

ABYSSAL BENTHIC FORAMINIFERA IN THE EASTERN EQUATORIAL PACIFIC (IODP EXP 320) DURING THE MIDDLE EOCENE

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Abstract—We report on the faunal transition of benthic foraminifera during the middle Eocene at Site U1333 (4862 m water depth, 3,560-3,720 m paleo-water depth) of Integrated Ocean Drilling Program Expedition 320 in the eastern equatorial Pacific Ocean. During the period \sim 41.5–40.7 Ma, which includes carbonate accumulation event 3 (CAE-3), the benthic foraminiferal accumulation rate (BFAR) increased gradually and then it declined rapidly. In contrast, BFAR was considerably lower during ~40.7–39.4 Ma, corresponding to the middle Eocene climatic optimum (MECO), and then it increased during \sim 39.3–38.4 Ma, including CAE-4. Diversity (E [S₂₀₀]) was slightly lower in the upper part of the study interval than in the lower part. The most common benthic foraminifera were Nuttallides truempyi, Oridorsalis umbonatus, and Gyroidinoides spp. in association with Globocassidulina globosa and Cibicidoides grimsdalei during the period studied. Quadrimorphina profunda occurred abundantly with N. truempyi, O. umbonatus, and G. globosa during \sim 39.4– 38.4 Ma, including CAE-4, although this species was also relatively common in the lower part of the study interval. Virgulinopsis navarroanus and Fursenkoina sp. A, morphologically infaunal taxa, were common during \sim 38.8–38.4 Ma, corresponding to the late stage of CAE-4. Based on Q-mode cluster analysis, four sample clusters were recognized and their stratigraphic distributions were generally discriminated in the lower and upper parts of the study interval. Thus, there was only a small faunal transition in the abyssal eastern equatorial Pacific during the middle to late-middle Eocene. The faunal transition recognized in this study may be related to recovery processes following intense carbonate corrosiveness in the eastern equatorial Pacific during MECO.

INTRODUCTION

EEP-SEA benthic foraminifera showed gradual faunal changes from the late-middle Eocene to the early Oligocene (e.g., Miller et al., 1992; Thomas, 1992, 2007; Nomura, 1995; Hayward et al., 2010). There were stepwise benthic foraminifera faunal changes in the late-middle Eocene and the late Eocene after an abrupt extinction across the Paleocene-Eocene transition. For example, a gradual decrease in relative abundance and subsequent extinction of Nuttallides truempyi was reported for the middle to late Eocene by, for example, Tjalsma and Lohmann (1983), who suggested that the "Nuttallides truempyi fauna" was replaced by the "Globocassidulina subglobosa fauna" at the middle-late Eocene transition in the abyssal depths of the Atlantic Ocean. It is recognized that changes in the characteristics of deep-ocean waters associated with the Cenozoic cooling trend contributed to such faunal changes (Tjalsma and Lohmann, 1983; Nomura et al., 1997).

Thomas and Gooday (1996) reported a latitudinal gradient in species richness between the Southern Ocean and the tropical ocean from the late Eocene to early Oligocene. They attributed the lower species richness in the Southern Ocean to gradual enhancement of seasonal food supply from the surface ocean. Hayward et al. (2010) discussed Cenozoic step-wise extinctions of elongate, cylindrical extinct taxa (e.g., Stilostomellidae and Pleurostomellidae). They reported on the greatest abundance and species richness of these taxa in various oceans during the middle Eocene to early Oligocene to the Cenozoic, and argued that changes of food source related to the rapid Eocene– Oligocene cooling event may have affected the subsequent decline in both the abundance and diversity of this group. Thus, the faunal composition of deep-sea foraminifera in the middle to late Eocene provides important insight for our understanding of the evolution of Cenozoic benthic foraminifera. However, lack of preservation of calcareous benthic foraminifera due to the relatively shallow calcium carbonate compensation depth (CCD) during the middle to late Eocene (e.g., van Andel et al., 1975; Pälike et al., 2012) is an obstacle to expanding our knowledge about middle Eocene benthic foraminifera, especially in the Pacific Ocean.

The results of Ocean Drilling Program (ODP) Leg 199 in the eastern equatorial Pacific (EEP) revealed several deep-sea paleoceanographic events in the early Cenozoic. Lyle et al. (2005) reported intermittent periods of carbonate sedimentation from the middle to late Eocene in the EEP, based on sediment geochemistry at ODP Sites 1218, 1219, and 1220. They recognized seven carbonate accumulation events (CAE-1 to CAE-7), and suggested that they were related to large CCD fluctuations. They also noted an interval between CAE-3 (~42.2-40.3 Ma) and CAE-4 (~39.9-38.2 Ma) that was characterized by almost no carbonate sedimentation, which they interpreted to correspond to the middle Eocene climatic optimum (MECO) of Bohaty and Zachos (2003). In particular, Lyle et al. (2005) reported that CAE-3 was the most prominent of the seven carbonate sedimentation events. Tripati et al. (2005) suggested that some CAEs, particularly CAE-3, were possibly associated with Antarctic glaciation in the middle Eocene, based on stable isotope data and Mg/Ca ratios of benthic foraminifera, although Edgar et al. (2007) argued that the magnitude of the glaciation was possibly overestimated. Nomura and Takata (2005) also reported on benthic foraminifera across the Paleocene-Eocene transition at ODP Sites 1215, 1220 and 1221. In addition, Takata et al. (2012) reported on



FIGURE 1-Location of Site U1333, IODP Exp 320 (after Pälike et al., 2010).

benthic foraminifera in the early Oligocene at ODP Sites 1218 and 1219, and IODP Site U1334. These instances of benthic foraminifera in the same area may be useful to characterize benthic foraminifera in the middle Eocene, comparing the data in the earliest Eocene and early Oligocene. Thus, various studies have provided information about middle to late Eocene paleoceanography in the EEP. The carbonate-rich sediment succession in the EEP and the CAEs there may provide opportunities to document the biotic responses of benthic foraminifera to environmental changes at abyssal depths during the middle Eocene.

Integrated Ocean Drilling Program (IODP) Expedition 320 collected continuous Paleogene sequences at five sites near ODP Leg 199 Site 1218 in the EEP (Pälike et al., 2010). Recently, Pälike et al. (2012) presented a detailed Cenozoic CCD evolution in the EEP and discussed its relation to carbon cycling. At Site U1333 (Fig. 1), an almost continuous sequence of middle Eocene to lower Miocene sediments was recovered. We investigated the faunal transition of benthic foraminifera in the middle Eocene at this site, in order to characterize the faunal

composition of deep-sea benthic foraminifera in the abyssal equatorial Pacific and compare that faunal composition to that of the early Oligocene (Thomas, 1985; Takata et al., 2010, 2012). In addition, we reviewed published research on middle Eocene benthic foraminifera in order to compare the occurrences of major benthic foraminifera in the EEP with those of other oceans.

MATERIALS AND METHODS

The present-day water depth (and estimated paleo-water depths during \sim 42.5–38.4 Ma) at Site U1333 (N 10°30.996', W 138°25.160') (Fig. 1) is 4862 m (paleo-water depth \sim 3,560 to \sim 3,720 m), with increasing paleo-water depths over that time span due to simple thermal subsidence (Pälike et al., 2010). The Eocene sequence we studied at this site is characterized by brownish radiolarian oozes and white, partially chalky, calcareous nannofossil oozes (Pälike et al., 2010). We used stratigraphic and chronological frameworks developed by the Shipboard Scientific Parties of IODP Expedition 320 (Pälike et al., 2010) and the composite depths (revised composite depth



FIGURE 2—Downcore profiles of Benthic Foraminiferal Number (BFN), Planktonic Foraminiferal Number (PFN), Benthic Foraminiferal Accumulation Rate (BFAR), Planktonic Foraminiferal Accumulation Rate (PFAR), the ratio of planktonic foraminifera/total foraminifera (P/T ratio) and diversity (E [S₂₀₀]) at Site U1333, IODP Exp. 320.

rmcd [m revised CCSF-A]; adjusted rmcd) of Westerhold et al. (2012). We followed the time scale of Cande and Kent (1995) (CK95). The age model was based on shipboard magnetostratigraphy (Pälike et al., 2010) corrected for the adjusted rmcd (Westerhold et al., 2012). The intervals representing CAE-3 and CAE-4 are diachronous among ODP sites; their stratigraphic positions vary with paleo-depth as demonstrated by Lyle et al. (2005) at ODP Sites 1218, 1219, and 1220. In this study, we considered the intervals representing CAE-3 and CAE-4 at Site U1333 to be 183.0-175.5 and 164.0-157.0 adjusted rmcd, respectively, based on carbonate concentrations and mass accumulation rates (Pälike et al., 2010; Khim, unpublished data). In addition, the stratigraphic position of the interval representing MECO (174.5-166.0 adjusted rmcd) at site U1333 was based on the lithologic description of Pälike et al. (2010) and carbonate concentrations and mass accumulation rates of Pälike et al. (2010) and Khim (unpublished data).

We analyzed the benthic foraminifera in 120 sediment samples spanning 42.4 to 38.4 Ma. The freeze-dried samples (approximately 10 cm³) were weighed, then soaked in warm water and washed using a 250-mesh (63 µm) sieve. The residues were dried at 40°C, after which they were weighed and the weight percentage of the coarse fraction (>63 µm) of each sample was calculated. We collected 200–300 specimens from the >105 µm size fraction of adequate split aliquots (1/2–1/32). For samples that contained very few benthic foraminifera, we collected the specimens from the >105 µm size fraction of the 1/4–1/2 split aliquots. These specimens were identified and counted using a stereo binocular microscope. Planktonic foraminifera were also counted in the >105 µm size fraction of the 1/16 aliquot for all samples.

Benthic and planktonic foraminiferal numbers (BFN and PFN, respectively; number of individuals per gram of bulk sediment) were calculated. The benthic foraminiferal accumulation rate

(BFAR; Herguera and Berger, 1991) was calculated as follows: BFAR (cm⁻² ky⁻¹)=BFN × LSR × DBD, where BFN is the number of benthic foraminifera per gram of bulk sediment, LSR is the linear sedimentation rate (cm ky^{-1}) based on the time scale of CK95, and DBD is the dry bulk density ($g \text{ cm}^{-3}$) of the sediment from Pälike et al. (2010). The planktonic foraminiferal accumulation rate (PFAR) was calculated by the same procedure. To evaluate carbonate dissolution, we calculated the ratio of the number of planktonic foraminifera to that of both benthic and planktonic foraminifera (P/T ratio), based on PFN and BFN. Diversity E (S_n) (the expected number of species in samples rarefied to n individuals; n=200) for each sample was calculated in the statistical programming environment R (R Development Core Team, 2010) by using the function from the Vegan community ecology package (Oksanen et al., 2010). Cluster analysis (Q-mode) was performed to determine sample groups, based on relative abundances of benthic foraminiferal taxa in each sample. The data matrix consisted of 65 taxa, for which at least three specimens occurred in each sample, and 86 samples that contained more than 150 specimens. Horn's index of overlap (Horn, 1966) was applied to determine the similarity between samples. The clustering was carried out by using the unweighted pair group method with arithmetic average in a program developed by Davis (1973) and modified by Hasegawa (1988).

RESULTS AND DISCUSSION

Both BFN and BFAR increased gradually and then declined rapidly in the 183–176 adjusted rmcd interval (\sim 41.5–40.7 Ma) (Fig. 2). However, both BFN and BFAR were very low in the 174–166 adjusted rmcd interval (\sim 40.6–39.4 Ma) (Fig. 2), which corresponds to the MECO (Bohaty and Zachos, 2003). There was an increase in the 164–158 adjusted rmcd interval (\sim 39.2–38.6 Ma) (Fig. 2). The former foraminifera-rich interval

corresponds to carbonate accumulation event 3 (CAE-3) and the latter to CAE-4 (Lyle et al., 2005). The profiles of PFN and PFAR were also almost zero in most samples of MECO (Fig. 2), whereas the variations were frequent in the other intervals. It has been reported that CCD shoaled considerably in the EEP during the MECO (Lyle et al., 2005; Pälike et al., 2012). Thus, the abundances of both benthic and planktonic foraminifera were related to stratigraphic distributions of CAE-3, MECO and CAE-4 (e.g., Pälike et al., 2010).

Sixty-four genera and 113 species were identified in the studied interval. Nuttallides truempyi, Oridorsalis umbonatus and Gyroidinoides spp. were the most common benthic foraminifera, in association with Cibicidoides grimsdalei, Globocassidulina globosa and Quadrimorphina profunda (Figs. 3, 4). Osangularia plummerae was found mainly in the lower sequence (185.1-172.8 adjusted rmcd), although it was scarce in the uppermost sample (157.0 adjusted rmcd) (Fig. 3). Globocassidulina globosa was common in the 183-176 and 160-157 adjusted rmcd intervals (~41.5-40.7 Ma and ~38.8-38.4 Ma, respectively) (Fig. 4). Quadrimorphina profunda was abundant in association with N. truempyi, O. umbonatus and G. globosa in the interval 165–157 adjusted rmcd (~39.4–38.4 Ma), although this species was also relatively common at around 178 m and 186 adjusted rmcd (Fig. 4). Virgulinopsis navarroanus and Fursenkoina sp. A in association with G. globosa increased in the interval 160–157 adjusted rmcd (\sim 38.7–38.4 Ma) (Fig. 4). In contrast, calcareous hyaline species having robust test walls or agglutinated form, such as Cibicidoides grimsdalei, N. truempyi and O. umbonatus and agglutinated from, such as Spiroplectammina spectabilis were common in MECO (Fig. 3). Hence, it is difficult to examine faunal change in this period. Diversity E (S_{200}) in the upper part of the study interval (166– 157 adjusted rmcd) (mean 33.6) was slightly lower than that of the lower part (187-174 adjusted rmcd) (mean 37.1) (Fig. 2).

Based on Q-mode cluster analysis four sample clusters were recognized (Fig. 5). Cluster A includes 34 samples belonging to the upper part of the study interval, except for two samples (178.6–178.4 adjusted rmcd) in the lower part (Fig. 4). In contrast, Cluster B includes 47 samples belonging to the lower part of the study interval (Fig. 4). Cluster C contains lower five samples of the study interval (186.8–183.4 adjusted rmcd), whereas Cluster D includes one sample in the upper part of the study interval (158.5 adjusted rmcd). Thus, the sample clusters are generally discriminated in the upper and lower parts of the study interval.

Occurrences of benthic foraminifera at Site U1333 in the middle Eocene are summarized as follows: 1) *Nuttallides truempyi, C. grimsdalei, O. umbonatus, Gyroidinoides* spp. and *G. globosa* are common constituents (Clusters B, C and partly Cluster A) and have slightly high E (S₂₀₀) in the ~42.4–40.6 Ma interval, including CAE-3; 2) benthic foraminifera are rare in the ~40.6–39.5 Ma interval, covering MECO and calcareous hyaline species having robust test walls or agglutinated form occurred; 3) *Quadrimorphina profunda, N. truempyi, C. grimsdalei, O. umbonatus, Gyroidinoides* spp. and *G. globosa* are common with *V. navarroanus* and *Fursenkoina* sp. A (Clusters A and D) and have slightly low E (S₂₀₀) in the ~39.5–38.4 Ma interval, including CAE-4. Additionally, the abundance of *V. navarroanus* and *Fursenkoina* sp. A increased during ~38.8–38.4 Ma.

The P/T ratio was almost zero in the interval 174–166 adjusted rmcd whereas it fluctuated markedly in the rest of the studied interval (Fig. 2). The low P/T ratio of this interval represents carbonate corrosiveness (e.g., Thunell, 1976). Carbonate corrosiveness might have hampered preservation of

calcareous benthic foraminiferal tests and thus affected the species composition of our samples. However, there is no clear relationship between the P/T ratio and BFN, BFAR, or E (S₂₀₀). In addition, preservation of benthic foraminifera was generally moderate with only minor secondary calcite overgrowth on test walls. Even small taxa with thin test walls (e.g., *Q. profunda*) were present, except for samples in the 174–166 adjusted rmcd interval that corresponds to MECO. In addition, there is no marked difference in the P/T ratios of the CAE-3 (mean 0.20) and CAE-4 (mean 0.13) intervals. Although we cannot dismiss post-mortem bias only on the basis of the abundance and species composition of benthic foraminifera, we believe that our foraminiferal data provide valid information on the timing of deposition, except for the MECO interval.

Quadrimorphina profunda, V. navarroanus and Fursenkoina sp. A increased in the upper part of the study interval, compared to the lower interval. There is little ecological information about these species. Quadrimorphina profunda is regarded as an opportunistic species that occurs in the recovery process after strong carbonate corrosiveness associated with the Paleocene-Eocene thermal maximum (e.g., Takeda and Kaiho, 2007). The common occurrence of this species in the early stage of CAE-4 might be equivalent to that of the Paleocene-Eocene transition, although we cannot completely exclude other possibilities (e.g., change of trophic conditions). Additionally, O. plummerae likely disappeared at this site during MECO and then occurred scarcely again after CAE-4 (Fig. 3), although this species and its equivalent (Osangularia mexicana of Tjalsma and Lohmann [1983]) occurred in the Atlantic Ocean in the middle Eocene, especially at shallower depths (<2000 m water depth) (e.g., Tjalsma and Lohmann, 1983; Ortiz and Thomas, 2006). The local disappearance of this species in the abyssal EEP during 40.3 to 38.4 Ma can be attributed to a recovery process after intense carbonate corrosiveness during the MECO. In addition, according to Miller et al. (1985, fig. 8), the relative abundance of Osangularia spp. was less common in Zone E13 (40.0-38.0 Ma) of Berggren and Pearson (2005) (originally described as Zone P14 of Blow [1979]) at DSDP Site 549 (2533 m water depth; eastern north Atlantic). The timing is roughly consistent with the period corresponding to MECO and the subsequent CAE-4. The local disappearance of O. plummerae might also have occurred in abyssal depths of the north Atlantic. Thus, the slightly low diversity in CAE-4 can be interpreted to reflect intense carbonate corrosiveness during MECO. In contrast, V. navarroanus and Fursenkoina sp. A increased during the late stage of CAE-4. These species have elongate morphology that is thought to be specific to an infaunal microhabitat, commonly under eutrophic or low-oxygen conditions (Gooday, 2003; Jorissen et al., 2007). However, BFAR, a proxy for paleoproductivity (Herguera and Berger, 1991), did not change markedly during this period (Fig. 2) and there is no lithologic evidence of low oxygen levels (Pälike et al., 2010). We suggest that trophic conditions might have changed and affected the faunal composition of benthic foraminifera, which corresponds to turnover of primary producers reported to have occurred in the late Eocene to early Oligocene (e.g., Thomas, 2007).

The faunal association of middle Eocene benthic foraminifera at Site U1333 is similar to that of benthic foraminifera in the early Eocene of the EEP (Nomura and Takata, 2005) in terms of abundant *N. truempyi*, *O. umbonatus*, and *Gyroidinoides* spp. in association with *A. dissonata and Cibicidoides grimsdalei*. However, abundant *Q. profunda* and common *V. navarroanus* and *Fursenkoina* sp. A in the latest middle Eocene were not recognized by Nomura and Takata (2005). We may have detected these species because of the smaller size fraction we



FIGURE 3—Occurrences of benthic foraminifera at Site U1333, IODP Exp. 320.

analyzed (>105 μ m) compared to that of the previous studies (>150 μ m). In contrast, the association we recognized is different from that of the early Oligocene in this area (Thomas, 1985; Takata et al., 2010, 2012). *Nuttallides umbonifer* was common in the Oligocene, instead of *N. truempyi*. The last known common occurrence of *N. truempyi* was the middle-late Eocene, and it became globally extinct at the Eocene-Oligocene transition (e.g., Tjalsma and Lohmann, 1983; Thomas, 2007). The abundance of *Q. profunda* was lower in the Oligocene than in the middle Eocene. The diversity of genus *Cibicidoides* was relatively low, and *C. grimsdalei* and *C. eocanus*, which have robust tests, were abundant in the middle Eocene. In contrast, *Anomalinoides* sp. A and *O. plummerae* were found only in the middle Eocene. Furthermore, Cassidulinidae were limited mostly to *G. globosa*. Other cassidulina sp., were almost absent in the middle Eocene. E (S_{200}) (32.0–47.6; mean 40.6) in the early Oligocene (~32–28 Ma) at IODP Site U1334 (Takata et al., 2012) was similar to that of the middle Eocene at Site U1333 of our study, in which middle Eocene paleo-depths at Site U1334. These findings confirm that there was no marked change



FIGURE 3—Continued.

of species richness in the EEP from the late Eocene to the early Oligocene, as proposed by Thomas and Gooday (1996).

To compare the relative abundances of major benthic foraminifera in the EEP with those of other oceans, we reviewed published research on middle Eocene benthic foraminifera. The faunal compositions of benthic foraminifera we found in the EEP are similar to those of the abyssal depths of the Atlantic Ocean during the Eocene (Tjalsma and Lohmann, 1983; Miller, 1983; Miller et al., 1985; Boltovskoy et al., 1992; Boltovskoy and Boltovskoy, 1989; Müller-Merz and Oberhänsli, 1991) and of the Pacific Ocean (Boltovskoy and Watanabe, 1994) where there were abundant *N. truempyi, O. umbonatus* and *Gyroidinoides* spp. in association with *Globocassidulina subglobosa* (equivalent to our *G. globosa*) and *A. dissonata*. In contrast, the faunal associations of benthic foraminifera at bathyal depths in the EEP were somewhat different from those at abyssal depths in the Atlantic and Indian Oceans. For example, common lenticulinids, buliminids, and *Osangularia* spp. have been identified at bathyal depths in the Atlantic and Indian Oceans (Tjalsma, 1983; Tjalsma and Lohmann, 1983; Miller and Katz, 1987; Nomura, 1995; Katz and Miller, 1996). These taxa were also less common in our study area.

We found little published information on the depth distribution during the middle Eocene of *G. subglobosa*, other than that provided by Tjalsma and Lohmann (1983, fig. 28) and Katz and Miller (1996, fig. 12). Katz et al. (2003, fig. 10) showed no clear relationship between the distribution of *G. subglobosa* and paleo-depth in the Atlantic Ocean during the Oligocene, whereas Takata et al. (2012) documented a decrease in the distribution of *G. subglobosa* with increasing paleo-depth in the abyssal EEP during the early Oligocene, probably reflecting a decrease of food supply with increasing water depth. According



FIGURE 4—Downcore profiles of relative abundance of major benthic foraminifera species at Site U1333, IODP Exp. 320 and stratigraphic distributions of the four clusters.

to ecological information, *G. subglobosa* prefers deep-sea environments with high concentrations of organic carbon (Miao and Thunell, 1993) or an environment characterized by pronounced seasonal food pulses (Gooday, 1994; Suhr et al., 2003; Suhr and Pond, 2006; Eberwein and Mackensen, 2006; Gooday et al., 2008). Thus, changes in the mode of food supply from the surface ocean, including its seasonality, may have affected the abundance of this species. In contrast, D'haenens et al. (2012) regarded *G. subglobosa* as an opportunistic species, as well as *Gyroidinoides* spp., in the early Eocene at DSDP Site 401 (2495 m water depth, eastern North Atlantic). Hence, the lack of an obvious relationship between water depth and the distribution of *G. globosa* and *G. subglobosa* among the oceans might be explained by a characteristic sensitivity of this species to regional and short-term paleoceanographic conditions.

The relative abundance of *Q. profunda* as reported in the literature is variable; we consider this to reflect in part the size fractions used. In particular, Boltovskoy and his collaborators, using the >63 μ m fraction, reported *Q. profunda* as a common species (e.g., Boltovskoy and Watanabe, 1994), whereas other studies using the >150 μ m fraction reported very few individuals of this species (e.g., Miller, 1983; Miller et al., 1985). These results imply that *Q. profunda* might have been common at abyssal depths during the late-middle Eocene, and may provide a clue for understanding paleoceanographic change around in MECO.

Tjalsma and Lohmann (1983) and Thomas (2007) reported a gradual faunal turnover in abyssal benthic foraminifera at the middle–late Eocene transition. We suggest that slightly lower E (S₂₀₀) during the early stage of CAE-4 than during CAE-3 was caused mainly by dominance of a few species (e.g., *Q. profunda*) after MECO. Similarly, slightly higher E (S₂₀₀) during the late stage of CAE-4 (Fig. 2) may be explained by subsequent increases of the abundances of other taxa, such as *V. navarroanus* and *Fursenkoina* sp. A. Hence, our results suggest that the small faunal transitions in the late-middle Eocene occurred at abyssal depths in the EEP, and that these transitions were probably related to severe carbonate corrosiveness during MECO. Further micropaleontological studies to clarify the

reasons for these faunal transitions will benefit from consideration of geochemical proxies.

CONCLUSIONS

We investigated middle Eocene benthic foraminifera at Site U1333 of IODP Expedition 320 in the EEP. At this site, BFN and BFAR increased gradually and then declined rapidly during the period \sim 41.5–40.7 Ma, which includes CAE-3. In contrast, BFN and BFAR were considerably lower during ~40.7-39.4 Ma, corresponding to MECO, and then they increased during \sim 39.4–38.4 Ma, which includes CAE-4. Diversity (E [S₂₀₀]) was slightly lower in the upper part of the study interval than in the lower part. Nuttallides truempyi, Oridorsalis umbonatus and Gyroidinoides spp. in association with Globocassidulina globosa and Cibicidoides grimsdalei were the most common benthic foraminifera during \sim 42.4–40.6 Ma. Additionally, Quadrimorphina profunda were abundant along with N. truempyi, O. umbonatus and G. globosa during \sim 39.4–38.4 Ma. Virgulinopsis navarroanus and Fursenkoina sp. A, morphologically infaunal taxa, increased during \sim 38.8–38.4 Ma, which includes the late stage of CAE-4. Our Q-mode cluster analysis revealed four sample clusters with distributions generally in the lower and upper parts of the study interval. Thus, a small faunal transition occurred in the abyssal EEP during the middle to late-middle Eocene. The faunal transition revealed in this study may be related to recovery processes following a period of intense carbonate corrosiveness at abyssal depths in the EEP after MECO.

SYSTEMATIC PALEONTOLOGY

Taxonomic assignments followed Cushman (1946, 1951), Brotzen (1948), Tjalsma and Lohmann (1983), Van Morkhoven et al. (1986), Jones (1994), Nomura (1995) and Nomura and Takata (2005). The generic classification of Loeblich and Tappan (1987) was used and updated in some instances, especially for the uniserial taxa presented by Hayward (2002) and Hayward et al. (2012).

> Class Foraminiferida Eichwald, 1830 Suborder Textulariina Delage and Hérouard, 1896



Superfamily RZEHAKINACEA Cushman, 1933 Family RZEHAKINIDAE Cushman, 1933 Genus Spirosigmoillinella Matsunaga, 1955 SPIROSIGMOILLINELLA COMPRESSA Matsunaga, 1955 1955 Spirosigmoillinella compressa MATSUNAGA, p. 50, textfigs. 1, 2. Occurrence.—This species was very rare in 177.7-176.0 adjusted rmcd. Superfamily LITUOLACEA de Blainville, 1827 Family LITUOTUBIDAE Loeblich and Tappan, 1984 Genus Paratrochamminoides Soliman, 1972 PARATROCHAMMINOIDES sp. Occurrence.--This species was very rare at 185.3 adjusted rmcd. Superfamily CYCLAMMINACEA Loeblich and Tappan, 1964 Family CYCLAMMIDAE Marie, 1941 Subfamily ALVEOLOPHRAGMINAE Saidova, 1981 Genus RETICULOPHRAGMIUM Maync, 1955 RETICULOPHRAGMIUM AMPLECTENS (Grzybowski, 1898) 1898 Cyclammina amplectens Grzybowski, p. 292, pl. 12, figs. 1–3. Occurrence.--This species was very rare in 182.2-175.7 adjusted rmcd. Superfamily TROCHAMMINICEA Schwager, 1877 Family TROCHAMMINIDAE Schwager, 1877 Subfamily TROCHAMMININAE Schwager, 1877 Genus TROCHAMMINA Parker and Jones, 1859 TROCHAMMINA Sp. Occurrence.-This species was very rare at 175.0 adjusted rmcd. Superfamily Spiroplectamminacea Cushman, 1927 Family Spiroplectamminidae Cushman, 1927 Subfamily Spiroplectammininae Cushman, 1927 Genus Spiroplectammina Cushman, 1927 SPIROPLECTAMMINA SPECTABILIS (Grzybowski, 1898) Figure 6.1-6.3 1898 Spiroplecta spectabilis GRZYBOWSKI, p. 293, pl. 12, fig. 12. Occurrence.--This species was common in 186.8-158.0 adjusted rmcd. Remarks.--We included some variety of this species with larger early whorl or presence of coating layer. Superfamily VERNEUILINACEA Cushman, 1911 Family VERNEUILIRIDAE Cushman, 1911 Subfamily DOROTHIINAE Balakhmatova, 1972 Genus MARSSONELLA Cushman, 1933 MARSSONELLA TROCHOIDES (Marsson, 1878) Figure 6.5 1878 Gaudryina crassa Marsson var. β trochoides MARSSON, p. 159, pl. 3, fig. 27d–27f. 2005 Marssonella trochoides (Marsson); NOMURA AND TAката, pl. P3, fig. 2a, 2b.

FIGURE 5—Dendrogram of showing the results of cluster analysis of benthic foraminifera at Site U1333, IODP Exp. 320. The four clusters (A, B, C and D) were recognized.



FIGURE 6—Scanning electron micrographs of benthic foraminifera at Site U1333, IODP Exp. 320. *1–3, Spiroplectammina spectabilis* (Grzybowski), samples 320-U1333B-15H-4, 88–90 cm, 320-U1333B-16H-5, 48–50 cm ad 320-U1333B-16H-5, 48–50 cm; *4, Textularia* sp. C, sample 320-U1333C-19H-2, 8–10 cm; *5, Marssonella trochoides* (Marsson), sample 320-U1333B-17H-6, 28–30 cm; *6, Valvulina spinosa* Cushman, sample 320-U1333B-16H-7, 28–30 cm; *7, Karreriella subglabra* (Cushman), sample 320-U1333B-15H-2, 8–10 cm; *8, Eggerella bradyi* (Cushman), sample 320-U1333B-17H-3, 68–70 cm; *9, Gaudryina* sp., sample 320-U1333B-16H-4, 28–30 cm; *10–12, Pleurostomella clavata* Cushman, samples 320-U1333B-15H-2, 128–130 cm, 320-U1333C-19H-2, 8–10 cm and 320-U1333C-19H-2, 8–10 cm; *13, Pleurostomella* sp. D, sample 320-U1333C-19H-2, 8–10 cm; *14, Pleurostomella subnodosa* (Reuss), sample 320-U1333B-17H-1, 108–110 cm. Scale bar=100 µm.

Occurrence.—This species was very rare in 186.8–157.0 adjusted rmcd.

Subfamily VERNEUILININAE Cushman, 1911 Genus GAUDRYINA d'Orbigny, 1839 GAUDRYINA sp. Figure 6.9

Occurrence.—This genus was rare in 186.8–157.8 adjusted rmcd.

Remarks.—In our specimens, this species has often coarsegrained test wall.

Family TRITAXIIDAE Plontnikova, 1979 Genus TRITAXIA Reuss, 1860 TRITAXIA HAVANENSIS (Cushman and Bermúdez, 1937)

1937 *Clavulinoides havanensis* Cushman and Bermúdez, p. 3, pl. 1, figs. 12, 13.

Occurrence.—This species was very rare in 184.8–184.0 adjusted rmcd.

Superfamily TEXTULARIACEA Ehrenberg, 1838 Family Eggerellidae Cushman, 1937 Subfamily Eggerellinae Cushman, 1937 Genus Eggerella Cushman, 1933 Eggerella Bradyi (Cushman, 1911) Figure 6.8

1911 Vereuilina bradyi CUSHMAN, p. 55, text-fig. 87a, 87b.

Occurrence.—This species was very rare in 182.8–159.6 adjusted rmcd.

Eggerella sp. A

Occurrence.—This species was very rare at 165.1 adjusted rmcd.

Genus Karreriella Cushman, 1933 Karreriella subglabra (Cushman, 1926) Figure 6.7

- 1926 *Textularia subglabra* Cushman, p. 584, pl. 15, fig. 7а-7с.
- 1928 Textularia chapapotensis Cole, p. 206, pl. 33 (2), fig. 9.

Occurrence.—This species was common in 187.0–158.0 adjusted rmcd.

KARRERIELLA cf. SUBGLABRA (Cushman, 1926)

Occurrence.—This species was very rare at 176.5 adjusted rmcd.

Genus Martinottiella Cushman, 1933 Martinottiella? sp.

Occurrence.—This species was very rare in 186.0–164.8 adjusted rmcd.

Family TEXTULARRIDAE Ehrenberg, 1838 Subfamily TEXTULARIINAE Ehrenberg, 1838 Genus BIGENERINA d'Orbigny, 1826 BIGENERINA sp.

Occurrence.—This species was rare in 186.8–157.5 adjusted rmcd.

Genus Textularia Defrance, 1824 Textularia sp. A Occurrence.—This species was very rare at 161.2 adjusted rmcd.

TEXTULARIA Sp. B

Occurrence.—This species was very rare in 186.8–183.648 adjusted rmcd.

TEXTULARIA sp. C Figure 6.4

Occurrence.—This species was rare in 186.4–157.5 adjusted rmcd.

Family VALVULINIDAE Berthelin, 1880 Genus VALVULINA d'Orbigny, 1826 VALVULINA SPINOSA Cushman, 1927 Figure 6.6

1927a Valvulina spinosa CUSHMAN, p. 111, pl. 23, fig. 1.

Occurrence.---This species was rare in 187.0-157.2 adjusted rmcd.

Remarks.—In our specimens, this species usually did not have uniserial part, except for large-size individuals.

Suborder LAGENINA Delage and Hérouard, 1896 Superfamily NODOSARINACEA Ehrenberg, 1838

Family VAGINULINIDAE Reuss, 1860

Subfamily LENTICULINAE Chapman, Parr and Collins, 1934

Genus LENTICULINA Schlumberger, 1881

LENTICULINA spp.

Figure 7.12

Occurrence.—This genus was rare in 185.8–157.5 adjusted rmcd.

Remarks.—We did not attempt to identify any of the species because the number of each species was too few.

Subfamily Marginuliniae Wedekind, 1937 Genus Marginulina d'Orbigny, 1826 Marginulina spp.

Occurrence.—This genus was very rare in 183.2–157.2 adjusted rmcd.

Remarks.—We did not attempt to identify any of the species because the number of each species was too few.

Superfamily Nodosarinacea Ehrenberg, 1838 Family Glandulinidae Reuss, 1860 Subfamily Glandulininae Reuss, 1860 Genus Glandulina d'Orbigny, 1839 Glandulina sp.

Occurrence.—This species was very rare in 161.4–159.2 adjusted rmcd.

Family Nodosariidae Ehrenberg, 1838 Subfamily Nodosariinae Ehrenberg, 1938 Genus Chrysalogonium Schubert, 1908 Chrysalogonium crassitestum (Schwager, 1866)

1866 Nodosaria crassitesta SCHWAGER, p. 224, pl. 5, fig. 55.
2012 Epelistoma crassitesta (Schwager); HAYWARD ET AL., pl. 6, figs. 8–13.

Occurrence.—This species was very rare in 184.8–159.2 adjusted rmcd.

CHRYSALOGONIUM EQUISETIFORMIS (Schwager, 1866)

1866 Nodosaria equisetiformis Schwager, p. 231, pl. 6, fig. 66.



FIGURE 7—Scanning electron micrographs of benthic foraminifera at Site U1333, IODP Exp. 320. 1, Nodosaria naumanni Reuss, sample 320-U1333B-17H-1, 88–90 cm; 2, Polymorphina? sp., sample 320-U1333B-17H-2, 68–70 cm; 3, Pyrulinoides acuminatus (d'Orbigny), sample 320-U1333B-15H3, 28–30 cm; 4, Siphonodosaria hispidula (Cushman), sample 320-U1333B-16H-6, 88–90 cm; 5, Siphonodosaria aculeata (Cushman and Renz), sample 320-U1333B-15H-2, 128–130 cm; 6, Stilostomella decurta (Bermúdez), sample 320-U1333B-17H-3, 68–70 cm; 7, Stilostomella sp. A, sample 320-U1333B-17H-1, 88–90 cm; 8, Nodosarella rotundata (d'Orbigny), sample 320-U1333C-19H-2, 68–70 cm; 9, Nodosarella sp. A, sample 320-U1333B-17H-2, 108–110 cm; 10, 11, Ellipsoidella pleurostomelloides Heron-Allen and Earland, samples 320-U1333B-17H-2, 128–130 cm and 320-U1333B-17H-3, 128–130 cm; 13, Ellipsoglandulina labiata (Schwager), sample 320-U1333B-17H-3, 48–50 cm. Scale bar=100 µm.

2012 *Chrysalogonium equisetiformis* (Schwager); HAYWARD et al., pl. 4, figs. 17–22.

Occurrence.—This species was very rare in 184.8–175.5 adjusted rmcd.

Genus DENTALINA Risso, 1826 DENTALINA spp.

Occurrence.—This genus was rare in 185.0–157.5 adjusted rmcd.

Remarks.—We did not attempt to identify any of the species because the number of each species was too few.

Genus Glandulonodosaria Silvestri, 1900 Glandulonodosaria Ambigua (Neugeboren, 1856)

1856 Nodosaria ambigua NEUGEBOREN, p. 71, pl. 1, figs. 13– 16.

1946 Nodosaria monile Hagenow; CUSHMAN, pl. 27, fig. 9.

- 2005 Nodosaria monile Hagenow; NOMURA AND TAKATA, pl. P4, figs. 7, 8.
- 2012 *Glandulonodosaria ambigua* (Neugboren); HAYWARD ET AL., pl. 7, figs. 33–37.

Occurrence.—This species was very rare in 186.8–157.8 adjusted rmcd.

Genus Nodosaria Lamarck, 1816 Nodosaria annulata Reuss, 1844

1844 Nodosaria annulata REUSS, not given.

1845 Nodosaria annulata var. dichotoma (?) REUSS, p. 27, pl. 8, fig. 67.

Occurrence.—This species was very rare in 179.2–161.7 adjusted rmcd.

Nodosaria naumanni Reuss, 1874 Figure 7.1

1874 Nodosaria naumanni REUSS, p. 82, pl. (II) 20, fig. 11.

Occurrence.—This species was rare in 186.8–157.0 adjusted rmcd.

NODOSARIA Sp. A

Occurrence.—This species was very rare at 184.3 adjusted rmcd.

NODOSARIA Sp. B

Occurrence.—This species was very rare at 158.9 adjusted rmcd.

Genus PSEUDONODOSARIA Boomgaart, 1949 PSEUDONODOSARIA APPRESSA (Loeblich and Tappan, 1955)

1955 *Rectoglandulina appressa* LOEBLICH AND TAPPAN, p. 126, pl. 1, figs. 1–4.

Occurrence.—This species was very rare in 184.5–180.9 adjusted rmcd.

Family LAGENIDAE Reuss, 1862 Genus LAGENA Walker and Jacob, 1798 LAGENA spp.

Occurrence.—This genus was very rare in 186.8–157.0 adjusted rmcd.

Remarks.—We did not attempt to identify any of the species because the number of each species was too few.

Family POLYMORPHINIDAE d'Orbigny, 1839

Subfamily FALSOGUTTULINIAE Loeblich and Tappan, 1986 Genus FALSOGUTTULINA Bartenstein and Brand, 1949 FALSOGUTTULINA sp.

Occurrence.—This species was very rare in 182.6–179.9 adjusted rmcd.

Subfamily POLYMORPHININAE d'Orbigny, 1939 Genus POLYMORPHINA d'Orbigny, 1826 POLYMORPHINA? sp. Figure 7.2

Occurrence.—This species was very rare in 185.5–162.3 adjusted rmcd.

Remarks.—This species sometimes had additional apertures.

Genus Pyrulinoides Marie, 1941 Pyrulinoides acuminatus (d'Orbigny, 1840) Figure 7.3

1840 Pyrulina acuminata D'ORBIGNY, pl. 4, figs. 18, 19.

2005 *Pyrulinoides acuminatus* (d'Orbigny); Nomura and Takata, pl. P4, fig. 16.

Occurrence.—This species was rare in 187.0–158.5 adjusted rmcd.

Family Ellipsolagenidae Silvestri, 1923 Subfamily Ellipsolageninae Silvestri, 1923 Genus Fissurina Reuss, 1850 Fissurina spp.

Occurrence.---This species was rare in 186.8--157.0 adjusted rmcd.

Remarks.—We did not attempt to identify any of the species because the number of each species was too few.

Suborder Rotalina Delage and Hérouard, 1896 Superfamily Pleurostomellacea Reiss, 1860 Family Pleurostomellidae Reuss, 1860 Genus Ellipsoglandulina Silvestri, 1900 Ellipsoglandulina Labiata (Schwager, 1866) Figure 7.13

- 1866 *Glandulina labiata* Schwager, p. 237, pl. 6, fig. 77a, 77b.
- 2012 *Ellipsoglandulina labiata* (Schwager); HAYWARD ET AL., pl. 25, figs. 11–19.

Occurrence.—This species was very rare in 186.0–157.5 adjusted rmcd.

Genus Ellipsoidella Heron-Allen and Earland, 1910 Ellipsoidella Pleurostomelloides Heron-Allen and Earland, 1910 Figure 7.10, 7.11

- 1910 *Ellipsoidella pleurostomelloides* HERON-ALLEN, p. 413, pl. 10, figs. 1–11; pl. 11, figs. 1, 2.
- 2012 Ellipsoidella pleurostomelloides Heron-Allen; HAY-WARD ET AL., pl. 27, figs. 6–11.

Occurrence.—This species was very rare in 186.6–158.7 adjusted rmcd.

ELLIPSOIDELLA cf. PLEUROSTOMELLOIDES Heron-Allen and Earland, 1910

1910 *Ellipsoidella pleurostomelloides* HERON-ALLEN, p. 413, pl. 10, figs. 1–11; pl. 11, figs. 1, 2.

Occurrence.—This species was very rare in 185.5–179.4 adjusted rmcd.

Genus Nodosarella Rzehak, 1895 Nodosarella rotundata (d'Orbigny, 1846) Figure 7.8

1846 Lingulina rotundata D'ORBIGNY, p. 61, pl. 2, figs. 48– 51.

Occurrence.---This species was rare in 187.0--158.5 adjusted rmcd.

Nodosarella sp. A Figure 7.9

Occurrence.—This species was rare in 185.1–157.2 adjusted rmcd.

NODOSARELLA Sp. B

Occurrence.—This species was very rare at 160.2 adjusted rmcd.

Genus PLEUROSTOMELLA Reuss, 1860 PLEUROSTOMELLA CLAVATA Cushman, 1926 Figure 6.10–6.12

1926 Pleurostomella clavata Cushman, p. 590, pl. 16, fig. 5a, 5b.

Occurrence.—This species was rare in 187.0–157.0 adjusted rmcd.

PLEUROSTOMELLA cf. CLAVATA Cushman, 1926

1926 Pleurostomella clavata Cushman, p. 590, pl. 16, fig. 5a, 5b.

Occurrence.—This species was very rare in 179.9–157.5 adjusted rmcd.

PLEUROSTOMELLA SUBNODOSA (Reuss, 1851) Figure 7.14

1851 Pleurostomella subnodosa REUSS, p. 24, pl. 8, fig. 2a, 2b.

Occurrence.—This species was rare in 187.0–157.0 adjusted rmcd.

PLEUROSTOMELLA Sp. A

Occurrence.—This species was very rare in 182.6–176.3 adjusted rmcd.

PLEUROSTOMELLA Sp. B

Occurrence.—This species was very rare in 183.8–158.5 adjusted rmcd.

PLEUROSTOMELLA Sp. C

Occurrence.—This species was very rare in 186.6–158.0 adjusted rmcd.

PLEUROSTOMELLA sp. D Figure 7.13

Occurrence.—This species was very rare in 157.0–159.4 adjusted rmcd.

Superfamily STILOSTOMELLACEA Finlay, 1947 Family STILOSTOMELLIDAE Finlay, 1947 Genus Orthomorphina Stainforth, 1952 Orthomorphina havanensis (Cushman and Bermúdez, 1937)

- 1937 Nodogenerina havanensis Cushman and Bermúdez, p. 14, pl. 1, figs. 47, 48.
- 2012 Orthomorphina perverse (Schwager); HAYWARD ET AL., pl. 8, figs. 35–38, pl. 9, figs. 1–4.

Occurrence.—This species was very rare in 183.2–159.9 adjusted rmcd.

Genus SIPHONODOSARIA Silvestri, 1924 SIPHONODOSARIA ACULEATA (Cushman and Renz, 1948) Figure 7.5

1881 Nodosaria abyssorum BRADY, p. 63, figs. 8, 9.

1948 Ellipsonodosaria nuttalli Cushman and Jarvis var. aculeata Cushman and Renz, p. 32, pl. 6, fig. 10.

Occurrence.—This species was sometimes common in 186.8–157.0 adjusted rmcd.

SIPHONODOSARIA HISPIDULA (Cushman, 1917) Figure 7.4

- 1917 Nodosaria lepidula var. hispidula Cushman, p. 654.
- 1921 Nodosaria lepidula var. hispidula, Cushman, pl. 36, fig. 7.

Occurrence.—This species occurred sometimes commonly in 187.0–157.0 adjusted rmcd.

SIPHONODOSARIA SPINATA (Cushman, 1934)

1934 Nodogenerina spinata CUSHMAN, p. 123, pl. 14, fig. 14.

Occurrence.—This species was very rare in 175.8–157.5 adjusted rmcd.

SIPHONODOSARIA Sp. A

Occurrence.—This species was very rare in 162.9–159.9 adjusted rmcd.

SIPHONODOSARIA Sp. B

Occurrence.—This species was very rare in 183.4–179.2 adjusted rmcd.

Genus Stilostomella Guppy, 1984 Stilostomella decurta (Bermúdez, 1937) Figure 7.6

1937 Ellipsonodosaria decurta BERMÚDEZ, p. 144, pl. 17, figs. 13, 14.

Occurrence.—This species was very rare in 182.8–1182.2 adjusted rmcd.

STILOSTOMELLA GRACILLIMA (Cushman and Jarvis, 1934)

1934 Ellipsonodosaria nuttalli Cushman and Jarvis var. gracillima Cushman and Jarvis, p. 72, pl. 10, fig. 7a, 7b.

Occurrence.—This species was very rare in 186.2–157.8 adjusted rmcd.

STILOSTOMELLA sp. A Figure 7.7

Occurrence.—This species was very rare in 177.9–158.0 adjusted rmcd.

Superfamily BOLIVINACEA Glaessuer, 1937

Family BOLIVINIDAE Glaessuer, 1937 Genus BOLIVINA d'Orbigny, 1839 BOLIVINA HUNERI HOWE, 1939

1939 Bolivina huneri Howe, p. 66, pl. 9, figs. 3, 4.

Occurrence.—This species was very rare in 177.7–160.7 adjusted rmcd.

Superfamily Cassidulinacea d'Orbigny, 1839 Family Cassidulinidae d'Orbigny, 1839 Subfamily Cassidulinae d'Orbigny, 1839 Genus Evolvecassidulina Eade, 1967 Evolvecassidulina cf. Howei (Cushman, 1946)

1946 Cassidulinoides howei CUSHMAN, p. 36, pl. 7, figs. 9, 10.

Occurrence.---This species was very rare at 115.8 adjusted rmcd.

Genus GLOBOCASSIDULINA Voloshinova, 1960 GLOBOCASSIDULINA GLOBOSA (Hantken, 1875) Figure 8.5

- 1875 *Cassidulina globosa* HANTKEN, 1875, p. 64, pl. 16, fig. 2a, 2b.
- 1999 Globocassidulina globosa (Hantken); NOMURA, p. 28, figs. 18.14a–18.14c, 18.15a–18.15c, 18.16a–18.16c, 19, 21.11, 21.12.

Occurrence.—This species occurred commonly in 187.0–157.0 adjusted rmcd.

Remarks.—This species has been usually identified as *Globocassidulina subglobosa* (Brady) in Paleogene deep-sea sediments. However, according to Nomura (1999), this form is different from the holotype of the Brady's collection. For this reason, we identified this species as *Globocassidulina globosa* (Hantken), following the taxonomic assignment of Nomura (1999).

GLOBOCASSIDULINA Sp. A

Occurrence.—This species was very rare at 174.7 adjusted rmcd.

GLOBOCASSIDULINA Sp. B

Occurrence.—This species was very rare at 180.1 adjusted rmcd.

Superfamily TURRILINACEA Cushman, 1927 Family Stainforthidae Reiss, 1963 Genus Virgulinopsis Hofker, 1956 Virgulinopsis navarroanus (Cushman, 1933) Figure 8.3

1933a Virgulina navarroana Cushman, p. 63, pl. 7, figs. 9a, 9b, 10a, 10b.

Occurrence.—This species occurred commonly in 184.1–157.0 adjusted rmcd.

Superfamily LOXOSTOMATACEA Loeblich and Tappan, 1962 Family LOXOSTOMATIDAE Loeblich and Tappan, 1962 Genus Aragonia Finley, 1939 Aragonia aragonensis (Nuttall, 1930)

1930 Textularia aragonensis Nuttall, p. 280, p. 23, fig. 6.

Occurrence.—This species was very rare in 186.8–183.0 adjusted rmcd.

Superfamily BULIMINACEA Jones, 1875 Family BULIMINIDAE Jones, 1875 Genus BULIMINA d'Orbigny, 1826 BULIMINA ALAZANENSIS Cushman, 1927 Figure 8.1

1927b Bulimina alazanensis Cushman, p. 161, pl. 25, fig. 4.

Occurrence.—This species was very rare in 181.1–162.3 adjusted rmcd.

BULIMINA MIDWAYENSIS Cushman and Parker, 1936 Figure 8.2

1936 Bulimina arkadelphiana Cushman and Parker var. midwayensis Cushman and Parker, p. 42, pl. 7, figs. 9, 10.

Occurrence.—This species was very rare in 185.5–160.4 adjusted rmcd.

Family BULIMINELLIDAE Hofker, 1951 Genus BULIMINELLA Cushman, 1911 BULIMINELLA PARVULA Brotzen, 1948

1948 Buliminella parvula Brotzen, p. 57, pl. 10, figs. 3, 4.

Occurrence.—This species was very rare in 184.5–158.9 adjusted rmcd.

Genus Globobulimina Cushman, 1927 Globobulimina sp.

Occurrence.—This species was very rare at 180.7 adjusted rmcd.

Family SIPHOGENERINOIDIDAE Saidova, 1981 Subfamily SIPHOGENERINOIDINAE Saidova, 1981 Genus Loxostomina Sellier de Civrieux, 1969 Loxostomina sp.

Occurrence.—This species was very rare in 179.6–160.2 adjusted rmcd.

Superfamily FURSENKOINACEA Loeblich and Tappan, 1961 Family FURSENKOINIDAE Loeblich and Tappan, 1961 Genus FURSENKOINA Loeblich and Tappan, 1961 Figure 8.4

FURSENKOINA Sp. A

Occurrence.—This species occurred sometimes commonly in 187.0–157.0 adjusted rmcd.

FURSENKOINA Sp. B

Occurrence.—This species was very rare in 184.1–178.2 adjusted rmcd.

FURSENKOINA Sp. C

Occurrence.—This species was very rare in 185.8–160.2 adjusted rmcd.

Superfamily DISCORBACEA Ehrenberg, 1838 Family Sphaeroidinidae Cushman, 1927 Genus Sphaeroidina d'Orbigny, 1826 Sphaeroidina bulloides d'Orbigny, 1826 Figure 8.9

1826 Sphaeroidina bulloides D'ORBIGNY, p. 267.

Occurrence.—This species was rare in 185.5–157.0 adjusted rmcd.



FIGURE 8—Scanning electron micrographs of benthic foraminifera at Site U1333, IODP Exp. 320. *1, Bulimina alazanensis* Cushman, sample 320-U1333B-15H-4, 48–50 cm; *2, Bulimina midwayensis* Cushman and Parker, sample 320-U1333B-15H-2, 48–50 cm; *3, Virgulinopsis navarroanus* (Cushman), sample 320-U1333B-15H-2, 108–110 cm; *4, Fursenkoina* sp. A, sample 320-U1333B-15H-1, 128–130 cm; *5, Globocassidulina globosa* (Hantken), sample 320-U1333B-15H-2, 128–130 cm; *6, Cibicidoides bradyi* (Trauth), sample (320-U1333B-17H-2, 108–110 cm; *7, 8, Cibicidoides eocaenus* (Gümbel), samples 320-U1333B-17H-2, 108–110 cm and 320-U1333B-17H-3, 88–90 cm; *9, Sphaeroidina bulloides* d'Orbigny, sample 320-U1333B-16H-7, 28–30 cm; *10, Cibicidoides grimsdalei* (Nuttall), sample 320-U1333B-15H-2, 128–130 cm.

Superfamily GLABRATELLACEA Loeblich and Tappan, 1964 Family HERONALLENIIDAE Loeblich and Tappan, 1964 Genus HERONALLENIA Chapman and Parr, 1931 HERONALLENIA sp.

Occurrence.—This species was very rare in 185.5–157.5 adjusted rmcd.

Superfamily DISCORBINELLACEA Sigal, 1952 Family PSEUDOPARRELLIDAE Voloshinova, 1952 Subfamily PSEUDOPARRELLINAE Voloshinova, 1952 Genus EPISTOMINELLA Husezima and Maruhasi, 1944 EPISTOMINELLA EXIGUA (Brady, 1884)

1884 Pulvinulina exigua BRADY, p. 696, pl. 103, figs. 13, 14.

Occurrence.—This species was very rare in 183.0–161.2 adjusted rmcd.

Superfamily DISCORBINELLACEA Sigal, 1952 Family PARRELLOIDIDAE Hofker, 1956 Genus CIBICIDOIDES Thalmann, 1939 CIBICIDOIDES BRADYI (Trauth, 1918) Figures 8.6, 13.2

1918 Truncatulina bradyi TRAUTH, not designated.

Occurrence.---This species was rare in 187.0-157.0 adjusted rmcd.

CIBICIDOIDES EOCAENUS (Gümbel, 1868) Figures 8.7, 8.8, 13.6, 14.1, 14.2

- 1868 Rotalia eocaena GÜMBEL, p. 650, pl. 2, fig. 87a, 87b.
- 2005 *Cibicidoides eocanus* (Gümbel); NOMURA AND TAKATA, pl. P14, fig. 2a–2c.

Occurrence.—This species was rare in 187.0–157.2 adjusted rmcd.

Remarks.—In our specimens, we discriminated this species from *Cibicidoides praemundulus* Berggren and Miller, by more convex spiral side, although it was sometimes difficult to separate both the species.

CIBICIDOIDES GRIMSDALEI (Nuttall, 1930) Figure 8.10

1930 *Cibicides grimsdalei* NUTTALL, p. 291, pl. 25, figs. 7, 8, 11.

Occurrence.—This species was sometimes common in 186.8–157.0 adjusted rmcd.

CIBICIDOIDES PRAEMUNDULUS Berggren and Miller, 1986 Figures 9.1, 13.4, 13.5

- 1986 *Cibicidoides praemundulus* Berggren and Miller; VAN MORKHOVEN ET AL., p. 264, text-figs. 5, 6, pl. 87, figs. 1–3.
- 2005 *Cibicidoides eocanus* (Gümbel); NOMURA AND TAKATA, pl. P14, fig. 1a–1c.

Occurrence.—This species was sometimes common in 187.0–157.0 adjusted rmcd.

CIBICIDOIDES SUBCARINATUS (Cushman and Deaderick, 1944) Figure 9.2

EA Sigal, 1952 Occurrence.—This species was very rare at 183.8 adjusted rmcd.

adjusted rmcd.

CIBICIDOIDES sp. B

CIBICIDOIDES Sp. A

2005 Cibicidoides subcarinatus (Cushman and Deaderick);

Occurrence.-This species was very rare in 184-157.0

Nomura and Takata, pl. P14, fig. 4a-4c.

Occurrence.—This species was very rare at 184.1 adjusted rmcd.

CIBICIDOIDES sp. C

Occurrence.—This species was very rare in 184.8–158.0 adjusted rmcd.

CIBICIDOIDES sp. D

Occurrence.--This species was very rare at 158.0 adjusted rmcd.

Superfamily Planorbulinacea Schweger, 1877 Family Cibicididae Hofker, 1956 Subfamily Cibicidinae Cushman, 1927 Genus Cibicidina Bandy, 1949 Cibicidina Walli Bandy, 1949

1949 Cibicidina walli BANDY, p. 95, pl. 15, fig. 5a-5c.

Occurrence.—This species was very rare in 162.3–158.0 adjusted rmcd.

Superfamily Asterigerinacea d'Orbigny, 1839 Family Epistomariidae Hofker, 1954

Subfamily Eponidellinae Seiglie and Bermúdez, 1965 Genus NUTTALLIDES Finlay, 1939 NUTTALLIDES TRUEMPYI (Nuttall, 1930)

Figure 10.1

1930 Eponides truempyi NUTTALL, p. 287, pl. 24, figs. 9, 13, 14.

Occurrence.—This species was abundant in 187.0–157.0 adjusted rmcd.

NUTTALLIDES UMBONIFER (Cushman, 1933) Figure 10.2

1933b Pulvinulinella umbonifera Cushman, p. 90, pl. 9, fig. 9a–9c.

Occurrence.—This species was very rare in 187.0–158.0 adjusted rmcd.

Superfamily NONIONACEA Schultze, 1854 Family NONIONIDAE Schultze, 1854 Subfamily NONIONINAE Schultze, 1854 Genus NONION de Monfolt, 1808 NONION AFFINIS (Reuss, 1851)

1851 Nonionina affinis REUSS, p. 72, pl. 5, fig. 32a, 32b.

Occurrence.—This species was very rare in 186.8–158.9 adjusted rmcd.

NONION HAVANENSE Cushman and Bermúdez, 1937 Figure 10.9

1937 Nonion havanense Cushman and Bermúdez, p. 19, pl. 2, figs. 13, 14.

¹⁹²⁹ Anomalina coonensis BERRY, p. 14, pl. 2, figs. 22-24.



FIGURE 9—Scanning electron micrographs of benthic foraminifera at Site U1333, IODP Exp. 320. *1*, *Cibicidoides praemundulus* Berggren and Miller, sample 320-U1333B-17H-2, 108–110 cm; *2*, *Cibicidoides subcarinatus* (Cushman and Deaderick), sample 320-U1333B-17H-1, 48–50 cm; *3*, *Anomalinoides spissiformis* (Cushman and Stainforth), sample 320-U1333C-19H-2, 8–10 cm; *4*, *Anomalinoides* sp. A, sample 320-U1333B-17H-2, 108–110 cm; *5*, *Valvalabamina depressa* (Alth), sample 320-U1333B-16H-7, 28–30 cm; *6*, *7*, *Paralabamina elevata* (Plummer), samples 320-U1333B-15H-1, 68–70 cm and 320-U1333B-16H-7, 28–30 cm. Scale bar=100 μm.



FIGURE 10—Scanning electron micrographs of benthic foraminifera at Site U1333, IODP Exp. 320. 1, Nuttallides truempyi (Nuttall), sample 320-U1333B-16H7, 8–10 cm; 2, Nuttallides umbonifer (Cushman), sample 320-U1333B-16H-7, 8–10 cm; 3, Alabamina dissonata (Cushman and Renz), sample 320-U1333B-15H-2, 128–130 cm; 4, 5, Pullenia jarvisi Cushman, samples 320-U1333B-15H-1, 128–130 cm and 320-U1333B-17H-1, 88–90 cm; 6, 7, Pullenia bulloides (d'Orbigny), samples 320-U1333B-17H-1, 128–130 cm; 8, Nonion havanensis Cushman and Bermúdez, sample 320-U1333B-17H-1, 88–90 cm; 9, Pullenia subcarinata (d'Orbigny), sample 320-U1333B-17H-1, 28–30 cm. Scale bar=100 μm.

Occurrence.—This species was rare in 186.8–158.5 adjusted rmcd.

Subfamily PULLENINAE Schwager, 1877 Genus PULLENIA Parker and Jones, 1862 PULLENIA BULLOIDES (d'Orbigny, 1846) Figure 10.6, 10.7

1846 Nonionina bulloides d'Orbigny, p. 107, pl. 5, figs. 9, 10.

Occurrence.—This species was rare in 187.0–157.0 adjusted rmcd.

PULLENIA JARVISI Cushman, 1936 Figure 10.4, 10.5

1936 Pullenia jarvisi CUSHMAN, p. 77, pl. 13, fig. 6.

Occurrence.—This species was rare in 187.0–157.0 adjusted rmcd.

Remarks.—We included specimens with five inflated chamber in the last whorl that are identical to *Pullenia quinqueloba* (Reuss) into this species, according to Cushman (1946).

> PULLENIA SUBCARINATA (d'Orbigny, 1839) Figure 10.9

1839 Nonionina subcarinata d'Orbigny, p. 28, pl. 5, figs. 23, 24.

Occurrence.—This species was rare in 187.0–157.0 adjusted rmcd.

Superfamily Chilostomellacea Brady, 1881 Family Chilostomellidae Brady, 1881 Subfamily Chilostomellinae Brady, 1881 Genus Allomorphina Reuss, 1849 Allomorphina Minuta Cushman, 1936 Figure 11.1

1936 Allomorphina minuta Cushman, p. 72, pl. 13, fig. 3a-3c.

Occurrence.—This species was rare in 186.2–157.5 adjusted rmcd.

Subfamily PALLAIMORPHININAE Loeblich and Tappan, 1981 Genus Abyssamina Schnitker and Tjalsma, 1980 Abyssamina Quadrata Schnitker and Tjalsma, 1980 Figure 11.3

1980 Abyssamina quadrata SCHNITKER AND TJALSMA, p. 237, pl. 1, figs. 1–6.

Occurrence.---This species was rare in 186.8--157.0 adjusted rmcd.

Remarks.—Schnitker and Tjalsma (1980) described *Abyssamina quadrata* and *A. Poagi*. However, it was difficult to distinguish both species based on their descriptions. For this reason, we just used *A. quadrata* in this study.

Family ALABAMINIDAE Hofker, 1951 Genus ALABAMINA Toulmis, 1941 ALABAMINA DISSONATA (Cushman and Renz, 1948) Figure 10.3

1948 Pulvinulinella atlantisae Cushman var. dissonata Cushman and Renz, p. 35, pl. 7, figs. 11, 12.

Occurrence.—This species was rare in 187.0–157.0 adjusted rmcd.

Alabamina Sp. A

Occurrence.—This species was very rare in 175.5–159.6 adjusted rmcd.

Family QUADRIMORPHINIDAE Saidova, 1981 Genus QUADRIMORPHINA Finlay, 1939 QUADRIMORPHINA PROFUNDA Schnitker and Tjalsma, 1980 Figure 11.2

1980 *Quadrimorphina profunda* SCHNITKER AND TJALSMA, p. 239, pl. 1, figs. 16–21.

Occurrence.—This species was sometimes abundant in 186.0–157.0 adjusted rmcd.

Genus VALVALABAMINA Reiss, 1963 VALVALABAMINA DEPRESSA (Alth, 1850) Figure 9.5

1850 Rotalina depressa ALTH, p. 266, pl. 13, fig. 21.

2005 Valvalabamina depress (Alth); Nomura and Takata, pl. P20, figs. 4a–4c, 5a–5c.

Occurrence.—This species was rare in 186.6–157.0 adjusted rmcd.

Remarks.—We used *Valvalabamina* for this species instead of *Anomalinoides* due to less perforate test wall on the umbilical side.

Family ORIDORSALIDAE Loeblich and Tappan, 1984 Genus ORIDORSALIS Andersen, 1961 ORIDORSALIS UMBONATUS (Reuss, 1851) Figure 12.1, 12.2

1851 Rotalina umbonata REUSS, p. 75, pl. 5, fig. 35.

Occurrence.—This species was abundant in 187.0–157.0 adjusted rmcd.

Remarks.—The variation in shape was high. Most specimens were plano-convex shape with more convex spiral side.

Family Osangulallidae Loeblich and Tappan, 1964 Genus Osangularia Brotzen 1940 Osangularia plummerae Brotzen, 1940 Figure 11.6

- 1940 Osangularia plummerae BROTZEN, p. 30, text-fig. 8.
- 1945 Osangularia mexicana (Cole); CUSHMAN AND STAIN-FORTH, p. 63, pl. 11, fig. 5a, 5b.

Occurrence.—This species was rare in 186.4–157.0 adjusted rmcd and disappeared in CAE-4.

Family HETEROLEPIDAE Gonzáles-Donoso, 1969 Genus Anomalinoides Brotzen, 1942

ANOMAILINOIDES SPISSIFORMIS (Cushman and Stainforth, 1945) Figure 9.3

- 1945 Anomalina alazanensis var. spissiformis Cushman and Stainforth, p. 71, pl. 14, fig. 5a–5c.
- 2005 Valvalabamina praeacuta (Vasilenko); Nomura and Таката, pl. P11, figs. 1a–1c, 2a–2c, 3a–3c.

Occurrence.—This species was rare in 187.0–157.0 adjusted rmcd.

Remarks.—Nomura and Takata (2005) identified this species to *Valvalabamina praeacuta* (Vasilenko), but we identified it to *Anomalinoides spissiformis* (Cushman and Stainforth) due to coarsely perforated test wall especially on the umbilical side and more round-shape periphery.

Anomailinoides sp. A Figure 9.4



FIGURE 11—Scanning electron micrographs of benthic foraminifera at Site U1333, IODP Exp. 320. 1, Allomorphina minuta Cushman, sample 320-U1333B-15H-2, 88–90 cm; 2, Quadrimorphina profunda Schnitker and Tjalsma, sample 320-U1333B-15H-2, 68–70 cm; 3, Abyssamina quadrata (Schnitker and Tjalsma), sample 320-U1333B-15H-2, 68–70 cm; 4, 5, Paralabamina lunata (Brotzen), samples 320-U1333B-16H-7, 8–10 cm; 6, Osangularia plummerae Brotzen, sample 320-U1333B-17H-2, 128–130 cm; 7, Linaresia semicribrata (Beckmann), sample 320-U1333C-19H-1, 128–130 cm. Scale bar=100 μm.



FIGURE 12—Scanning electron micrographs of benthic foraminifera at Site U1333, IODP Exp. 320. 1, 2, Oridorsalis umbonatus (Reuss), sample 320-U1333B-15H-2, 128–130 cm; 3, Gyroidioides beisseli (White), sample 320-U1333B-16H-5, 108–110 cm; 4, Gyroidioides nitidus (Reuss), samples 320-U1333B-15H-4, 128–130 cm; 5, Gyroidinoides soldanii (d'Orbigny), sample 320-U1333B-15H-2, 128–130 cm; 6, Gyroidinoides subangulatus (Plummer), sample 320-U1333B-15H-2, 128–130 cm; 7, Gyroidinoides globosus (Hagenow), sample 320-U1333C-19H1, 128–130 cm. Scale bar=100 μm.



FIGURE 13—Light micrographs of benthic foraminifera at Site U1333, IODP Exp. 320. 1, Paralabamina lunata (Brotzen), sample 320-U1333B-16H-7, 8–10 cm; 2, Cibicidoides bradyi (Trauth), sample 320-U1333B-17H-2, 108–110 cm; 3, Anomalinoides sp. A, sample 320-U1333B-17H-1, 88–90 cm; 4, 5, Cibicidoides praemundulus Berggren and Miller, samples 320-U1333B-17H-1, 48–50 cm and 320-U1333B-15H-1, 128–130 cm; 6, Cibicidoies eocaenus (Gümbel), sample 320-U1333B-17H-2, 108–110 µm.



FIGURE 14—Light micrographs of benthic foraminifera at Site U1333, IODP Exp. 320. 1, 2, Cibicidoies eocaenus (Gümbel), samples 320-U1333C-19H-2, 68–70 cm and 320-U1333C-19H-2, 8–10 cm. Scale bar=100 μm.

1951 *Anomalina acuta* (Plummer) Cushman, pl. 18, figs. 3a– 3c, 4a–4c, 5, 6.

Occurrence.—This species was very rare in 186.8–157.0 adjusted rmcd.

Remarks.—This species resembled to *Anomalinoides spissi-formis* (Cushman and Stainforth), but there were granular shell materials in umbilicus.

Family GAVELINELLIDAE Hofker, 1956 Subfamily GYROIDINOIDINAE Saidova, 1981 Genus GYROIDINOIDES Brotzen, 1942 GYROIDINOIDES BEISSELI (White, 1928) Figure 12.3

- 1928 Gyroidina beisseli WHITE, p. 291, pl. 39, fig. 7a-7c.
- 2005 *Gyroidina beisseli*; Nomura and Takata, pl. P20, fig. 1a–1c.

Occurrence.—This species was abundant in 187.0–157.0 adjusted rmcd.

Gyroidinoides globosus (Hagenow, 1842) Figure 12.7

1842 Nonionina globosa Von HAGENOW, p. 574, not given.

Occurrence.—This species was rare in 187–158.5 adjusted rmcd.

GYROIDINOIDES NITIDUS (Reuss, 1844) Figure 12.4

- 1844 Rotalia nitida REUSS, not given.
- 2005 *Gyroidinoides nitidus* (Reuss); NOMURA AND TAKATA, pl. P21, fig. 3a–3c.

Occurrence.---This species was rare in 185.8--157.8 adjusted rmcd.

GYROIDINOIDES SOLDANII (d'Orbigny, 1826) Figure 12.5

- 1826 Gyroidina soldanii D'ORBIGNY, p. 278, not given.
- 1846 Gyroidina soldanii D'ORBIGNY, pl. 8, figs. 10-12.
- 1871 *Gyroidina soldanii*; Parker, Jones and Brady, pl. 12, fig. 151.
- 1995 *Gyroidinoides soldanii* (d'Orbigny); Nomura, pl. 4, figs. 3a–3c, 4a–4c.

Occurrence.---This species was rare in 186.8--157.0 adjusted rmcd.

Gyroidinoides subangulatus (Plummer, 1927) Figure 12.6

1927 Rotalia soldanii (d'Orbigny) var. subangulata PLUM-MER, p. 154, pl. 12, fig. 1a-1c.

Occurrence.---This species was rare in 184.8-157.0 adjusted rmcd.

Gyroidinoides sp. A

Occurrence.—This species was very rare in 162.3–159.2 adjusted rmcd.

Subfamily Gavelinellinae Hofker, 1956 Genus Linaresia González-donoso Linaresia semicribrata (Beckmann, 1954) Figure 11.7

- 1954 Anomalina pomploides Galloway and Heminway var. semicribrata BECKMANN, p. 400, pl. 27, fig. 3, text-figs. 24, 25.
- 1986 Anomalinoides semicribratus (Beckman); VAN MORK-HOVEN ET AL., pl. 48, figs. 1–3.
- 2005 *Linaresia semicribrata* (Beckmann); NOMURA AND TAKATA, pl. P11, fig. 6a–6c.

Occurrence.—This species was very rare in 186.8–157.2 adjusted rmcd.

Remarks.—This species has been thought to be probably a continuous cline with *Anomalinoides globulosus* (Chapman and Parr), *Anomalinoides rubiginosus* (Cushman), *Anomalinoides capitatus* (Gümbel), according to Van Morkhoven et al. (1986).

Genus Paralabamina Hansen, 1970 Paralabamina elevata (Plummer, 1927) Figure 9.6, 9.7

- 1927 Truncatulina elevata PLUMMER, p. 142, pl. 11, fig. 1a-1c.
- 2005 Paralabamina elevata (Plummer); NOMURA AND TAKA-TA, pl. P18, figs. 4a–4c, 8a–8c, 9a–9c.

Occurrence.—This species was very rare in 180.1–157.2 adjusted rmcd.

PARALABAMINA LUNATA (Brotzen, 1948) Figures 11.4, 11.5, 13.1

- 1948 Eponides lunata BROTZEN, p. 77, pl. 10, figs. 17, 18.
- 2005 *Paralabamina lunata* (Brotzen); NOMURA AND TAKATA, pl. P12, figs. 6a–6c, 7a–7c, pl. P18, figs. 5a–5c, 7a–7c.

Occurrence.—This species was very rare in 158.1–162.3 adjusted rmcd.

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