Survivorship of benthic foraminifera across the Danian Warm World

Thulasi Thena[1]*, Dhananjai K Pandey[1], Raj K Singh[2], Nisha Nair[1], K S Roshni[1]

[1]*National Centre for Polar and Ocean Research (NCPOR), Ministry of Earth Sciences, Goa 403804, India*

[2]*School of Earth, Ocean, and Climate Sciences, Indian Institute of Technology Bhubaneswar, 752050, Odisha, India*

**Corresponding author e-mail and orcid: thenadoss@ncpor.res.in ; tinathulasi@gmail.com ; https://orcid.org/0000-0002-9304-8665*

Abstract

Three major geological events: The cretaceous-Paleogene (K/Pg) transition, Dan-C2, and the Latest Danian Event (LDE) during the Early Paleocene geologic period caused potential impacts over mass extinctions of several marine life and also rapid change in climate from icehouse to warmhouse condition. The effects of these events on the marine community in the Indian Ocean are not well understood in comparison to other oceans. Here we investigate benthic foraminiferal diversity patterns, morphotypes, and oxygen conditions along with the carbonates and magnetic susceptibility records in the Indian Ocean sediments to understand the Danian Warm World (DWW). Deep-sea sediments from the International Ocean Discovery Program (IODP) Site U1457 (Laxmi basin, Northern Indian Ocean) at ~1100 meters below the seafloor (mbsf) of the Danian period (*c.* 66 – 61.6 Ma) are examined, which suggest that the foraminifera subsisted across major events. Species belonging to *Bolivina*, *Glandulina*, *Hoeglundina*, *Parrelloides* and *Quadrimorphina* genus were dominant above the K/Pg boundary whereas *Bolivina*, *Bulimina*, *Cassidulina*, *Cornuspira*, *Gyroidinoides*, *Melonis*, *Oolina*, *Pullenia*, *Reussoolina* and *Rutherfordoides* were dominated across the hyperthermal events. We also calculated the average oxygen content at 0.16 ml/L in accordance with oxyphilic species abundance, which serves as supportive evidence, in defining Laxmi basin favours a suboxic to dysoxic environment. The benthic foraminiferal diversity pattern, primary anomalies of calcium carbonates, magnetic susceptibility, and previous global datasets of carbon and oxygen isotopes attempted to mark the period of geologic events at the study site.

Keywords*: Benthic foraminifera, Laxmi basin, K/Pg, Danian, Northern Indian Ocean.*

Key Points

- New insight on the existence of benthic foraminifera during the early Paleocene from IODP Site U1457 of Laxmi basin, Northern Indian Ocean.
- The survivorship heat sustained foraminiferal shells define the ecological condition and tolerance in an oxygen-poor habitat.
- Foraminiferal diversity patterns suggest to define the possibility of major geological events across the Danian warm period.

Plain Language Summary

Foraminifera are single-celled organisms found in marine environments which play a vital role in marine ecosystems and biogeochemical cycling processes. They exist in marine environments since *c*. 500 Ma and are adapted to different ecological conditions owing to their sensitivity. Foraminiferal fossils considered as crucial tool for reconstructing the past environment and climatic conditions. Sixty-six million years ago, large asteroid impact caused the loss of approximately 75% of living organisms on Earth, including dinosaurs. This event is marked and known as the Cretaceous-Paleogene (K/Pg) extinction event. Examining the geological record is one technique to test how the Earth would behave in climates warmer than the one we currently experience. Hence, we analyzed deep-sea marine sediments from the Laxmi basin in the Northern Indian Ocean to determine the foraminiferal survivorship across the Danian warmhouse period (*c*. 66 – 61.6 Ma). We analyzed the quantitative accumulation of foraminifera based on various parameters, the concentration of carbonate deposition, and magnetic susceptibility and found 37 benthic foraminifera species sustained during the warmer climatic period. These results also aided in defining the possibility of K/Pg boundary, and short-term hyperthermal events that occurred in the Laxmi basin.

1. Introduction

The Cenozoic Era is the most recent geological era that began about 66 million years ago and continues today (Zachos et al., 2001). The Danian epoch (*c*. 66 - 61.6 Ma) of early Paleogene (*c*. 66 - 56 Ma) is significant owing to the commencement of a new era in Earth's history, extinction of non-avian dinosaurs, diversification of mammals, geological events, and a stratigraphic boundary used for studying Earth's history (Lyson et al., 2019; Condamine et al., 2021). Short-range hyperthermal events Dan-C2 (*c*. 65.2 Ma), Latest Danian Event (LDE; *c*. 62.2 Ma), and the major Chicxulub crater (*c*. 66 Ma) discovery stood as key evidence supporting the

concept that an asteroid impact was responsible for the mass extinction of foraminifera, planktic organisms, and benthic organisms throughout Cretaceous/Paleogene (K/Pg) transition (Kring, 2007; Khozyem et al., 2019; Chiarenza et al., 2020; Lyons et al., 2020; Bornemann et al., 2021; Nauter-Alves et al., 2023). Contemporaneous tectonic activities led to the separation of India from Madagascar and Seychelles followed by the formation of the Northern Indian Ocean (NIO). The associated geodynamic developments substantially impacted global oceanic circulation patterns (Kent and Muttoni, 2008). The Laxmi basin lies between an isolated morphological high of the Laxmi ridge to the west and the Indian subcontinent to the east (Pandey et al., 2019; 2022). Its genesis is closely linked to the broader geological history of the NIO. Over time, it has been shaped by a range of geological processes, including rifting, seafloor opening, volcanic activity, and post-rift sedimentation. The modern seafloor in this region is characterized by features such as submarine canyons, seamounts, and ridges. Despite a broad evolutionary understanding, the precise genesis of the Laxmi basin has remained enigmatic. Accordingly, it has attracted the attention of geologists and oceanographers across the globe because of its key geographic location between the Indo-Arabian tectonic plates (Pandey et al., 2019).

Warm and shallow marine conditions with a high sea level characterized the early Paleocene period in global oceans (Zachos et al., 2001). The warm conditions were likely driven by high atmospheric carbon dioxide levels and increased greenhouse gas concentrations (Zachos et al., 1993). Analyses of marine sediment cores suggest that the bottom water conditions may have significantly impacted marine life in those areas (Pandey et al., 2016). However, NIO's early Paleocene deep ocean environmental signals are not well known due to a lack of direct observations and measurements. Micropaleontological studies are frequently linked to sources of sediment transportation at assorted oxygen conditions, bottom water warming, and stability of bottom water ecosystem owing to their prominent wealth among the marine community (Thena et al., 2021a). Foraminiferal responses in the Early Paleocene or Danian provide valuable insights into rapid global warming, carbon cycle perturbations, and recovery and evolution of marine ecosystems after a major extinction event (Arreguín-Rodríguez et al., 2022; Alegret et al., 2009; Jehle et al., 2015; Molina 2015). The warming of the surface and bottom waters and ecosystem disturbance influenced the individual species as well as assemblage diversity observed across the global ocean (Arreguín-Rodríguez et al., 2022, 2021; Rogers, 2015; Zeppilli et al., 2018; Paulus, 2021; Jameson et al., 2022; Nauter-Alves et al., 2023). Few commonly reported benthic foraminiferal genera in Early Paleocene sediments include *Bolivina*, *Bulimina*,

Cibicidoides, *Nuttallides*, *Spiroplectammina*, *Seabrookia*, *Planulina* and *Uvigerina*, etc. (Algret and Thomas, 2004, 2005, 2007; Arreguín-Rodríguez et al., 2022, 2021; Sprong et al., 2012; Farouk and Jain, 2018). The presence of *Nuttallides* suggests that the seafloor was well-oxygenated, while the presence of *Cibicidoides* indicates the presence of low-oxygen conditions (Galazzo et al., 2013). These genera are typical deep-sea benthic foraminifera found in various sediment types, including chalks, limestones, and siliceous sediments. Changes in the ratio of these and other benthic foraminifera provide information about changes in ocean circulation patterns and other environmental factors (Gupta et al., 2008). Benthic foraminifera witnessed through all these geologic events are termed "survivors" in the present study. The current manuscript chiefly focuses on documenting their survivorship at the Laxmi basin, NIO during the Danian Warm World (DWW) and their global responses.

2. Site Description and Methodology

The International Ocean Discovery Program (IODP) Expedition 355 carried out scientific ocean drilling at two sites, namely U1456 and U1457, in the Laxmi basin of NIO (Fig. 1). Drilling and coring operations in ~3600m deep water depths retrieved a total of about 1700 m sediment and igneous basement cores from both sites. Although most of the sediment cores ranged between the Recent to mid-late Miocene period, a condensed Paleocene segment overlying the igneous basement of the late Cretaceous age was recovered from Site U1457 (Pandey et al., 2016, 2019). Here we investigate the sediment cores from Site U1457 (17°9.9486′N and 67°55.8121′E; Water depth ~3523 m; Fig. 1). This particular site is located at ~490 km west of the Indian coastal margin and ~750 km south of present-day Indus River. Geologically, the region lies within the Laxmi basin of NIO. The total sediment thickness around the Laxmi basin ranges between 1.1 and 3.5 km, with the rate of sedimentation during the Paleocene estimated to be 18-20 cm/ka (Pandey et al., 2017; Nair et al., 2021). The total depth of penetration at Site U1457 reached around ~1100 m below the sea floor (mbsf) and the cored section was divided into five lithologic units by the shipboard scientists (Pandey et al., 2016). The present study focuses on unit V consisting of claystone and volcanoclastic sediments overlayed on the basaltic basement of early Paleocene / Danian (*c*. 66 – 61.6 Ma). The age datum of the samples is correlated at two depth intervals from the revised chronostratigraphic record of calcareous nannofossil biostratigraphy (Routledge et al., 2019).

The sediment samples between ~1060 and 1095 mbsf were processed following the standard procedures: sediments were soaked in distilled water for more than 12 hours; wet sieved over 63 µm mesh using a clean jet of water; the remains were oven-dried and stored in labelled vials

(Gupta and Thomas, 1999; Mohan et al., 2011; Thena et al., 2021a). Benthic and planktic foraminifera >125 µm in the samples were quantitatively analyzed under the microscope as a whole fraction. Statistical analysis was performed using PAST software that correlates the benthic foraminiferal diversity patterns, events and changes to compare our results across the global ocean datasets (Arreguín-Rodríguez et al., 2022). The benthic foraminiferal identification, taxonomic concepts, and nomenclature in the manuscript are after Loeblich and Tappan, (1964; 1984); Pawlowski et al. (2013).

In addition, to relate the findings with carbonate composition and sediment sources, procured samples were also tested with a few other proxies: inorganic carbon (IC) and magnetic susceptibility, respectively. Low-frequency magnetic susceptibility (MS) measurements were carried out using a Bartington MS2B sensor, and 30-40 mg of samples were oven-dried at 60°C, homogenized to measure the IC using CM5017 CO_2 coulometer. Carbonate concentration in sediments is calculated by multiplying 8.333 with obtained IC values at each depth interval (Johnson et al., 2014). Stable isotope records of carbon and oxygen of global oceans are obtained from previously published records to enhance the understanding of the study region (Table 1; Quillevere et al., 2002; Westerhold et al., 2011; 2018; Barnet et al., 2019). The oxygen content at each depth was calculated using the oxygen transfer function of Drinia et al. (2004) and Thena et al. (2021b). The geodynamic settings of the Laxmi basin during the Paleocene time make it an important site to investigate the DWW and its possible climatic implications.

3. Results and Discussions

3.1. Faunal stability across DWW

Benthic foraminifera in the Laxmi basin was identified and measured in terms of their relative abundance, diversity, morphogroups, shell composition, favored habitual conditions, and ecological sustainability. A proper quantitative analysis was performed to know the relative abundance of calcareous and agglutinated benthic foraminifera and planktic foraminifera. Based on population abundance, the average accumulation of benthic calcareous foraminifera constitutes 73.16%, agglutinated foraminifera at 4.52%, and planktic foraminifera 8.66%. Thirty-seven species of benthic foraminifera belonging to 29 genera are recognized in the present study that survived across the DWW (Table 2). However, due to their lower range of preservation in the analyzed samples, benthic foraminifera identified as having an abundance rate of greater than 5% at least in two samples at the generic level are plotted against the analyzed depth (Fig. 2). Further, based on habitual preferences, benthic foraminifera are grouped as infaunal (27.68%)

and epifaunal (20.14%) species (Murray et al., 2011; Arreguin-Rodriguez et al., 2018; Venturelli et al., 2018). Even though the present study covering the Danian period has poor preservation of foraminifera, considerable calcareous (40.05%) shell material is dominated in the samples (Fig. 3). The benthic foraminifera are grouped into eight morphotypes that include average accumulation of uniserial (0.68%), biserial (8.73%), triserial (2.10%), unilocular (4.56%), planispiral (3.59%), tubular (1.21%), trochospiral (24.43%) and 1.20% of milioline (Fig. 4; Corliss and Fois, 1990; Alegret et al., 2021). Each benthic foraminiferal species responds differently to the availability of dissolved oxygen, where the calculated oxygen content at each depth ranged between 0.1 and 0.6 ml/L. Hence, benthic foraminifera is grouped into oxic (12 species), suboxic (15 species), and dysoxic (8 species) groups following Kaiho, (1994), and Singh et al. (2015) and their inter-correlation among each parameter is quantitatively measured for a better understanding (Fig. 5; Table 3).

3.2. Benthic foraminiferal tolerance in oxygen-poor habitats

Based on our results, the studied core comprises 44.57% foraminiferal abundance pertaining to two different depositional environments evidenced by a higher abundance of trochospiral morphogroups assemblages (Fig. 4). The water column depth of the region defines the samples fit bathyal zone also characterized by the dominance of dysoxic to suboxic (*Bolivina*, *Bulimina*, *Cassidulina*, *Cornuspira*, *Parrelloides*, *Reussoolina*) and few oxic taxa (e.g., *Cibicidoides*, *Epistominella*, *Gavelinopsis*, *Laticarinina*) species. The benthic foraminiferal assemblages also delineate the biotic events (K/Pg, Dan-C2, and LDE) that occurred during the early Paleocene period in NIO. Through the anticipated K/Pg transition, we find a high number of dysoxic to suboxic benthic foraminiferal assemblages belonging to *Bolivina*, *Glandulina*, *Hoeglundina*, *Parrelloides*, and *Quadrimorphina* genus (Fig. 2). However, their abundance decreased after the short-term Danian hyperthermal events. This study suggests that the survival of *Bolivina*, *Bulimina*, *Cassidulina*, *Cornuspira*, *Gyroidinoides*, *Melonis*, *Oolina*, *Pullenia*, *Reussoolina*, and *Rutherfordoides* genera across the Dan-C2, but their abundance decreased in the later interval. The oxic species has an inclining trend at the Laxmi basin between Dan-C2 and ~63.25 Ma (Fig. 5), evidenced by the dominance of planispiral and trochospiral morphogroup species (Fig. 4; Table 3). However, in the younger interval, the dysoxic and suboxic foraminifera having biserial or unilocular morphogroup proved to be dominant, which strongly suggests a dysoxic to the suboxic environment at the Laxmi basin (Figs.2, 4, 5; Kranner et al., 2022).

3.3. Stable isotopes - Faunal diversity interconnections

Stable isotope record from the Danian age describes the complex interactions between biotic and abiotic factors that drove environmental change during this important time period in Earth's history (Keller et al., 2020). The perception of the past isotopic compositions from the Pacific and Atlantic Oceans signifies a decrease in the primary productivity and leads to predicting better the time range of climatic events that happened during the Danian age (Fig. 6). The global faunal diversity pattern turns as an indicative proxy of the post-impact K/Pg event, evidencing from impulsive incursions in $\delta^{13}C$ and $\delta^{18}O$ at *c*. 66 Ma (Fig. 6a-d; Zachos et al., 2001; Quillevere et al., 2002; Barnet et al., 2019). The benthic foraminiferal diversity pattern suggests an increasing trend up to ~1084 mbsf and subsequently decreases toward ~1074 mbsf followed by minor variations (Fig. 6e-h). This faunal pattern observed from the Laxmi basin of NIO (Fig.6i) is closely correlated to similar data collected from various oceans for the same period. Earlier to the K/Pg transition (*c*. 68 - 66 Ma) decreasing diversity trend is observed in the Pacific, Atlantic, and Southern Oceans whereas an increasing trend is observed in the Tethys (Fig. 6e-h). After that across the K/Pg transition and Dan-C2 period (*c*. 66 – 65 Ma), diversity decreased, except for the Southern Ocean. A major turnover in the foraminifera and nannofossil abundance was observed across the world (Coccioni et al., 2010). Nauter-Alves et al. (2023) suggest volcanic activity as the main cause of the reduction of the foraminifera and nannofossil abundance during the Dan-C2 (Fig. 6e-h). This study also observed the reduction in foraminiferal diversity across the Dan-C2 till ~63.25 Ma. A constant and gradual faunal diversity range is observed throughout the warmer world heading towards LDE (*c*. 62.5 Ma; Fig. 6i). Correspondingly, the Pacific Ocean reports the infaunal foraminifera dominance indicating oligotrophic nature, whereas the mixed ratio of epifaunal and infaunal foraminifera signifies the mesotrophic condition in the Atlantic, Southern Ocean and at Site U1457 of Laxmi basin (Figs.5, 6). These findings are compatible with the aphotic condition and substituting heterogenous sedimental sources (Alegret et al., 2021; Giusberti et al., 2016).

3.4. Sediment geochemistry inferences

The determined IC values in the section do not exceed 1.0% and averaged 0.33%. The $CaCO_3$ records during the warm house period ranged between 0.1 and 5.9%, an estimated average of 2.78% (Fig. 3g). Lower carbonate content across the DWW signals low productivity and also clues the chance of a rise in calcium compensation depth since the interval experiences short-term hyperthermal events (Slotnick et al., 2015; Rostami et al., 2020). The measurements of MS vary from 0.8×10^{-8} to 21.46×10^{-8} SI units, and at one particular interval (~1090.18 mbsf), its value peaks high, 102.10×10^{-8} SI units when compared to overall samples (Fig. 3h). Lower

the values of MS is an immense temperature-dependent proxy in deep-sea sediments suggesting warmer climatic condition throughout the early Paleocene epoch (Ouyang et al., 2016; Radaković et al., 2019). The lithology of the formation is highly correlated to the MS results, and pelagic carbonates deposition shows low values at intervals between ~1060 and 1080 mbsf. The impulsive peak in the above-discussed depth signals may be the impact owing to the *Deccan-Reunion hotspot* (*c*. 65.2 Ma) concurring with the K/Pg transition interval (Dyment 1998; Mahoney et al., 2002; Bhattacharya, G. C., and Yatheesh; 2015; Khozyem et al., 2019; Pandey et al., 2020; Noronha-D'Mello et al., 2021).

4. Conclusions

Benthic foraminifera showed their persistence across the Danian warmer period at the Laxmi basin, NIO. The present research attempts to correlate the faunal patterns, isotopic evidence, and sediment deposition interpretations to demarcate the K/Pg zone and hyperthermal events recorded in IODP Site U1457. The benthic and planktic faunal assemblage patterns are inversely correlated, and the rate of survival capability after the mass extinction of the major calcareous planktic foraminifera genus at the K/Pg boundary is strongly evidenced at ~1090 mbsf. The summation of infaunal and epifaunal benthic foraminiferal morphogroups defines the species are favourable to aphotic or bathypelagic oceanographic bottoms. The dysoxic to suboxic benthic foraminifera in the *Bolivina, Bulimina, Cassidulina, Cornuspira, Parrelloides, Reussoolina* genus region are highly sustained to oxygen deficient conditions. All global ocean records display benthic foraminiferal diversity < 20%, whereas, in the Laxmi basin, it is < 8%, suggesting low productivity. Similarly, magnetic susceptibility and carbonate results describe the environmental conditions and probabilities of sedimental sources that prevailed during the time. Overall, the early Paleocene epoch was a time of significant geological and climatic changes in the Laxmi Basin and worldwide. The presented manuscript and ongoing research projects hooked on sedimentation and fossils record of the Tertiary period will benefit to shed new light on the evolution of the geological history of the Indian Ocean.

Conflict of Interest

The authors declare no conflicts of interest in relevance to this manuscript.

Open Research

The data archiving is underway. The data will be made available at PANGAEA repository. The stable isotope records of carbon and oxygen for Pacific and Atlantic in Figure 6a-b is taken from Westerhold et al. (2011) and Barnet et al. (2019). Indian Ocean isotope data in Figure 6c-

d through Quillevere et al. (2002). Fisher α diversity patterns from global oceans in Figure 6e-h is after Alegret et al. (2021). The software used for mapping and statistical purposes are open source: GeoMapApp and PAST.

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Figure 1. Bathymetry map showing the location of Laxmi basin (IODP U1457), Northern Indian Ocean (NIO) with Deep Sea Drilling Project (DSDP) and Ocean Drilling Project (ODP) sites, considered in this study. The reconstructed map of 66 Ma is backdropped using web-based platform http://www.odsn.de/odsn/services/paleomap/paleomap.html (Hay et al., 1999).

Figure 2. Dominant benthic foraminifera taxa survived at various depth interval across the Danian Warm World (DWW). Species are grouped at genus level together and plotted against depth, due to lower abundance.

Figure 3. Records of foraminiferal abundance (%), habitat (%) and shell composition (%) in Laxmi basin across lowermost Paleogene. (a) Relative abundance of benthic foraminifera (b) Abundance of Planktic foraminifera (c) Infaunal benthic foraminifera (d) Epifaunal benthic foraminiferal (e) Calcareous benthic foraminifera (f) Agglutinated benthic foraminifera (g) Magnetic susceptibility (χ_{lf} $10^{-8}m^{3}kg^{-1}$) (h) Calcium carbonate (%).

Figure 4. Morphotype classification and dispersal rate of benthic foraminifera in IODP Site U1457, Laxmi basin, NIO.

Figure 5. Distribution of (a) oxic, (b) suboxic and (c) dysoxic benthic foraminifera with the calculated (d) oxygen content in Laxmi basin.

Figure 6. Benthic foraminiferal diversity in IODP Site U1457 (vs depth; purple) across Danian in comparison with global benthic foraminiferal diversity (vs age). Pacific Ocean (black), Atlantic Ocean (red), Southern Ocean (blue) and Tethys (green). Stable carbon ($\delta^{13}C$; pink, orange, olive) and oxygen ($\delta^{18}O$; indigo, sky blue, pink) isotope records from Pacific, Atlantic and Indian Ocean are stacked along diversity pattern respectively. The datasets utilized in this figure are from various published sources detailed in Table 1.

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Table 1. Geographic and paleogeographic site descriptions of IODP Site U1457, Laxmi basin, NIO and associated information's of inter-related global ocean records.

Age	Site	Present day geographic location			Paleolatitude	Data source
DANIAN (66 – 61.6 Ma)	DSDP 465	Pacific Ocean	33°49′N	178°55′E	20.7° N	Westerhold et al., 2011; 2018; Barnet et al., 2019; Alegret et al., 2021
	ODP 865		18°26′N	179°33′W	5.5° N	
	ODP 1210		32°22′N	158°25′W	18.5° S	
	ODP 1049	Atlantic Ocean	30°08′N	76°06′W	27.7° N	
	ODP 1262		27°13'S	1°32'E	40.0° S	
	ODP 690	Southern Ocean	65°09′S	1°12'E	70.2° S	Alegret et al., 2021
	Agost	Tethys Ocean	--		31.0° N	
	ODP 122	Indian Ocean	16°44'S	115°32'E	41.9° S	Quillevere et al., 2002
	IODP 1457	N. Indian Ocean	17°9′N	67°55′E	23.8° S	*Present study*

Table 2. List of benthic foraminifera sustained across K/Pg and short-term hyperthermal events recorded throughout Danian in Laxmi basin.

Benthic foraminifera							
Infaunal morphogroups		**%**	**O_2**	**Epifaunal morphogroups**		**%**	**O_2**
Uniserial	*Rutherfordoides*	4.35	DO	Milioline	*Miliolinella*	1.54	DO
	Siphonodosaria	3.08	SO		*Quinqueloculina*	5.26	O
Biserial	*Bolivina*	34.45	DO		*Spiroloculina*	1.67	O
	Sahulia	0.83	O		*Spirosigmoilina*	0.83	O
	Cassidulina	25.00	SO		*Triloculina*	1.54	O
Triserial	*Bulimina*	13.05	DO	Trochospiral	*Cibicidoides*	58.70	O
Unilocular	*Glandulina*	1.11	SO		*Epistominella*	43.48	O
	Oolina	8.89	SO		*Gavelinopsis*	16.92	O
	Reussoolina	25.00	SO		*Gyroidinoides*	6.57	SO
Planispiral	*Lenticulina*	0.83	SO		*Hoeglundina*	1.67	SO
	Melonis	4.35	SO		*Laticarinina*	50.00	O
	Pullenia	5.18	SO		*Oridorsalis*	0.83	SO
Tubular	*Cornuspira*	13.33	DO		*Parrelloides*	15.79	SO

Table 3. Correlation matrix of various foraminiferal parameters used in the present study during the Danian interval.

	Depth	Benthic	Planktic	Infauna	Epifauna	Calcareous	Agglutinated	Oxic	Suboxic	Dysoxic	Oxygen content
Depth	1.00										
Benthic	-0.55	1.00									
Planktic	0.12	0.06	1.00								
Infauna	-0.58	0.46	0.06	1.00							
Epifauna	-0.23	0.37	-0.07	-0.13	1.00						
Calcareous	-0.14	0.62*	0.45	0.04	-0.08	1.00					
Agglutinated	0.37	0.22	0.08	-0.23	-0.26	0.67*	1.00				
Oxic	-0.31	0.44	-0.21	0.11	0.93**	-0.12	-0.31	1.00			
Suboxic	-0.59	0.36	0.07	0.83**	-0.16	-0.01	-0.25	-0.10	1.00		
Dysoxic	-0.51	0.43	0.28	0.84**	-0.31	0.34	0.16	-0.22	0.81**	1.00	
Oxygen content	-0.33	0.45	-0.20	0.12	0.92**	-0.10	-0.32	0.99**	-0.09	-0.20	1.00

*. Correlation is significant at the 0.05 level (2-tailed).

**. Correlation is significant at the 0.01 level (2-tailed).

Figure 1.

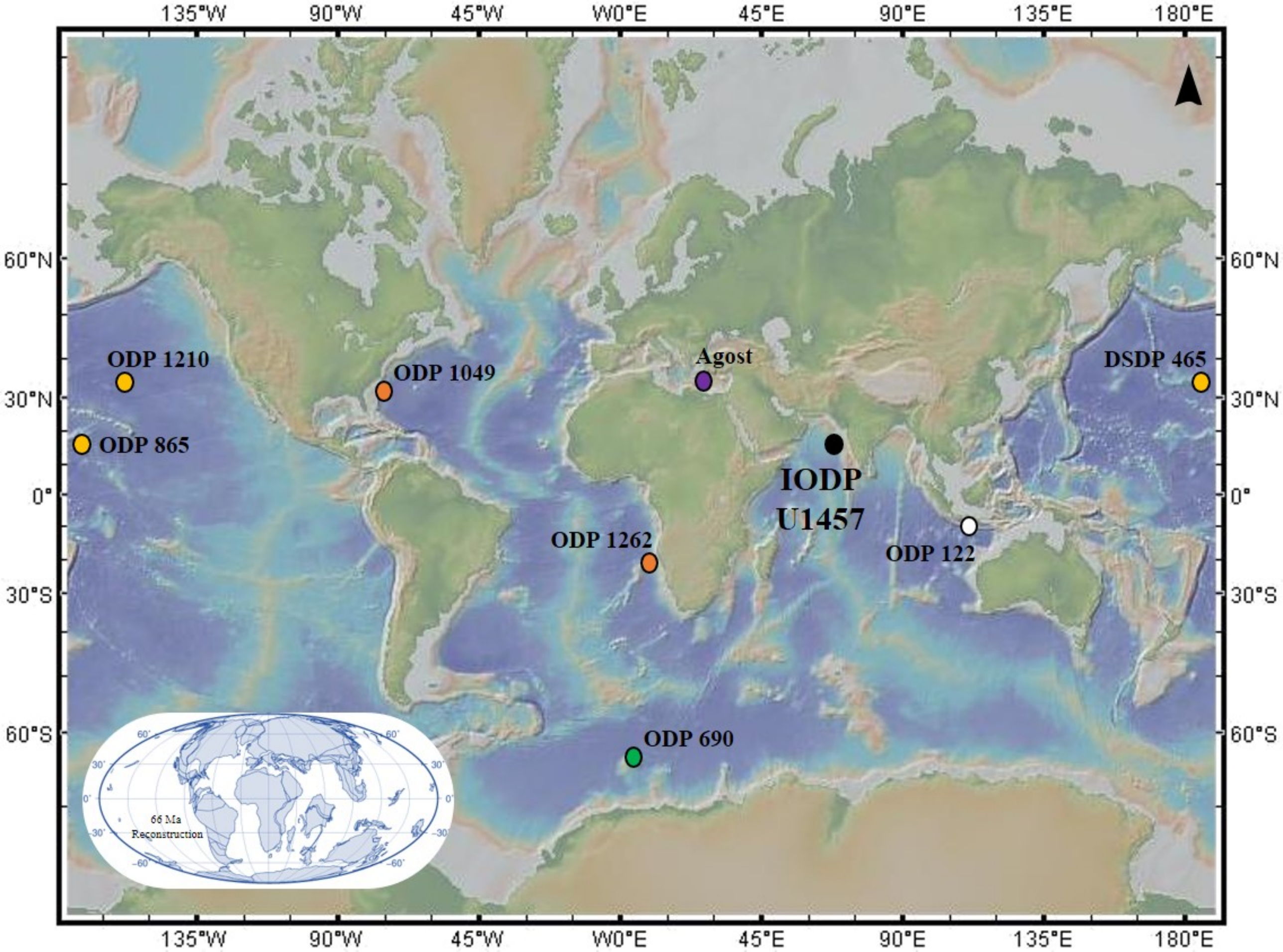

135°W
90°W
45°W
W0°E
45°E
90°E
135°E
180°E
60°N
30°N
0°
30°S
60°S
ODP 1210
ODP 1049
Agost
DSDP 465
ODP 865
IODP
U1457
ODP 1262
ODP 122
ODP 690
66 Ma
Reconstruction

Figure 2.

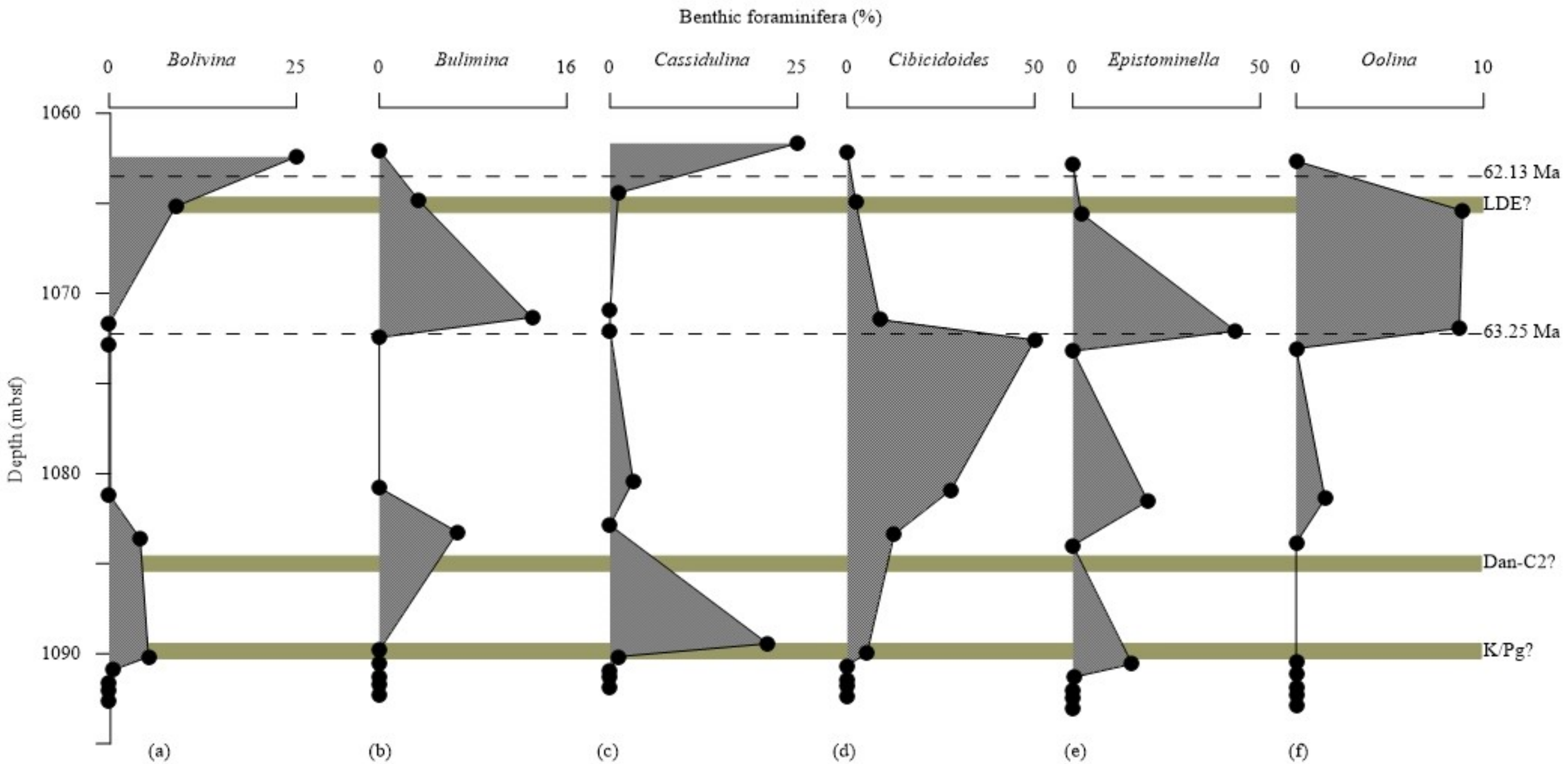

Benthic foraminifera (%)
Bolivina
Bulimina
Cassidulina
Cibicidoides
Epistominella
Oolina
0
25
16
50
10
Depth (mbsf)
1060
1070
1080
1090
62.13 Ma
63.25 Ma
LDE?
Dan-C2?
K/Pg?
(a)
(b)
(c)
(d)
(e)
(f)

Figure 3.

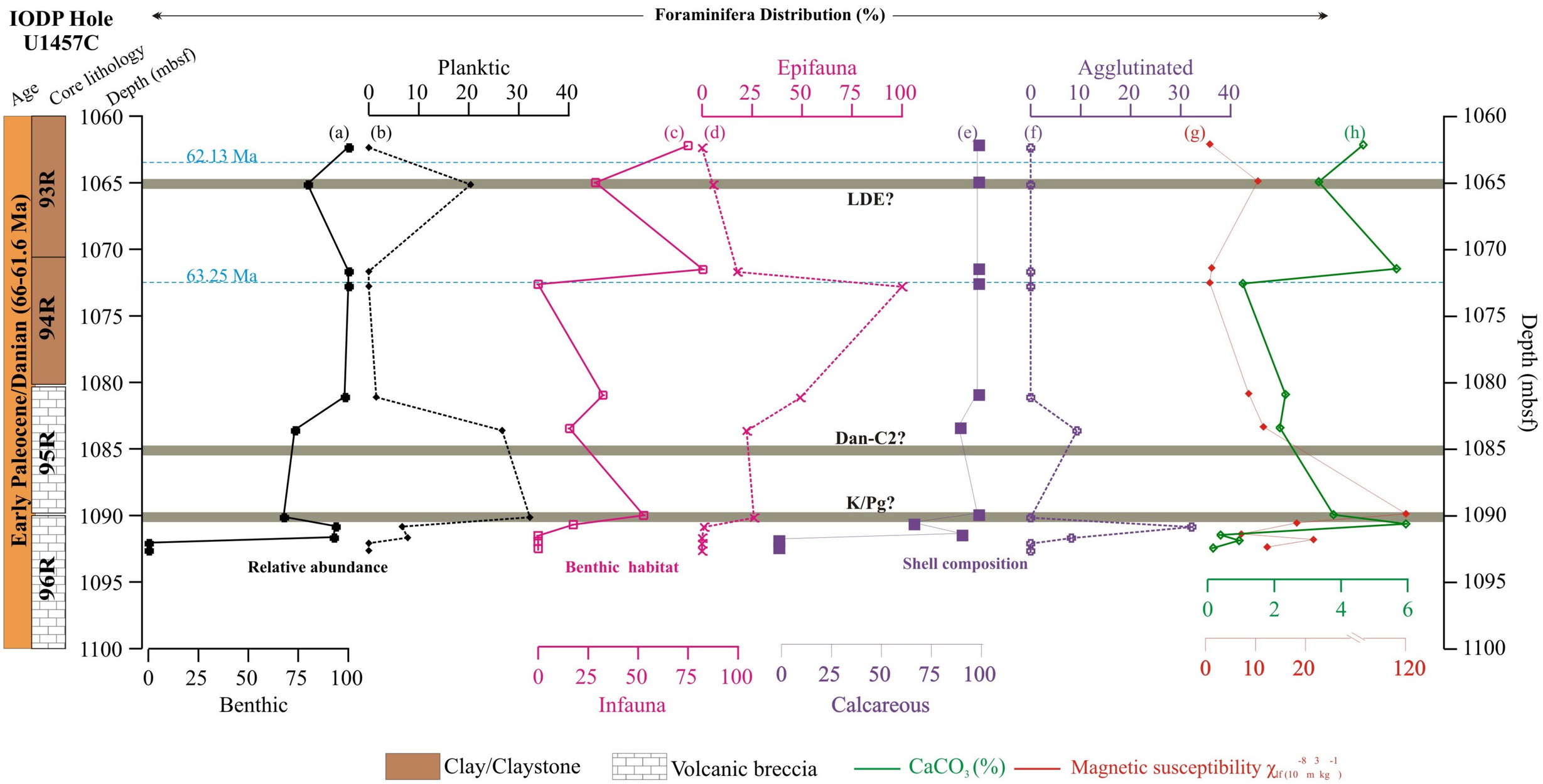

IODP Hole U1457C
Foraminifera Distribution (%)
Age
Core lithology
Depth (mbsf)
Early Paleocene/Danian (66-61.6 Ma)
93R
94R
95R
96R
62.13 Ma
63.25 Ma
LDE?
Dan-C2?
K/Pg?
Planktic
Epifauna
Agglutinated
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Relative abundance
Benthic habitat
Shell composition
Benthic
Infauna
Calcareous
Depth (mbsf)
Clay/Claystone
Volcanic breccia
CaCO3 (%)
Magnetic susceptibility χlf (10-8 m3 kg-1)

Figure 4.

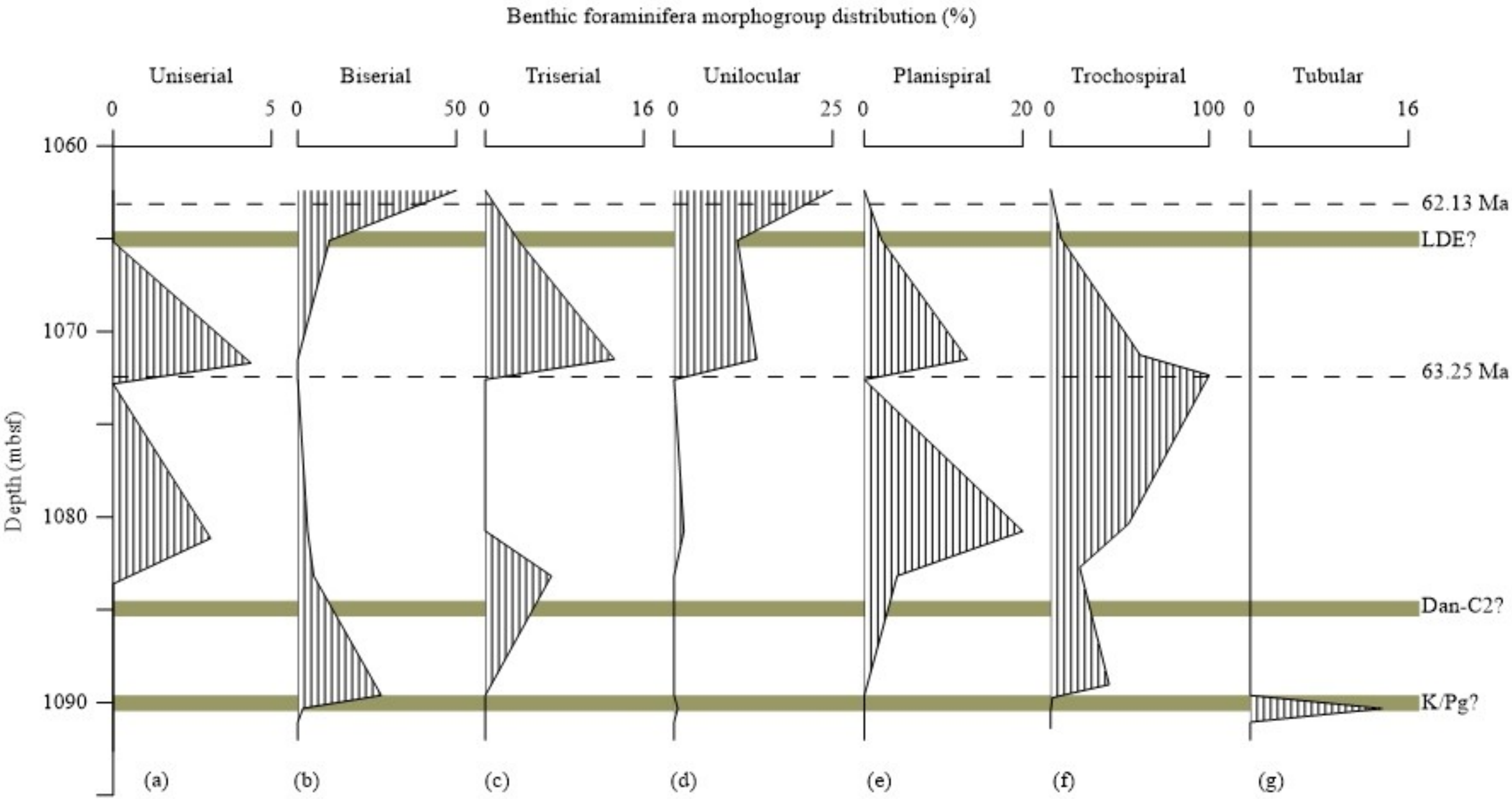

Benthic foraminifera morphogroup distribution (%)
Uniserial
Biserial
Triserial
Unilocular
Planispiral
Trochospiral
Tubular
0
5
0
50
0
16
0
25
0
20
0
100
0
16
1060
1070
1080
1090
Depth (mbsf)
62.13 Ma
LDE?
63.25 Ma
Dan-C2?
K/Pg?
(a)
(b)
(c)
(d)
(e)
(f)
(g)

Figure 5.

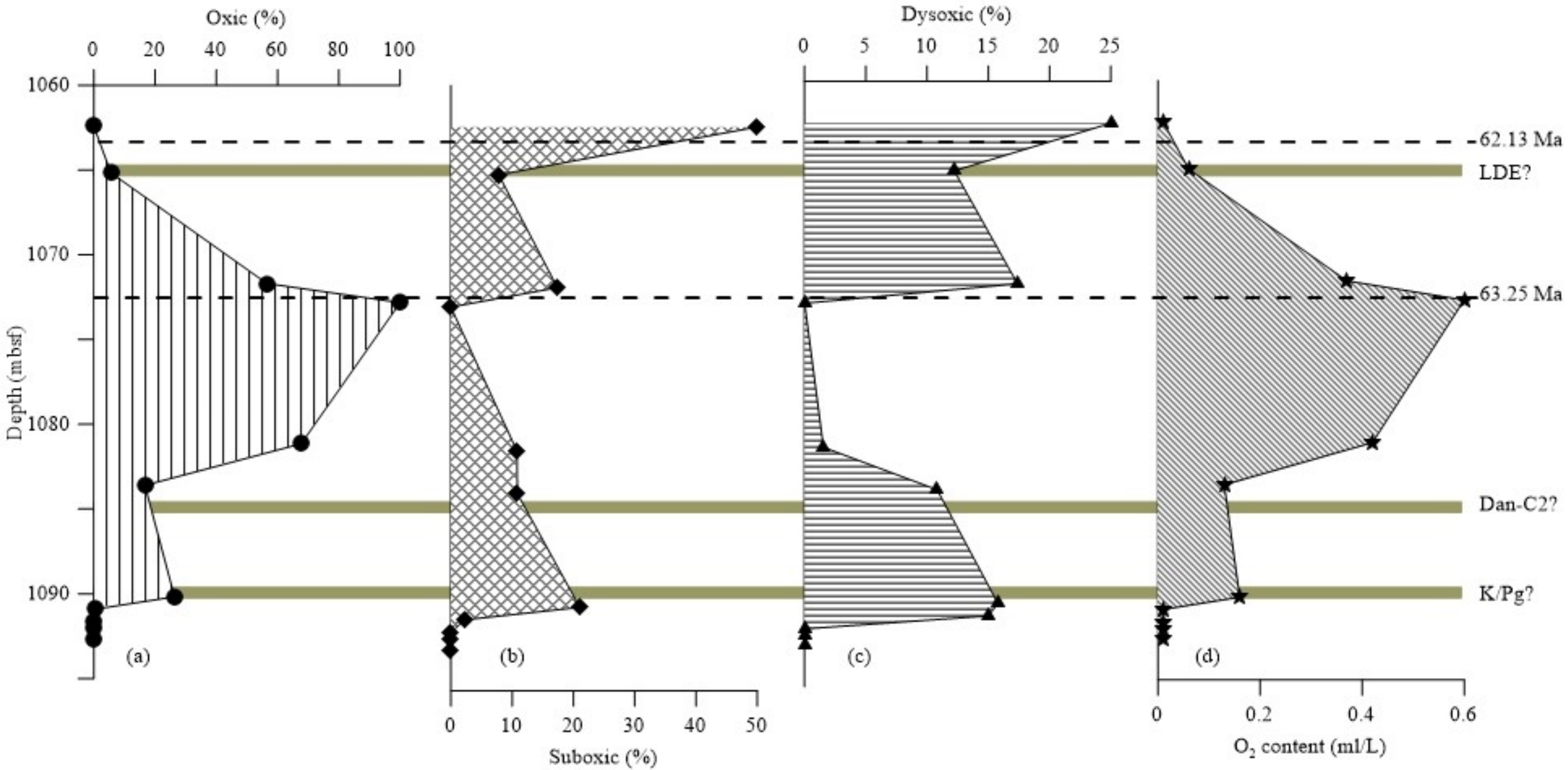
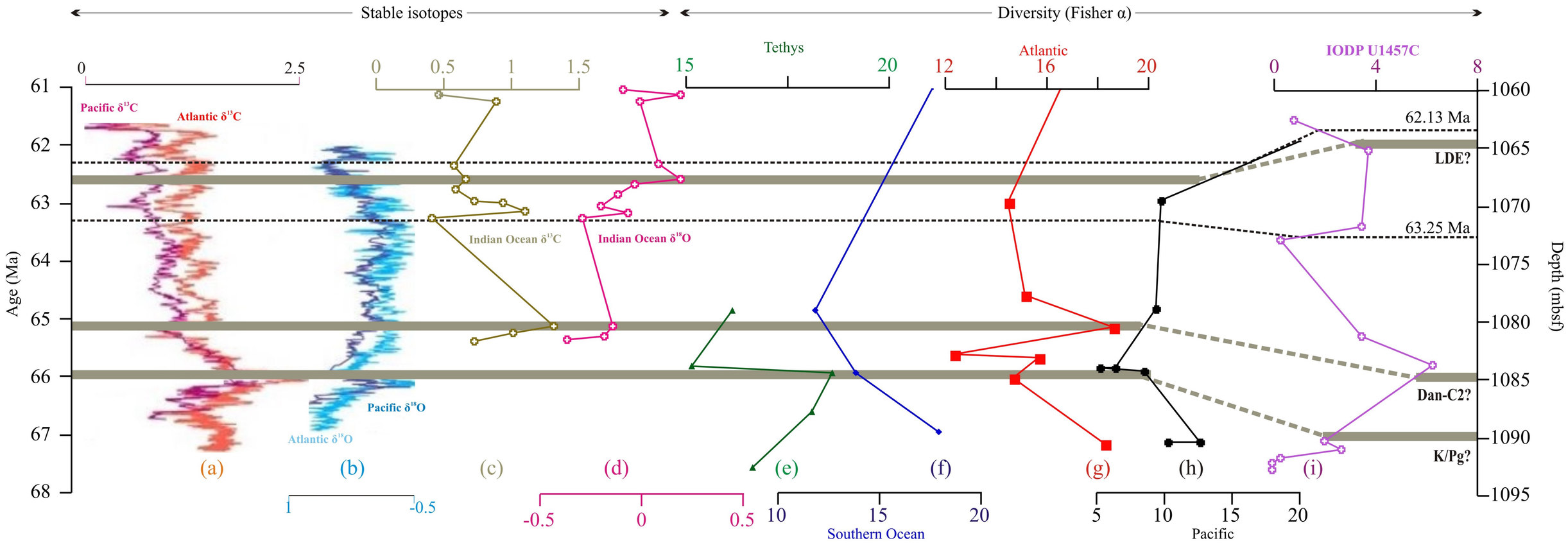

Oxic (%)
0
20
40
60
80
100
Dysoxic (%)
0
5
10
15
20
25
1060
1070
1080
1090
Depth (m bsf)
62.13 Ma
LDE?
63.25 Ma
Dan-C2?
K/Pg?
(a)
(b)
(c)
(d)
0
10
20
30
40
50
Suboxic (%)
0
0.2
0.4
0.6
O2 content (ml/L)

Figure 6.


Stable isotopes
Diversity (Fisher α)
Tethys
Atlantic
IODP U1457C
Pacific δ13C
Atlantic δ13C
Indian Ocean δ13C
Indian Ocean δ18O
Pacific δ18O
Atlantic δ18O
62.13 Ma
63.25 Ma
LDE?
Dan-C2?
K/Pg?
Age (Ma)
Depth (mbsf)
Southern Ocean
Pacific
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)