
Exmouth Plateau
600
700
750
800
43X
44X
45X
46X
47X
48X
49X
50X
51X
52X
53X
54X
55X
56X
57X
58X
59X
60X
61X
62X
63X
64X
65X
66X
67X
68X
69X
70X
71X
72X
73X
74X
IVA
White to light green-gray nannofossil chalk and green-gray clayey nannofossil chalk
IVB
Light green-gray nannofossil chalk and reddish brown nannofossil claystone
IVC
White to very light green-gray nannofossil chalk with foraminifers and green-gray nannofossil claystone
IVD
Light green-gray nannofossil chalk with foraminifers and brown clayey nannofossil chalk
MAASTRICHTIAN
CAMPANIAN
SANTONIAN
CON.
TUR.

Fig. 3


Ma
66
67
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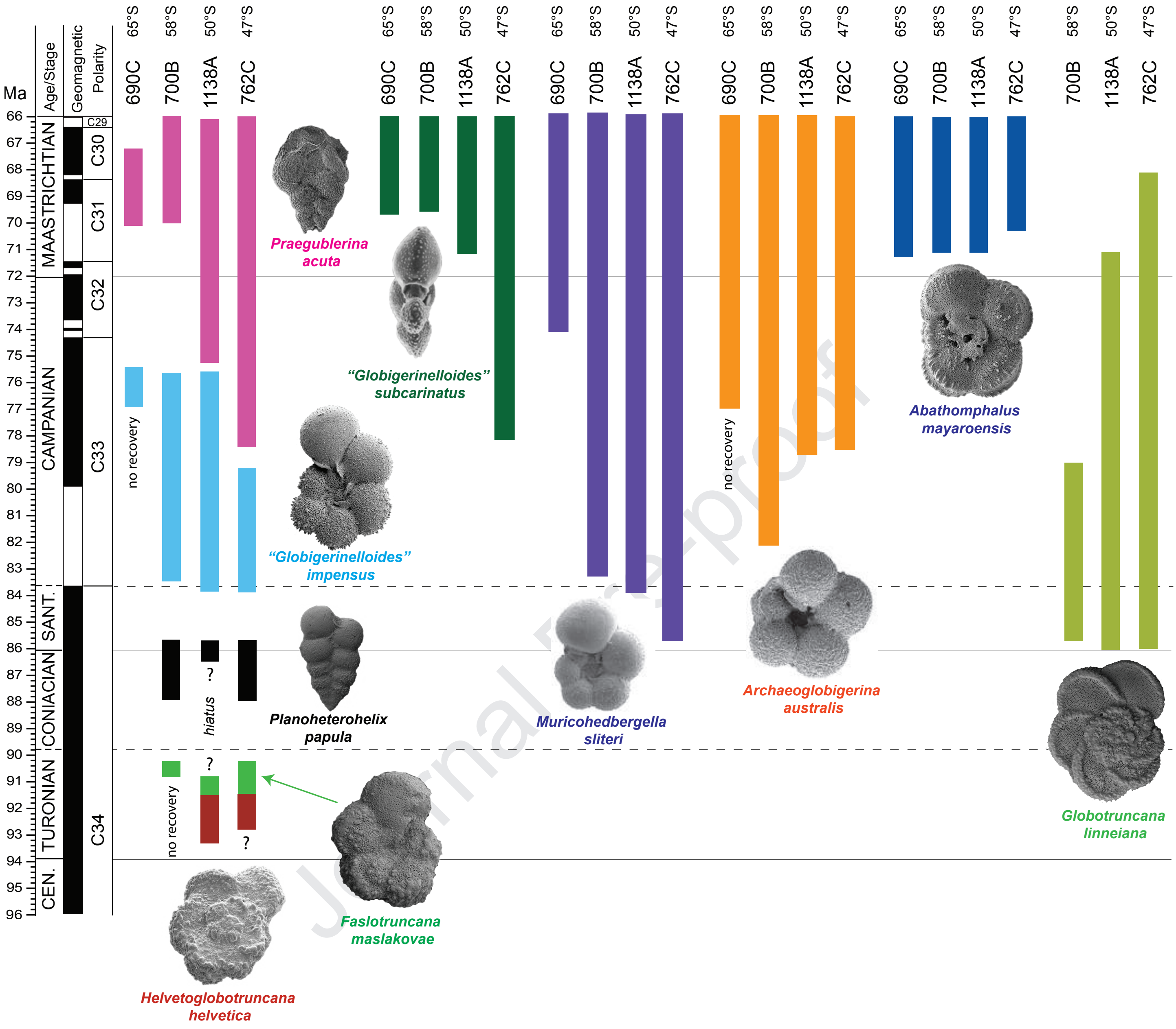
92
93
94
95
96
Age/Stage
MAASTRICHTIAN
CAMPANIAN
SANT.
CONIACIAN
TURONIAN
CEN.
Geomagnetic Polarity
C29
C30
C31
C32
C33
C34
Austral (Huber 1992) and Transitional (Petrizzo 2003) biozones
A. mayaroensis
G. havanensis
"G." impensus
P. papula
Ma. marg.
F. m.
H. helv.
paleolatitude 65°S
Hole 690C
Maud Rise
BIOEVENTS
BIOZONES This Study
LO "G." subcarinatus
LO P. acuta
LO A. mayaroensis
LO R. circumnodifer
LO M. sliteri
LO G. havanensis
HO "G." impensus
A. mateola
A. australis
A. mayaroensis
A. australis
"G." impensus
paleolatitude 58°S
Hole 700B
Northeast
Georgia Rise
BIOEVENTS
BIOZONES This Study
LO "G." subcarinatus
LO R. circumnodifer
LO P. acuta
LO A. mayaroensis
LO G. havanensis
HO "G." impensus
LO A. australis
LO "G." impensus
LO M. sliteri
HO P. papula
LO G. linneiana
LO P. papula
HO F. maslakovae
A. mayaroensis
A. australis
"G." impensus
G. linneiana
P. pa.
Margin. spp.
F. m.
paleolatitude 50°S
Hole 1138A
Kerguelen
Plateau
BIOEVENTS
BIOZONES This Study
LO R. fructicosa
LO "G." subcarinatus
LO A. mayaroensis
LO G. havanensis
LO P. acuta
LO R. circumnodifer
HO "G." impensus
LO G. rajagopalani
LO A. australis
LO "G." impensus
LO M. sliteri
HO P. papula
LO G. linneiana
LO P. papula
HO F. maslakovae
LO F. maslakovae
HO H. helvetica
LO H. helvetica
HO "G." bentonensis
A. mayaroensis
A. australis
"G." impensus
G. linneia.
p.
Margin. spp.
F. m.
H. helv.
paleolatitude 47°S
Hole 762C
Exmouth
Plateau
BIOEVENTS
BIOZONES This Study
LO R. fructicosa
LO C. contusa
LO A. mayaroensis
LO G. havanensis
LO G. rajagopalani
LO "G." subcarinatus
LO P. acuta
LO A. australis - P. elegans
LO C. plummerae
HO "G." impensus
HO D. asymetrica
LO "G." impensus
LO M. sliteri
HO P. papula
LO G. linneiana
LO G. neotricarinata
LO D. asymetrica
LO P. papula
HO F. maslakovae
LO F. maslakovae
HO H. helvetica
LO H. helvetica
A. mayaroensis
A. australis
"G." impensus
G. linneia.
P. pa.
Ma. spp.
F. m.
H. helv.
HO = highest occurrence
LO = lowest occurence
F. m. = F. maslakovae
P. pa. = P. papula
p. = P. papula
H. helv. = H. helvetica
Margin. spp. = Marginotruncana spp.
Ma. marg.= M. marginata
Ma. spp.= Marginotruncana spp.
G. linneia. = G. linneiana

Fig. 4


Ma
Age/Stage
Geomagnetic Polarity
66
67
68
69
70
71
72
73
74
75
76
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78
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80
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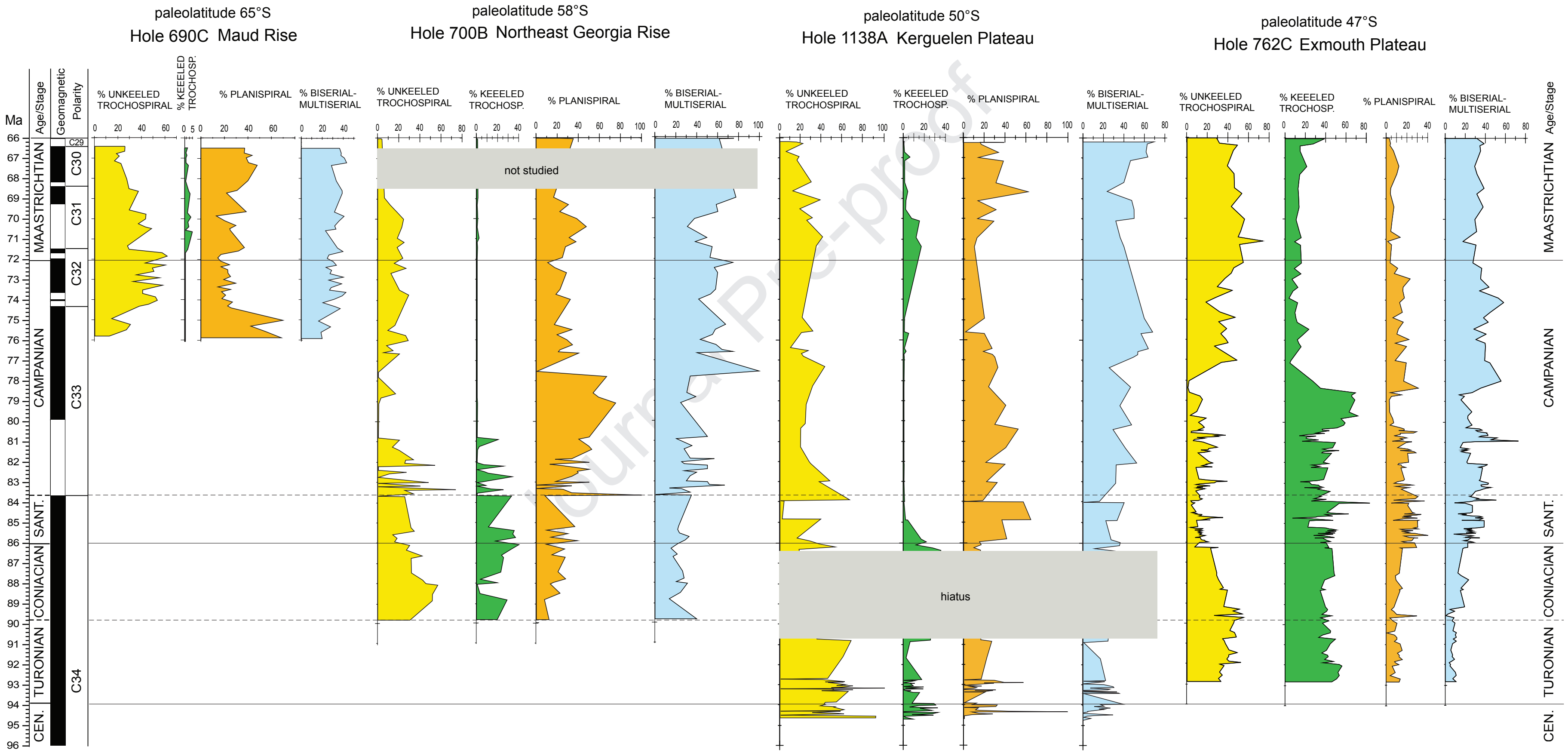
95
96
MAASTRICHTIAN
CAMPANIAN
SANT.
CONIACIAN
TURONIAN
CEN.
C29
C30
C31
C32
C33
C34
690C 65°S
700B 58°S
1138A 50°S
762C 47°S
no recovery
?
hiatus
?
?
no recovery
Praegublerina acuta
"Globigerinelloides" subcarinatus
"Globigerinelloides" impensus
Planoheterohelix papula
Faslotruncana maslakovae
Helvetoglobotruncana helvetica
Muricohedbergella sliteri
no recovery
Archaeoglobigerina australis
Abathomphalus mayaroensis
700B 58°S
1138A 50°S
762C 47°S
Globotruncana linneiana

Fig. 5


paleolatitude 65°S
Hole 690C Maud Rise
paleolatitude 58°S
Hole 700B Northeast Georgia Rise
paleolatitude 50°S
Hole 1138A Kerguelen Plateau
paleolatitude 47°S
Hole 762C Exmouth Plateau
Ma
Age/Stage
Geomagnetic Polarity
% UNKEELED TROCHOSPIRAL
% KEEELED TROCHOSP.
% PLANISPIRAL
% BISERIAL-MULTISERIAL
MAASTRICHTIAN
CAMPANIAN
SANT.
CONIACIAN
TURONIAN
CEN.
C29
C30
C31
C32
C33
C34
not studied
hiatus
66
67
68
69
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71
72
73
74
75
76
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Fig. 6

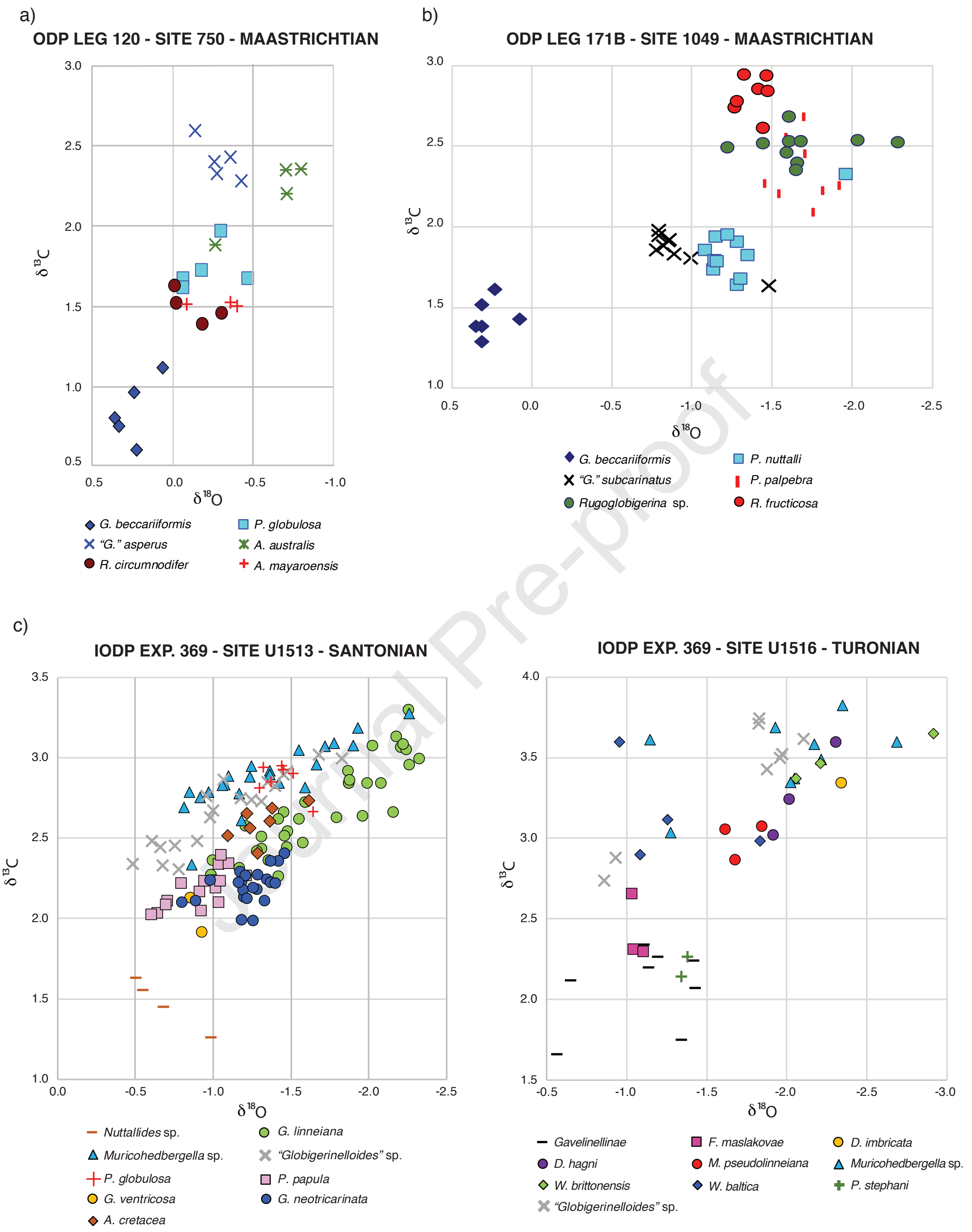

a)
ODP LEG 120 - SITE 750 - MAASTRICHTIAN
δ13C
3.0
2.5
2.0
1.5
1.0
0.5
0.5
0.0
-0.5
-1.0
δ18O
G. beccariiformis
"G." asperus
R. circumnodifer
P. globulosa
A. australis
A. mayaroensis
b)
ODP LEG 171B - SITE 1049 - MAASTRICHTIAN
δ13C
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
δ18O
G. beccariiformis
"G." subcarinatus
Rugoglobigerina sp.
P. nuttalli
P. palpebra
R. fructicosa
c)
IODP EXP. 369 - SITE U1513 - SANTONIAN
δ13C
3.5
3.0
2.5
2.0
1.5
1.0
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
δ18O
Nuttallides sp.
Muricohedbergella sp.
P. globulosa
G. ventricosa
A. cretacea
G. linneiana
"Globigerinelloides" sp.
P. papula
G. neotricarinata
IODP EXP. 369 - SITE U1516 - TURONIAN
δ13C
4.0
3.5
3.0
2.5
2.0
1.5
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
δ18O
Gavelinellinae
D. hagni
W. brittonensis
"Globigerinelloides" sp.
F. maslakovae
M. pseudolinneiana
W. baltica
D. imbricata
Muricohedbergella sp.
P. stephani

Fig. 7

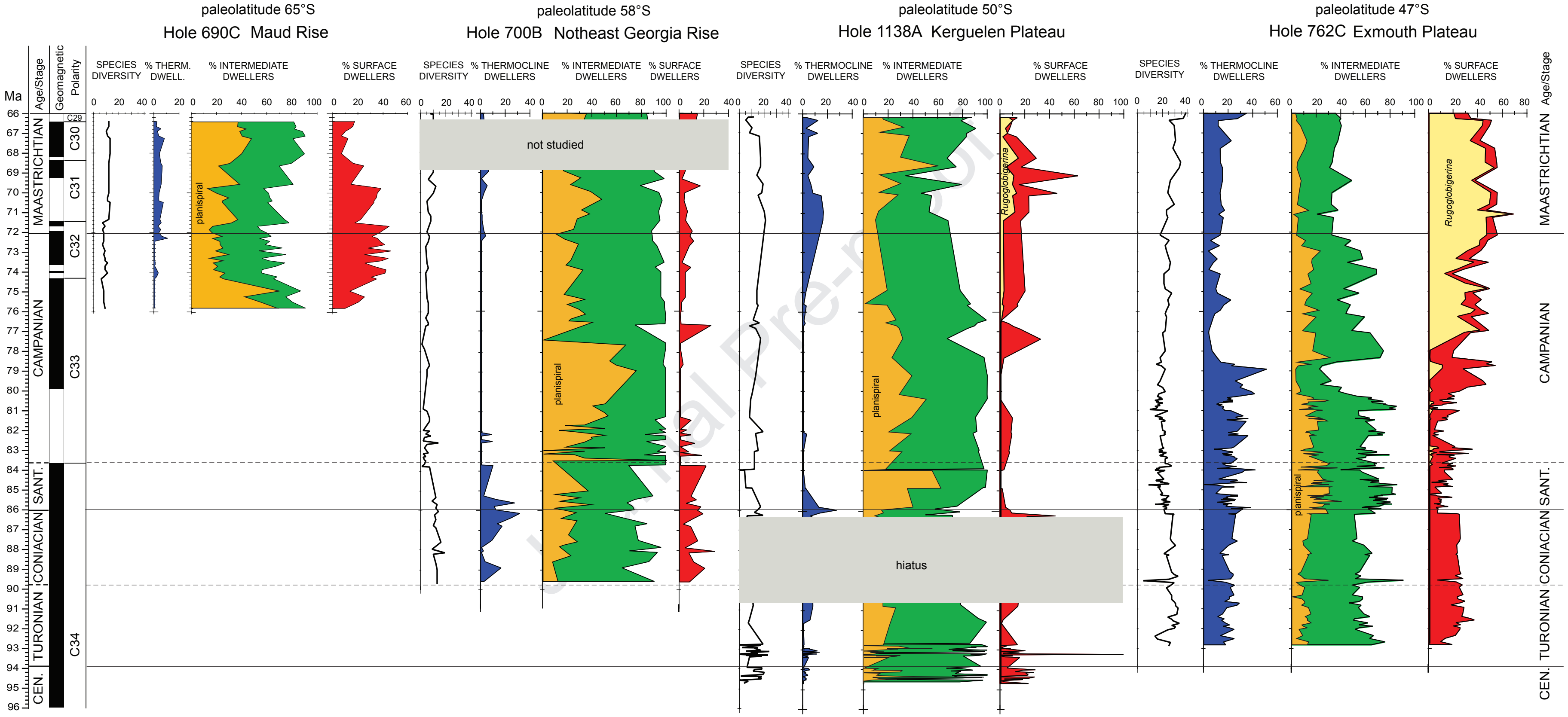
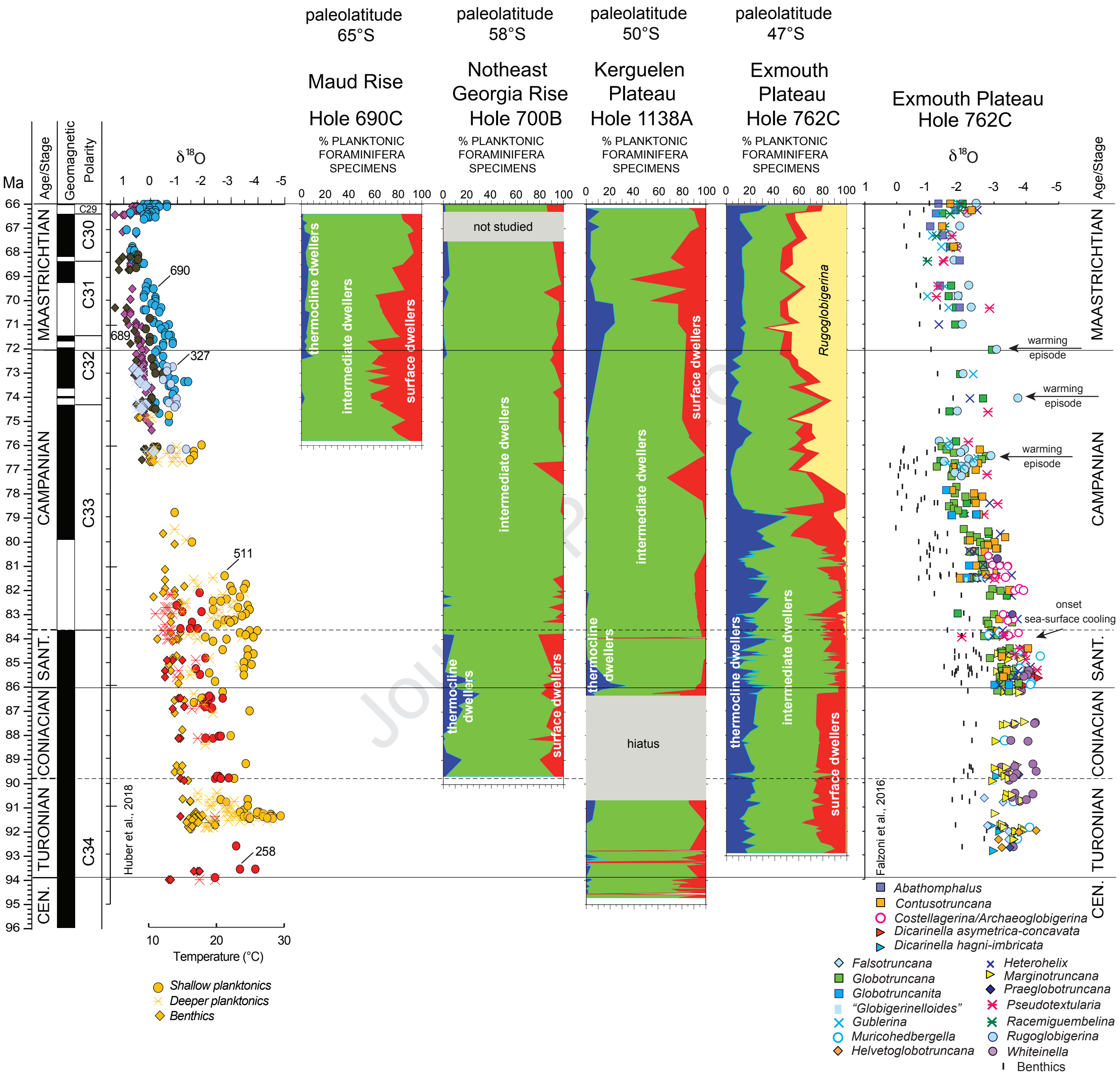

paleolatitude 65°S
Hole 690C Maud Rise
paleolatitude 58°S
Hole 700B Notheast Georgia Rise
paleolatitude 50°S
Hole 1138A Kerguelen Plateau
paleolatitude 47°S
Hole 762C Exmouth Plateau
Ma
Age/Stage
Geomagnetic Polarity
SPECIES DIVERSITY
% THERM. DWELL.
% THERMOCLINE DWELLERS
% INTERMEDIATE DWELLERS
% SURFACE DWELLERS
0 20 40 60 80 100
66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96
MAASTRICHTIAN
CAMPANIAN
SANT.
CONIACIAN
TURONIAN
CEN.
C29
C30
C31
C32
C33
C34
planispiral
Rugoglobigerina
not studied
hiatus

Fig. 8



paleolatitude 65°S
Maud Rise
Hole 690C
paleolatitude 58°S
Notheast Georgia Rise
Hole 700B
paleolatitude 50°S
Kerguelen Plateau
Hole 1138A
paleolatitude 47°S
Exmouth Plateau
Hole 762C
Exmouth Plateau
Hole 762C
% PLANKTONIC FORAMINIFERA SPECIMENS
Ma
Age/Stage
Geomagnetic Polarity
δ18O
1 0 -1 -2 -3 -4 -5
0 20 40 60 80 100
66
67
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76
77
78
79
80
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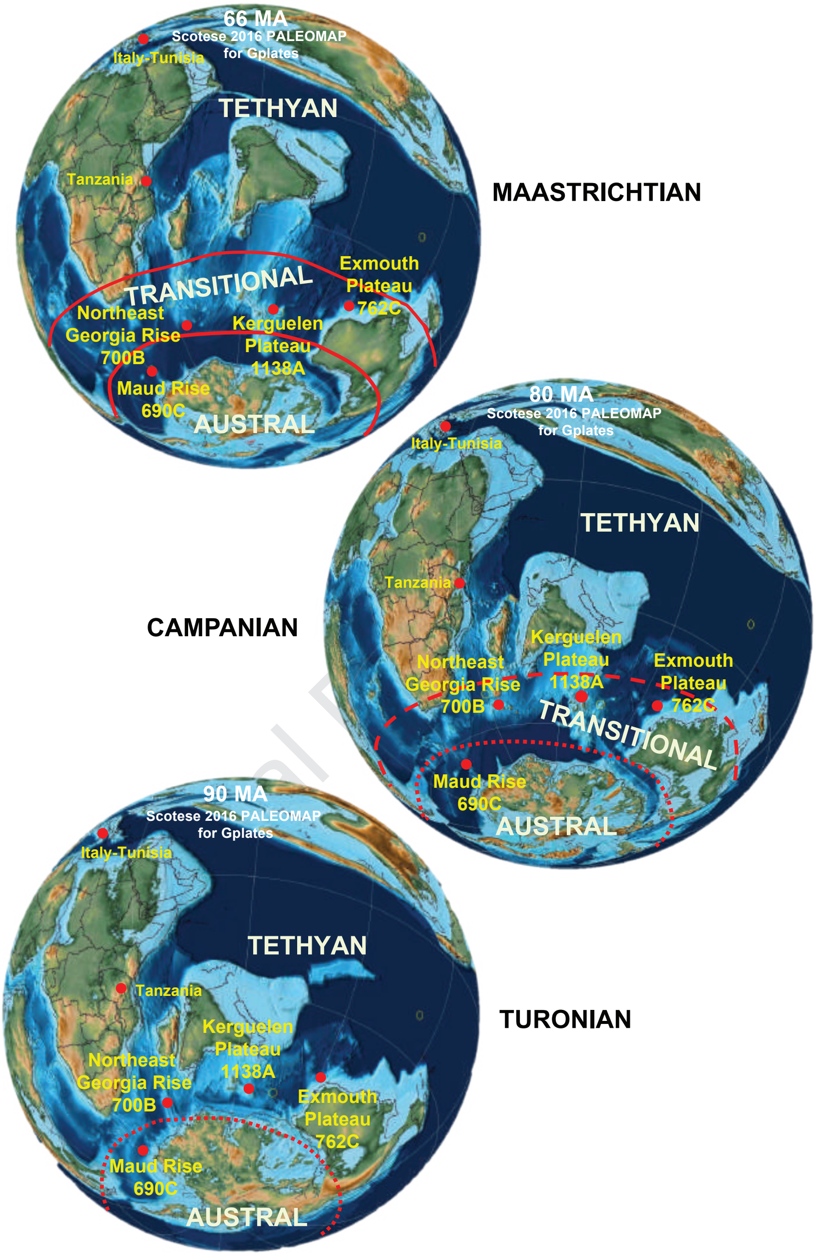
96
MAASTRICHTIAN
CAMPANIAN
SANT.
CONIACIAN
TURONIAN
CEN.
C29
C30
C31
C32
C33
C34
690
689
327
511
258
Huber et al., 2018
10 20 30
Temperature (°C)
Shallow planktonics
Deeper planktonics
Benthics
thermocline dwellers
intermediate dwellers
surface dwellers
not studied
hiatus
Rugoglobigerina
warming episode
warming episode
warming episode
onset sea-surface cooling
Falzoni et al., 2016
Abathomphalus
Contusotruncana
Costellagerina/Archaeoglobigerina
Dicarinella asymetrica-concavata
Dicarinella hagni-imbricata
Falsotruncana
Globotruncana
Globotruncanita
"Globigerinelloides"
Gublerina
Muricohedbergella
Helvetoglobotruncana
Heterohelix
Marginotruncana
Praeglobotruncana
Pseudotextularia
Racemiguembelina
Rugoglobigerina
Whiteinella
Benthics

Fig. 9


66 MA
Scotese 2016 PALEOMAP for Gplates
Italy-Tunisia
TETHYAN
Tanzania
MAASTRICHTIAN
Exmouth Plateau 762C
TRANSITIONAL
Northeast Georgia Rise 700B
Kerguelen Plateau 1138A
Maud Rise 690C
AUSTRAL
80 MA
Scotese 2016 PALEOMAP for Gplates
Italy-Tunisia
TETHYAN
Tanzania
CAMPANIAN
Kerguelen Plateau 1138A
Northeast Georgia Rise 700B
Exmouth Plateau 762C
TRANSITIONAL
Maud Rise 690C
AUSTRAL
90 MA
Scotese 2016 PALEOMAP for Gplates
Italy-Tunisia
TETHYAN
Tanzania
TURONIAN
Kerguelen Plateau 1138A
Northeast Georgia Rise 700B
Exmouth Plateau 762C
Maud Rise 690C
AUSTRAL

Highlights

- Planktonic foraminifera biozonation for the circum-Antarctic region
- Planktonic foraminifera quantitative data permit interpretation of changes in the pattern of surface water stratification
- Poleward and equatorward migration of planktonic foraminiferal species
- Paleoecology of Late Cretaceous planktonic foraminifera
- Paleogeographic boundaries of the Austral, Transitional and Tethyan Bioprovinces
- Links between species distribution patterns and transition from the hot greenhouse climate of the Turonian to the cooler greenhouse of the Maastrichtian

All authors have contributed to the manuscript and have approved the final version of the manuscript.
Petrizzo: Conceptualization, Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualization.
Huber, Falzoni, MacLeod: Investigation, Writing - Review & Editing.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: