Biostratigraphy, paleobathymetry and paleobiogeography of Lower Cretaceous benthic foraminifera from Shatsky Rise (ODP Leg 198) in the central Pacific Ocean

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Abstract

Benthic foraminiferal assemblages in ODP holes 1207B, 1214A, 1213A, and 1213B drilled on Shatsky Rise (Pacific Ocean) provided an opportunity to compare all taxa recorded from the Hauterivian to the Albian. The benthic foraminiferal assemblage abundances and compositions confirm an evolutionary deepening of the Shirshov and Tamu Massif during the Early Cretaceous. In the Hauterivian, recovered only at ODP holes 1213A and 1213B, an outer neritic setting (100 - 200 m) is inferred. The benthic foraminiferal assemblages display a deepening from an upper bathyal setting (200 - 500 m) during the Barremian to a lower bathyal (1000 - 2000 m) environment during the Albian.

The comparison of the Pacific benthic foraminiferal assemblages with records worldwide indicates that, during the Hauterivian, only very few taxa documented in ODP holes 1213A and 1213B, occur in all bioprovinces, probably because of the shallow-water environment (outer neritic: 100 - 200 m) characterizing the Shatsky Rise. Barremian to Albian benthic foraminiferal assemblages observed at Shatsky Rise reveal an affinity with taxa reported from other bioprovinces.

Specifically, a strong affinity is observed between the benthic foraminifera from the Shatsky Rise and those documented from the Atlantic Ocean, whereas the affinity with taxa of the Boreal Province and the Western Tethys is less pronounced.

The cosmopolitan character of most benthic foraminifera probably benefited from a very efficient circulation interconnecting various oceans in the Early Cretaceous. Concomitantly, many benthic foraminiferal taxa were able to populate different bioprovinces, showing no preference for any particular setting or paleo-latitudes. Differences between benthic foraminiferal assemblages from Shatsky Rise and other bioprovinces seem related to the geographical distance (biogeography) and site-specific paleobathymetry.

1. Introduction

The Cretaceous benthic foraminifera occurring in the Pacific Ocean are studied in sedimentary records drilled by the Deep-Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP), and only rare taxa are reported from onshore stratigraphic sections (e.g., Douglas, 1971; Sliter and Baker, 1972; Luterbacher, 1975; Bralower et al., 2002; Sager et al., 2010). Specifically, the benthic foraminifera of the Lower Cretaceous in the Pacific Ocean have not been widely examined, due to the gaps in the stratigraphic records and the poor core recovery of sedimentary rocks in drilled sites. In addition, many studies were often only preliminary reports or documentation of isolated findings and, thus, lack detailed taxonomic analysis with specimens identified only at genus level due to discrepant concepts or poor preservation. On the contrary, the Lower Cretaceous benthic foraminiferal record from the Atlantic Ocean has been extensively examined as corroborated by the countless taxonomic, paleobathymetric, paleoecological, and palaeoceanographic studies performed in northern and southern Atlantic Ocean (e.g., Bartenstein and Bolli, 1977; Bolli et al., 1994; Koutsoukos and Klasz, 2000; Holbourn et al., 2001a; Friedrich, 2005; Kochhann et al., 2014).

The biogeographic distribution of benthic foraminifera during the Early Cretaceous was documented by Bartenstein (1976, 1985, 1987) and Bolli et al. (1994) that identified a strict correlation between species from Northwest Germany (Boreal Bioprovince) and Trinidad (Atlantic Bioprovince). Koutsoukos and Klasz (2000) reported a close affinity of benthic foraminifera between the Brazilian-Caribbean-Gulf Coast Province and species from the Austral, the Boreal and NE Tethyan Realms during the Late Cretaceous. In addition, Holbourn et al. (2001a) highlighted the affinity among species occurring along the Atlantic Ocean and Western Tethys during the late Albian. Widmark and Malmgren (1992) documented Late Cretaceous benthic foraminifera in both the Pacific Ocean (DSDP Site 465 Hess Rise) and the Atlantic Ocean (South Atlantic: DSDP Sites 356, 516, 525, 527; North Atlantic: DSDP Site 384).

Benthic foraminifera live abundantly on the seafloor and can inhabit in shelf (0 - 200 m), bathyal (200 - 2000 m) and abyssal (> 2000 m) environments (Widmark and Malmgren, 1992; van der Zwaan et al., 1999; Murray, 2006; Jorissen et al., 2007; Gooday and Jorissen, 2012). They are extremely sensitive to changes in salinity, temperature, oxygen availability, and nutrient supply, thus their distribution and assemblage composition in the fossil record allow reconstructing the paleodepth and the paleoenvironmental conditions at the seafloor (e.g., Sliter and Barker, 1972; van Hinsbergen et al., 2005).

Here we report a detailed compilation and taxonomic review of the benthic foraminifera of the Lower Cretaceous (lower Hauterivian to the upper Albian interval) from the Pacific Ocean recorded on the Shatsky Rise (ODP holes 1207B, 1214A, 1213A, and 1213B) in the Pacific Ocean. The primary aims of this study are as follows: 1) revision of species from the Pacific Ocean to derive their stratigraphic ranges into the geological time scale; 2) documentation of the quantitative changes in the composition of the benthic foraminiferal assemblages; 3) reconstruction of the evolution of the paleobathymetry at the Shatsky Rise; and 4) the assessment of the cosmopolitan distribution of some Lower Cretaceous benthic foraminifera occurring in the Pacific Ocean and their relationship with the other bioprovinces (i.g., Atlantic Ocean Bioprovince, Boreal Bioprovince, Western Tethys Bioprovince, Indian Ocean Bioprovince and Antarctica Bioprovince).

2. Material and studied Sites

Lower Cretaceous (lower Hauterivian to upper Albian) benthic foraminiferal assemblages were studied at ODP sites 1207, 1213, and 1214 drilled during Leg 198 on the Shatsky Rise considered a medium-sized large igneous province (LIP) in the west-central Pacific Ocean (Fig. 1A). It is 1650 km long and 450 km wide and consists of three prominent highs (Southern, Central, and Northern), resulting from effusive flood basalt-style volcanism. These highs include volcanic edifices surrounded by normal oceanic lithosphere and a group of ~80 seamounts (Sager et al., 1999; Bralower et al., 2002). The paleogeographic position of Shatsky Rise during the Lower Cretaceous has been reconstructed at equatorial latitudes in the southern hemisphere and gradually drifted north over the last 90 Ma (Larson et al., 1992; Bralower et al., 2002)

2.1. ODP Site 1207

ODP Hole 1207B (37°47.4370′N - 162°45.0534′E) is the northernmost site drilled on the Shatsky

Rise, located in lower bathyal (3103 m) water depth (Shirshov Massif; Fig. 1B). At Hole 1207B, the lower Turonian to upper Barremian sedimentary rocks assigned to Lithological Unit III (from cores 198-1207B-20R-1, 0 cm to 49R-1, 39 cm; Shipboard Scientific Party, 2002a; Fig 1C) are characterized, from top to bottom, by changes from friable chalk to limestone. A sequence of dark greenish gray limestones was recovered in the lower Aptian in section 198-1207B-43R-1. A dark-colored claystone of ~45-cm of thickness rich in C_{org} content (ranging between 1.7 and 34.7 wt%) was recorded in the interval 198-1207B-44R-1, 60-105 cm. The base of Unit III (lower Aptian to Barremian) is characterized by limestones highly bioturbated, which contain pyritized radiolarians and small nodules of pyrite. Chert fragments with common inclusions and/or coatings of porcellanite were observed in Unit III (Shipboard Scientific Party, 2002a). Twelve samples from 198-1207B-49R-CC (Barremian) to sample 198-1207B-28R-CC (Albian) were analyzed for benthic and planktonic foraminifera.

2.2. ODP Site 1214

ODP Hole 1214A (31°52.0254′N - 157°28.7178′E) is located at 3402 m water depth on the southern flank of the Southern High of Shatsky Rise (Tamu Massif; Fig. 1B). In Hole 1214A Lithological Unit II comprises the late Albian to Hauterivian sedimentary rocks (from 198-1214A-2R-1, 0 cm to 25R-1; Shipboard Scientific Party, 2002b; Fig 1C) which are characterized by fragments (drilling breccia) of chert and porous calcareous porcellanite. Nannofossil claystone, limestone with radiolarians, and nannofossil chalk are present in minor amounts into the sedimentary succession (Shipboard Scientific Party, 2002b). Twenty-four samples from 198-1214A-25R-1, 19-20 cm (Hauterivian) to 198-1214A-6R-1, 4-5 cm (Albian) were analyzed for benthic and planktonic foraminifera.

2.3. ODP Site 1213

ODP holes 1213A (31°34.6402′N - 157°17.8605′E) and 1213B (31°34.6576′N - 157°17.8621′E), are the southernmost and deepest holes drilled on the Shatsky Rise depth transect and are located in lower bathyal (3883 m) water depth on the southern flank of the Southern High of Shatsky Rise (Tamu Massif; Fig. 1B). The Cretaceous sequence penetrate rocks from the early Cenomanian to Berriasian (198-1213A-10R to 21R and 198-1213B-1R to 27R; Shipboard Scientific Party, 2002c; Fig 1C) that are included in Lithologic Unit III, which is subdivided into five subunits, mainly on the basis of chert color and changes in associated lithologies. The subunits IIIA and IIIB are characterized by porcellanites (from early Cenomanian to early late Aptian). The subunit IIIC is marked by interbedded C_{org}-rich clayey porcellanite and radiolarian porcellanite (early Aptian). The subunit IIID spans the interval from the Hauterivian to the Berriasian, and is composed by chert, porcellanite, and nannofossil chalk to clayey nannofossil (Shipboard Scientific Party, 2002c). Fourteen samples from 198-1213B-10R-1, 21-22 cm (Hauterivian) to 198-12113A-18R-1, 30 cm (Albian) were analyzed for benthic and planktonic foraminifera.

3. Methods

A total of 50 samples were studied for benthic and planktonic foraminifera from ODP holes 1207B, 1214A, 1213A and 1213B (Supplementary Data Tables 1 and 2). At the studied sites sampling resolution is variable from core to core because of poor core recovery. The studied samples were previously investigated for planktonic and benthic foraminifera by the Shipboard Scientific Party (2002a, b, c).

Samples for the micropaleontological analysis were processed according to the standard procedure (see Shipboard Scientific Party, 2002a, b, c) and three size fractions were obtained (>63 µm. > 125 µm and >250 µm). The residues were examined under a stereomicroscope and all specimens present in each sample were counted, identified and permanently stored in Plummer slides.

Absolute abundances of benthic foraminifera are reported as the number of specimens per 10 grams of residue (n/10g; BFN). Shannon-Weaver diversity (HS; Shannon and Weaver, 1949) was calculated for each sample using the Past software (Hammer et al., 2001). The Shannon-Weaver has been used for determining the diversity of taxa in determined environments. Shannon-Weaver values > 2 reflect the presence of well-diversified benthic foraminiferal assemblages, consequently, values of Shannon-Weaver between 1 and 2 are indicative of lower diversity assemblages. Extremely low diversity assemblages display Shannon-Weaver values between 0 and 1. The Past software (Hammer et al., 2001) was also used to calculate the Pearson-correlation coefficients of the common species of benthic foraminifera displaying a worldwide geographic distribution during the Lower Cretaceous.

Benthic foraminifera were identified at species level whenever possible, following the taxonomy by Ellis and Messina (1942-2015), Luterbacher (1975) Mjatliuk (1988), Weidich (1990), Meyn and Vespermann (1994), Holbourn (1996), Holbourn and Kaminski (1997), Holbourn and Kuhnt (2001), and Holbourn et al. (2001a). The most common taxa were photographed using the light microscope Leica MZ12.5 with a camera Leica DFC295 at the Dipartimento di Scienze della Terra "A. Desio" of the Università degli Studi di Milano.

The paleobathymetric interpretation is based on the subdivision proposed by Nyong and Olsson (1984) and van Morkhoven et al. (1986) as follows: inner-neritic (IN: 0 - 50 m), middle-neritic (MN: 50 - 100 m), outer-neritic (ON: 100 - 200 m), upper bathyal (UB: 200 - 500 m), middle bathyal (MB: 500 - 1000 m), lower bathyal (LB: 1000 - 2000 m), and abyssal (AB: > 2000 m).

A revision and update of the planktonic foraminiferal biozonation, previously published by Shipboard Scientific Party (2002a, b, c), was performed in this study, on the same samples used for benthic foraminifera. Planktonic foraminiferal taxonomy follows the pforams@mikrotax database at http://www.mikrotax.org/pforams (Huber et al., 2016) and the biozonation follows Robaszynski and Caron (1995), Premoli Silva and Sliter (1995), and Gale et al. (2020).

Age assignments of the studied sites (ODP holes 1207B, 1214A, 1213A, and 1213B) are based on the integrated calcareous nannofossils (Bown, 2005) and planktonic foraminifera (this study) biostratigraphic data.

4. Results

4.1 Planktonic foraminifera biostratigraphy

Planktonic foraminifera recorded in ODP holes 1207B, 1214A, 1213A, and 1213B are characterized by low abundances and several samples are barren of foraminifera. Preservation is generally poor to moderate and specimens are mainly observed in the small-sized fraction (63-125μm). The poor core recovery hampered the identification of a reliable sequence of lowest and highest occurrences and thus the zonal assignments are mainly based on the composition of the assemblages and the concurrent occurrence of species that are indicative of distinctive biozones although the biozonal markers are absent.

In Hole 1207B (Supplementary Data Table. 2) the stratigraphic interval from the base (core 49R) to core 41R yield only one specimen of *Hedbergella mitra* and thus it is not zoned. The presence of *H. mitra* and *Hedbergella trocoidea* allow to assign core 40R to the *Globigerinelloides ferreolensis* - *Globigerinelloides algerianus* Zones. Samples from core 33R to 28R contain *Muricohedbergella wonders*i, *Ticinella primula*, and *Biticinella breggiensis* indicative of the *B. breggiensis* zone.

The presence of *Hedbergella luterbacheri*, *Hedbergella aptiana*, *Hedbergella excelsa* and *Hedbergella praetrocoidea* in Hole 1213B (Supplementary Data Table. 2) from the top of core 9R to 6R may allow identification of the *Globigerinelloides ferreolensis* - *Globigerinelloides algerianus* Zones. Core 2R and 1R in Hole 1213B and cores 21R and 20R in Hole 1213A are assigned to the *B. breggiensis* Zone according to the concurrent occurrence of *M. wonders*i, *T. primula*, *B. breggiensis*, *Muricohedbergella astrepta*, and *Globigerinelloides bentonensis*. The topmost core 18R yield *B. breggiensis*, *M. astrepta*

Muricohedbergella praelibyca, and *Globigerinelloides ultramicrus*, typical of the *Thalmanninella appenninca* Zones.

The base of Hole 1214A (cores 25R and 24R) (Supplementary Data Table. 2) is assigned to the *Globigerinelloides blowi* Zone based on the presence of *Globigerinelloides duboisi, Globigerinelloides aptiensis* and *H. aptiana*. The stratigraphic interval form core 23R to core 19R is included in the *Globigerinelloides ferreolensis - Globigerinelloides algerianus* Zones according to the composition of the assemblage. Samples from core 17R and 16R are tentatively assigned to the *T. primula* Zone. The occurrence of *T. primula, B. breggiensis, T. praeticinensis* in the interval from core 14R to 9R allow identification of the *B. breggiensis* Zone. The topmost samples in cores 7R and 6R contain fragments of *Planomalina buxtorfi* to indicate the *T. appenninica* Zone.

4.2 Benthic foraminifera

Benthic foraminifera recorded in ODP holes 1207B, 1214A, 1213A and 1213B are characterized by low abundances and several samples are barren of foraminifera (Fig. 2).

4.2.1 ODP Hole 1207B

Benthic foraminiferal numbers (BFNs) vary between 0 and 7309/10g (Fig. 2). The lower part of the studied interval (Barremian) is characterized by a peak in BFN reaching 2576/10g in sample 596.59 mbsf (meters below sea floor), whereas benthic foraminifera are absent in the two examined samples upward in the Barremian (585.70 mbsf) and in the Aptian (565.00 mbsf). A slight increase in the BFN is recorded in sample 526.65 mbsf with 1034/10g. The uppermost part of the studied interval assigned to the Albian is marked by a variation of BFN between 348/10g (498.69 mbsf) and 7309/10g (431.49 mbsf). Shannon diversity (H_S) fluctuates between 1.3 in the Aptian (in samples 526.65 mbsf) and 2.4 (in samples 460.30 mbsf) in the Albian (Fig. 2).

The calcareous foraminifera dominate in the studied samples, ranging from 61.7% to 100% (Fig. 2). On the contrary, the agglutinated foraminifera fluctuate from 0 to 38.3% (Fig. 2), being abundant only in samples 614.70 mbsf (Barremian) and 431.49 mbsf (Albian) with 38.3% and 27.2%, respectively (Fig. 2). The family Rotaliida is the most common group and fluctuate in abundance between 20.7% and 85.9% (Fig. 2), followed by the family Lagenida that ranges from 8.93% to 63.6% (Fig. 2). The family Textulariina is less abundant reaching the highest value of 36.1% (Fig. 2).

4.2.2 ODP Hole 1214A

Benthic foraminiferal number varies between 0 and 1258/10g (Fig. 2). The lower part of the studied interval (Hauterivian, Barremian and Aptian) contains no benthic foraminifera, except for sample 197.62 mbsf (Aptian) where the BFN display a peak up to 306/10g (Fig. 2). From sample 178.30 mbsf to sample 6.90 mbsf (Albian), the BFN increase to reach a maximum value of 1258/10g in sample 52.61 mbsf, with BFN mean value in this interval of 345/10g (Fig. 2). Shannon diversity (H_S) displays relative low values, ranging from 0 (samples 178.30 mbsf and 81.83 mbsf) to 2.7 in sample 52.61 mbsf (Fig. 2).

Calcareous foraminifera are the most abundant group, ranging from 67.8 to 100% (Fig. 2). The agglutinated foraminifera vary from 0 to 32.1% (Fig. 2). The Rotaliida, the most abundant family, fluctuate between 21.4% and 100% except for sample 178.0 mbsf where no taxa belonging to this family are recorded (Fig. 2). The second most abundant family is the Lagenida that ranges from 11.1% and 57.1% (Fig. 2), and is absent in some samples (81.83 mbsf, 91.40 mbsf, 101.22 mbsf, 120.51 mbsf, 121.37 mbsf, 130.16 mbsf, 178.30 mbsf). Textulariina are less abundant varying from 3.7 to 26.9%, except in sample 178. 30 msbf where they compose the 100% of the assemblage (Fig. 2).

4.2.2 ODP Holes 1213A and 1213B

Benthic foraminiferal number fluctuates between 0 and 10928/10g (Fig. 2). In the Hauterivian interval, a sharp increase in the BFN reaching 5506/10g (267.10 mbsf) is opposite to the absence of benthic foraminifera in sample 266.57 mbsf (Fig. 2). Benthic foraminifera are also absent in some samples of the Aptian and Albian interval (samples 257.92 mbsf, 192.27 mbsf, 179.60 mbsf, 160.30 mbsf, 143.10 mbsf). A slight increase in the BFN is recorded in sample 248.23 mbsf (1226/10g) in the Aptian. During the Albian, the BFN ranges from 53/10g (199.30 mbsf) to 10928/10g (238.61 mbsf). The values of H_S display ranges from 0.9 to 2.7 in samples 123.90 mbsf and 189.30 mbsf respectively (Fig. 2). The calcareous foraminifera are the most important group in the studied samples, fluctuating from 59.4% to 100% (Fig. 2). In turn, the agglutinated foraminifera display abundances between 0 to 40.5% (Fig. 2).

The Rotaliida is the most abundant family fluctuating between 8.1% and 100% (Fig. 2), followed by the Lagenida and Textulariina, which ranges from 9.2% and 66.6% and 32% and 40.5% respectively, except in sample 189.30 mbsf, where no taxa belonging to these families have been observed (Fig. 2). The Textulariina is the less abundant family reaching maximum values of 36.1% (Fig. 2).

4.3 Benthic foraminiferal assemblages

A total of 26 genera and 36 species of benthic foraminifera have been identified in ODP holes 1207B, 1214A, 1213A and 1213B spanning the Hauterivian - Albian interval (Figs. 3 A, B). Benthic foraminifera belonging to Rotaliina, Lagenina and Textulariina are assigned to 19 families following the classification by Loeblich and Tappan (1987). The Rotaliina are well represented (mean abundance of 46.38%) in the assemblages with the continuous presence and relative high abundance of Gavelinellidae (*Gavelinella*, *Gyroidinoides*), Osangulariidae (*Osangularia*), and Pleurostomellidae (*Pleurostomella*). The second most abundant group is the Lagenina (mean abundance of 38.16%), which is dominated by Nodosariidae (*Dentalina*, *Laevidentalina*), Vaginulinidae (*Astacolus*, *Lenticulina*), and Polymorphinidae (*Globulina*). The Textulariina are less abundant (mean abundance of 15.46%) and the assemblages are characterized by Eggerellidae (*Marssonella*) and Verneulinidae (*Gaudryina*).

The distribution of the most abundant benthic foraminiferal taxa is described below (Figs. 3A, B and 4A, B). The abundances in terms of suborders and families of the benthic foraminiferal assemblages expressed as BFN are given in the Supplementary Data Table 1.

4.3.1 ODP Hole 1207B

The dominant species in the Barremian interval is *Gavelinella barremiana* that shows an increase in abundance from 45/10g to 592/10g. *Globulina prisca* that displays an increase in abundance from 2/10g to 551/10g during the Barremian shows a major decrease in abundance during the Aptian and Albian (from 46/10g to 6/10g). *Astacolus calliopsis* records an increase in abundance up to 248/10g in the Barremian followed by a marked decrease to 21/10 in sample 526.50 mbsf (Aptian). *Lenticulina muensteri* varies from 2/10g to 207/10g (Barremian) and decreases in abundance through the Aptian and Albian to 12/10g to 11/10g, respectively. *Marssonella subtrochus* is recorded only in the Barremian fluctuating from 45/10g to 282/10g. *Gavelinella intermedia* varies from 17/10g and 758/10g in the Aptian. During the Albian, the abundance values of *G. intermedia* range from 21/10g to 664/10g. Taxa as *Gyroidinoides infracretaceus*, *Gyroidinoides* sp., and *Pleurostomella* sp. display low abundances during the Aptian (5/10g, 7/10g, 2/10g, respectively), and *G. infracretaceus* increases in abundance up to 664/10g in the Albian. Taxa recorded only in the Albian as *Clavulina gaultina* (from 1/10g to 332/10g), *Fissurina* sp. (from 1/10g to 332/10g), and *Tritaxia pyramidata* (from 1/10g to 664/10g) display high abundances. *Pleurostomella reussi* displays increase in abundance up to18/10g.

4.3.2 ODP Hole 1214A

In the Hauterivian, Barremian, and in most part of the Aptian interval, the studied samples are barren of benthic foraminifera. *Gavelinella barremiana* is the dominant taxon during the Aptian (in sample 197.6 mbfs), reaching abundance values up to 230/10g. *Fursenkoina viscida and Astacolus* sp. recorded low abundances of 38/10g.

In the Albian interval, *Osangularia insigna* displays abundances ranging from 2/10g to 268/10g. In addition, *Gaudryina dividens* (from 26/10g to 508/10g), *G. intermedia* (from 10/10g to 375/10g), *G. infracretaceus* (from 38/10g to 482/10g) show high abundances during this time interval. Taxa as *Dentalina* sp. (from 26/10g to 105/10g), *Ellipsodimorphina* sp. (from 19/10g to 88/10g), *G. prisca* (from 94/10g to 129/10g), *Gyroidinoides nitida* (from 72/10g to 150/10g), *Gyroidinoides* sp. (from 26 /10g to 94/10g), *Praebulimina elata* (from 34/10g to 89/10g), and *Valvulineria gracillima* (from 33/10g to 94/10g) are characterized by intermediate to low abundances.

4.3.2 ODP Holes 1213A and 1213B

The Hauterivian benthic foraminiferal assemblages are characterized by taxa as *Lenticulina grata* (from 31/10g to 446/10g), *Marssonella praeoxycona* (up to 595/10g), *M. subtrochus* (from 8/10g to 1637/10g), and *Vaginulinopsis schloenbachi* (up to 298/10g) with the latter two that are the most common and abundant. The Aptian is marked by low to intermediate abundances of taxa as *Astacolus calliopsis* (up to 40/10g), *Dentalina* sp. (up to 198/10g), *G. intermedia* (up to 119/10g), *G. prisca* (up to 119/10g), *L. muensteri* (up to 119/10g), and *Pleurostomella* sp. (up to 79/10g).

In the Albian, high abundance values are recorded for *G. dividens* (from 4/10g to 1068/10g), *G. intermedia* (from 12/10g to 2930/10g), *G. infracretaceus* (from 7/10g to 2350/10g), *O. insigna* (from 5/10g to 1435/10g). Intermediate to low abundances are characteristic of taxa as *Dentalina* sp. (from 19/10g to 239/10g), *Ellipsodimorphina* sp. (from 3/10g to 122/10g), *F. viscida* (from 1/10g to 202/10g), *Gyroidinoides* sp. (from 3/10g to 305/10g), *T. pyramidata* (from 18/10g to 305/10g), and *V. gracillima* (from 14/10g to 519/10g).

4.4 Stratigraphic distribution of benthic foraminifera at Shatsky Rise

The stratigraphic distribution of selected benthic foraminifera from ODP holes 1207B, 1214A, 1213A, and 1213B are illustrated in Figs. 3A, B. Some of the analyzed taxa show the same stratigraphic distribution at the three sites, while other taxa were found in only one or two sites. Possible explanations could be related to: a) low recovery of sediments at the three sites (ODP 1207, 1214, and 1213), b) Hauterivian sediments are recorded only at holes 1214A and 1213B, while Barremian sediments are only recovered at Hole 1207B, c) specific geographic locations, recording different taxa between the Shirshow Massiv (Hole 1207B) and Tamu Massif (holes 1214B, 1213A, and 1213B), and d) many samples are barren, especially in the Hauterivian and Aptian stratigraphic intervals.

Although most of the taxa recorded are known to have a wide stratigraphic distribution from the Jurassic Period to modern times as documented in the literature (Ellis and Messina, 1942-2015; Loeblich and Tapan, 1987; Holbourn, 1996; Supplementary Data Figure S1), some taxa are characterized by having their first and last occurrences levels (FOs and LOs, respectively) within the Hauterivian - Albian interval, allowing the recognition of the most important benthic foraminiferal events of the Early Cretaceous, which are widely correlatable.

In the Hauterivian, taxa as *Astacolus* sp., *Astacolus planiusculus*, *Astacolus scitula*, *Citharina* sp., *Dentalina* sp., *Dentalina cylindroides*, *Ellipsodimorphina* sp., *G. prisca*, *Lagena* sp., *Lenticulina grata*, *M. praeoxycona*, *M. subtrochus*, *Saracenaria* sp., and *V. schloenbachi* were exclusively recorded at ODP Site 1213. According to the literature, three events, namely the FOs of *D. cylindroides*, *M. praeoxycona* and *M. subtrochus* were observed during the Hauterivian (Fig. 3A; Supplementary Data

Figure S1).

The Barremian interval is characterized by the occurrence of the following taxa *Astacolus calliopsis*, *Dentalina nana*, *Dentalina communis*, *Gavelinella* sp., *G. barremiana*, *Globulina* sp., *Lenticulina* sp., *Lenticulina subalata*, *Lenticulina turgidula*, *Marginulina linearis*, *Marssonella oxycona*, *Nodosaria* sp., *Pseudonodosaria humilis*, and *Pyrulina cylindroides*. Within this group four biostratigraphic events were recognized during the Barremian: the FOs of *Gavelinella* sp., *G. barremiana*, *M. linearis*, and *P. cylindroides* (Fig. 3A; Supplementary Data Figure S1).

Taxa as *Bathysiphon brosgeri*, *Fissurina* sp., *F. viscida*, *Gaudryina* sp., *G. dividens*, *Gaudryina gradata*, *G. intermedia*, *Gyroidinoides* sp., *G. infracretaceus*, *L. muensteri*, *Marginulina* sp., *Marssonella kummi*, *Pleurostomella* sp., *Pseudonodosaria* sp., *Ramulina* sp., *Spiroplectammina* sp., and *V. excentrica* are observed in the Aptian at Shatsky Rise. Some significant biostratigraphic events were identified during the Aptian: the FOs of *G. dividens*, *G. intermedia*, *Gyroidinoides* sp., and *G. infracretaceus* and the of *G. barremiana* and *M. praeoxycona* (Fig. 3B; Supplementary Data Figure S1).

The Albian assemblages are characterized by the presence of *C. gaultina*, *Eponides* sp., *Globorotalites* sp., *Guttulina* sp., *G. nitida*, *Lingulina* sp., *Marginulina inaequalis*, *O. insigna*, *P. reussi*, *Pleurostomella subnodosa*, *Praebulimina* sp., *P. elata*, *Pyrulina* sp., *T. pyramidata*, *Vaginulina* sp., and *V. gracillima*. The following biostratigraphic events were recorded during the Albian: the FOs of *C. gaultina*, *Eponides* sp., *Globorotalites* sp., *O. insigna*, *P. reussi*, *P. elata*, and *V. gracillima* and the LOs of *F. viscida*, *G. dividens*, *G. gradata*, *L. grata*, *L. Turgidula*, *M. inaequalis*, *M. linnearis*, *M. kummi*, *P. elata*, *V. excentrica*, *V. schloenbachi*, and *V. gracillima* (Fig. 3A, B; Supplementary Data Figure S1).

5. Discussion

5.1 Paleobathymetric evolution of Shatsky Rise

Reconstruction of the Shatsky Rise paleobathymetry during the Cretaceous using benthic foraminiferal assemblages is based on comparisons with modern benthic data and on the statistical analysis of the assemblages of paleo-slopes, opposite to the depths estimated from backstripping (e.g. Sliter and Baker, 1972; Sikora and Olsson, 1991; Holbourn et al.,2001a).

Some of these methods for reconstructing the paleobathymetry, such as backtracking methods and estimation using micro and macro-fauna (e.g., benthic foraminifera, mollusks), have been previously applied to the Cretaceous sedimentary sections recovered at ODP and DSDP sites drilled on Shatsky Rise, Hesse Rise and the Mid-Pacific Mountains (Fig. 1B; Table. 1). In the attempt to improve the understanding of the paleobathymetric changes of the Shatsky Rise during the Lower Cretaceous, the occurrence of benthic foraminifera observed in this study, provides new insights into the composition of the deep-water assemblages, which were not documented by the Shipboard Scientific Party (2002a, b, c).

Although several benthic foraminifera display a relatively wide paleo-depth range typical of neritic and/or bathyal environments (Fig. 5A), some marker species and particular benthic foraminiferal assemblages are used to determine specific paleobathymetrical setting. Outer neritic settings are characterized by the increase in abundance of Lagenina (e.g., *Planularia*, *Citharina*, and *Astacolus*), Textulariina (e.g., *Dorothia*, *Marssonella*, *Gaudryina*, *Spiroplectinata*, *Spiroplectinella*, and *Clavulinoides*) and by less abundant rotaliids (e.g., *Praebulimina* and *Neobulimina*) which can vary in abundance according to the paleoenvironmental condition of the basin (Sliter and Baker, 1972; Nyong and Olsson, 1984; Sikora and Olsson, 1991).

The upper and middle bathyal environments are generally represented by common to abundant benthic foraminifera belonging to the suborders Rotaliina and common Textulariina, and especially *Osangularia* and *Gyroidinoides*, and siliceous agglutinated foraminifera, such as, *Bathysiphon* and

Rhizammina (Sliter and Baker, 1972; Nyong and Olsson, 1984; Sikora and Olsson, 1991; Koutsoukos and Hart, 1990). In turn, the lower bathyal environments are characterized by assemblages that contain abundant Rotaliina and abundant Textulariina (Sliter and Baker, 1972; Sliter, 1977a; Holbourn et al., 2001a).

According to the increase of the suborders of benthic foraminifera found at ODP sites 1207, 1214, and 1213 the data set reveals a paleobathymetric trend towards deepening of the sites during the Early Cretaceous (Fig. 5B). Specfically, an increase in abundance of Lagenina followed by the Textulariina was evidenced in the Barremian and Hauterivian, whereas the Rotaliina displayed a considerable increase in abundance during the Aptian and Albian. Similar increases and decreases in the abundance of taxa belonging to these suborders were previously described in the Cretaceous assemblages by Sliter and Baker (1972) and Holbourn et al. (2001a) in the Pacific and the Atlantic Ocean, respectively.

5.1.1 Hauterivian

The benthic foraminiferal assemblages at ODP holes 1213A and 1213B of the Hauterivian interval are composed by Lagenina (*Astacolus*, *Lenticulina*, *Vaginulinopsis*) and Textulariina (*Marssonella*) (Fig. 2). These taxa have a wide paleobathymetrical range thriving in neritic and bathyal environments (Fig. 5A). However, since the aforementioned foraminiferal assemblages are marked by abundant Lagenina with some increase of Textulariina taxa, which are typical of outer neritic setting (Sliter and Baker, 1972), an outer neritic setting (100 - 200 m) is here suggested for the Shatsky Rise during the Hauterivian.

Hauterivian benthic foraminifera (e.g., *Astacolus*, *Citharina*, *Dentalina*, *Frondicularia*, *Laevidentalina*, *Lenticulina*, *Planularia*, *Psilocitharella*, *Saracenaria*, and *Vaginulinopsis*) and ostracods recorded at IODP Site U1346, which is located at the Shirshov Massif close to ODP Hole

1207B, have been interpreted by thrived in an inner neritic setting shallower than 20 m (Yasuhara et al., 2017).

In this study, an outer neritic setting (100 - 200 m) is inferred for the Tamu Massif (ODP holes 1213A and 1213B; Fig. 5B), contrasting with the inner neritic (<20m) setting suggested for the Shirshov Massif during the Hauterivian (Yasuhara et al., 2017).

5.1.2 Barremian

The benthic foraminiferal assemblages at ODP Hole 1207B display an increase in abundance of the suborders Lagenina (*Astacolus*, *Dentalina*, *Globulina prisca*, *Lenticulina*) and a decrease in abundance of suborder Rotaliina (*Gavelinella barremiana*) and Textulariina (*Marssonella*) (see Fig. 2). Sliter and Baker (1972) observed that the major increase of Lagenina in the assemblages is related to outer neritic and slope settings. Taxa as *G. barremiana*, *G. prisca*, *Lenticulina*, *Astacolus*, and *Marssonella* have been considered by inhabiting different environments (Fig. 5A) but are especially found in shelf and slope settings (Riegraf, 1989; Koutsoukos, 1989; Frenzel, 2000; Holbourn and Kuhnt, 2001; Holbourn et al., 2001a; Giraldo-Gómez et al., 2018). According to the aforementioned benthic foraminiferal assemblages, an outer neritic-upper bathyal setting (200 - 500 m) is inferred for ODP Hole 1207B during the Barremian (Fig. 5B).

5.1.3 Aptian

During the Aptian, an increase in palaeodepth is reconstructed for Shatsky Rise holes 1207B, 1214A, 1213A, and 1213B (Fig. 5B). The Rotaliina are the dominant taxa (*G. barremiana*, *G. intermedia*, *Gyroidinoides*, *O. insigna*) associated to the Lagenina (*Astacolus*, *Dentalina*, *Globulina prisca*, *Lenticulina*), indicating a deepening in the Tamu and Shirshov Massif (Fig. 2). The increase in abundance of *G. barremiana* especially in Hole 1214A, of *G. intermedia* in Hole 1207B, and the slight increase in abundance of *O. insigna*, *G. prisca*, and *Gyroidinoides* allow inferring a depositional middle bathyal setting (500 - 1000 m) during the Aptian for the three studied sites (Fig. 5B).

5.1.4 Albian

During the Albian, a deepening of the Shatsky Rise paleodepth, is evidenced at ODP holes 1207B, 1214A, 1213A and 1213B. This is based on a continuous increase of the suborder Rotaliina (*G. intermedia*, *O. insigna*, *Pleurostomella*, *V. gracillima, G. infracretaceus*) that reaches more than the 60% of the benthic foraminiferal assemblages in the Albian (Fig. 2), whereas the Lagenina (*Dentalina*, *G. prisca*) and Textulariina (*C. gaultina*, *Gaudryina*, *T. pyramidata*) suborders are less abundant (Fig. 2). The most abundant taxa *G. intermedia*, *O. insigna*, and *Gyroidinoides* are characteristics of deeper waters (e.g., Sliter and Baker, 1972; Nyong and Olsson, 1984; Sikora and Olsson, 1991), thus an inferred paleobathymetry of lower bathyal (1000 - 2000 m) is suggested for the Albian interval at the three Shatsky Rise sites (Fig. 5B).

5.2 The Pacific benthic foraminiferal bioprovince at Shatsky Rise compared to the worldwide bioprovinces

Paleobiogeography is defined as the study of the geographical distribution of faunas and floras in the past, estimating extinction events and species ranges in a determinate geographical space. The biogeographical distribution of the fossils as well as of the recent benthic foraminiferal assemblages are controlled by the environmental conditions, such as salinity, temperature, oxygen availability, and nutrient supply, which modify the water-mass conditions of the oceans (e.g., Widmark and Malmgren, 1992; van der Zwaan et al., 1999; Murray, 2006; Jorissen et al., 2007; Gooday and Jorissen, 2012). In turn, the variation in the diversity (Shannon-Weaver (H_S) and species richness) of benthic foraminifera shows changes in the distribution of typical species in diverse environments, increasing diversity from shelf to deep sea (Buzas and Culver 1989; Murray, 2007). At Shatsky Rise, the values of Shannon-Weaver range between 1 and > 2 (Fig. 2), indicating the presence of relative well-diversified benthic foraminiferal assemblages (especially in ODP holes 1207B, 1213A, and 1213B). In turn, the Shannon-Weaver values recorded at ODP Hole 1214A fluctuate from 0 and 2 (Fig. 2), suggesting less diversified assemblages.

In the paleobiogeographical review performed in this study, we compare 35 species recorded at Shatsky Rise (Fig. 6) with records from different biogeographic provinces during the Early Cretaceous (see Fig. 6 for further information and references). The examined bioprovinces are: the Atlantic Ocean (western central Atlantic, eastern central Atlantic, south Atlantic and north Atlantic), Western Tethys, Boreal Realm, Indian Ocean and Antarctica. Most of the revised onshore sections, ODP and DSDP sites were located in deep-water settings, according to benthic foraminiferal reconstructions (see description of the onshore sections and ODP and DSDP sites in Fig. 6).

Most studies of benthic foraminifera occurring in the Pacific Ocean only describe taxa at genus level (e.g., Bralower et al., 2002; Sager et al., 2010). An exception is the detailed study of the Lower Cretaceous of the Shatsky Rise (DSDP sites 305 and 306) published by Luterbacher (1975) who described most of the taxa also observed in the present study.

Benthic foraminiferal records from other localities include the works of: i) Bartenstein (1976, 1985, 1987) and Bolli et al. (1994) that reported the correlation between species from northwest Germany (Boreal Bioprovince) and Trinidad (Atlantic Bioprovince) during the Early Cretaceous. ii) Koutsoukos and Klasz (2000) who reported the existence of the Brazilian-Caribbean-Gulf Coast Province where benthic foraminifera had a close affinity with species from the Austral Realm, the Boreal and NE Tethyan Realm during the Late Cretaceous. iii) The detailed study by Holbourn et al. (2001a) on the distribution of benthic foraminifera in the Atlantic Ocean, which shows the affinity among species from the Atlantic Ocean and the Western Tethys during the late Albian.

However, in many studies, a species is described with different names in distant regions, thus taxonomy is revised in this study (see taxonomic appendix) in order to produce a comprehensive review and overcome the synonym problems that hamper the understanding of the real geographical extent of several species through the geological record (e.g., Berggren and Aubert, 1975; van Morkhoven et al., 1986; Widmark and Malmgren, 1992).

In our review, very few species were observed to occur in all bioprovinces during the Hauterivian (Fig. 5B). Out of 8 species observed at Shatsky Rise (*L. grata*, *M. subtrochus*, *D. cylindroides*, *V. schloenbachi*, *A. scitula*, *M. praeoxycona*, *A. planiusculus*, *G. prisca*) only *G. prisca* is documented in the Indian Ocean during the Hauterivian (Figs. 6, 7A). This could be explained by the fact that sediments in ODP holes 1213A and 1213B were deposited in a shallow-water environment.

The Barremian interval recorded at ODP Hole 1207B and at DSDP sites 305 and 306 display 12 species that also occur in the Atlantic Bioprovince (*M. praeoxycona*, *G. prisca*, *P. cylindroides*, *L. turgidula*, *D. communis*, *D. nana*, *G. barremiana*, *A. calliopsis*, *L. subalata*, *M. kummi*, *L. muensteri*, *T. pyramidata*), six species that are common with the Western Tethys Bioprovince (*A. planiusculus*, *L. turgidula*, *M. oxycona*, *G. barremiana*, *L. muensteri*, *T. pyramidata*), and only 4 species that are found in the Boreal Bioprovince (*A. scitula*, *M. praeoxycona*, *D. communis*, *G. barremiana*) (Figs. 6, 7A). The Aptian was marked by a larger number of cosmopolitan taxa, with 17 species recorded at both Shatsky Rise and in the Atlantic Bioprovince (*L. grata*, *M. subtrochus*, *M. praeoxycona*, *G. Prisca*, *L. turgidula*, *D. communis*, *G. barremiana*, *A. calliopsis*, *M. linearis*, *M. kummis*, *G. dividens*, *G. intermedia*, *G. gradata*, *G. infracretaceus*, *L. muensteri*, *V. excentrica*, *T. pyramidata*). In turn, 13 and 12 common species were documented in the Western Tethys and Boreal bioprovinces, respectively (Figs. 6, 7A).

The group of cosmopolitan taxa (27 species) found in the Pacific Bioprovince (Shatsky Rise) and the Atlantic Bioprovince increased during the Albian and includes typical species such as *L. grata*, *M.*

subtrochus, *D. cylindroides*, *V. schloenbachi*, *A. scitula*, *M. praeoxycona*, *G. prisca*, *D. communis*, *M. oxycona*, *A. planiusculus*, *A. calliopsis*, *G. dividens*, *G. intermedia*, *G. gradata*, *F. viscida*, *G. infracretaceus*, *L. muensteri*, *V. excentrica*, *B. brosgei*, *T. pyramidata*, *P. elata*, *P. subnodosa*, *V. gracillima*, *O. insigna*, *P. reussi*, *C. gaultina*, *M. inaequalis* (Figs. 6, 7A). Moreover, in the Albian interval, the Boreal and Western Tethys bioprovinces display a decrease of common taxa (13 species) with respect to the Pacific Bioprovince (Figs. 6, 7A).

The Pearson correlation based on 35 species recorded in Shatsky Rise (Pacific Bioprovince) displays different degrees of affinity with the common species observed in the biogeographic provinces worldwide (Atlantic Ocean, Western Tethys, Boreal, Indian Ocean, and Antarctica; Figs. 7 A, B). An increase in number of species occurring in both the Pacific and the Atlantic bioprovinces is observed for the Barremian - upper Albian interval (Fig. 7A), and the high positive value of the Pearson correlation coefficients, suggest a clear affinity of the benthic foraminifera between the Pacific and Atlantic Ocean (Fig. 7B). Although the number of the species in common between the Shatsky Rise and the Boreal bioprovinces is not very high, the strong positive correlation indicates a high degree of affinity between the two bioprovinces (Fig. 7B). Conversely, a weaken affinity of benthic foraminifera of the Shatsky Rise and the Western Tethys bioprovinces is evidenced by the low positive correlation (Fig. 7B). A weak relationship is also reported with the taxa from Antarctica, while a high negative correlation is displayed with the Indian Bioprovince (Fig, 7B). These results suggest that the species occurring at the Shatsky Rise had no affinity with the assemblages of the Indian Ocean and the Antarctica bioprovinces. Conversely, there was a stronger relationship between the benthic foraminifera from the Pacific and the Atlantic Ocean. This datum corroborates the study by Widmark and Malmgren (1992) who observed the occurrence of the same species in both the Pacific (Hess Rise: DSDP Site 465) and Atlantic oceans (South Atlantic: DSDP Sites 356, 516, 525, 527; North Atlantic: DSDP Site 384) during the Late Cretaceous.

5.3 The cosmopolitan distribution of benthic foraminifera during the Lower Cretaceous

Species that have a widespread geographic distribution in a specific time interval are considered cosmopolitan. It is especially debated if the cosmopolitan modern benthic foraminifera are more abundant in deep-water settings or in shallow environments (e.g., Murray, 2006; Gooday and Jorissen, 2012). Several studies report endemic species mainly distributed in coastal and sublittoral settings, while other studies document cosmopolitan taxa distributed widely in bathyal and abyssal environments (Gooday and Jorissen, 2012). The results of this study confirm that most deep-water benthic foraminifera were cosmopolitan during the Mesozoic and Cenozoic (e.g., Berggren and Aubert, 1975; van Morkhoven et al., 1986; Koutsoukos, 1992; Widmark and Malmgren, 1992; Koutsoukos and de Klasz, 2000; Holbourn and Kuhnt, 2000; Holbourn et al., 2001a).

The Cretaceous benthic foraminiferal taxa recovered at Shatsky Rise show a clear pattern of progressive diversification from the Barremian to the Albian (Figs. 3A, B). Probably, based on a successful dispersal mode, these species were capable of crossing all barriers to occupy ecological niches located at different latitudes and diverse biogeographic provinces: Pacific Ocean (Shatsky Rise), Atlantic Ocean (including western central Atlantic, eastern central Atlantic, south Atlantic, and north Atlantic), Western Tethys, Indian Ocean, Boreal and Antarctica (Fig. 6).

Most of the 35 species documented in the Pacific Ocean were described in at least one additional bioprovince. Among the most important species of benthic foraminifera of the Early Cretaceous (from Hauterivian to Albian), *L. muensteri* is the only species occurring in the six bioprovinces (Fig. 6). Species such as *G. prisca*, *D. communis*, *G. barremiana*, *A. calliopsis* and *G. intermedia* are documented in five bioprovinces (Pacific Ocean, Atlantic Ocean, Western Tethys, Indian Ocean, and Boreal; Fig. 6). *Gavelinella barremiana* is an important stratigraphic marker of the Barremian that occurs in five bioprovinces (Pacific Ocean, Atlantic Ocean, Western Tethys, Indian Ocean, and Boreal), while for the Aptian interval it is recorded in four bioprovinces (Pacific Ocean, Atlantic Ocean, Western Tethys and Boreal). *Gavelinella intermedia* is documented in only four bioprovinces (Pacific Ocean, Atlantic Ocean, Western Tethys and Boreal) in the Aptian, whereas it is recorded in five bioprovinces in the Albian (Pacific Ocean, Atlantic Ocean, Western Tethys, Indian Ocean, and Boreal; Fig. 6). On the other hand, *M. subtrochus*, *L. turgidula*, *M. oxycona*, *G. dividens*, *G. gradata*, *G. infracretaceus*, *B. brosgei*, *T. pyramidata*, *V. gracillima*, *P. reussi*, and *M. inaequalis* were observed in four bioprovinces. For example, *G. infracretaceus* and *B. brosgei* are documented in the Aptian - Albian and Hauterivian - Albian intervals, respectively, in the Pacific Ocean, Atlantic Ocean, Western Tethys and Indian Ocean, but not in the Boreal Bioprovince (Fig. 6). Species as *L. grata*, *D. cylindroides*, *A. scitula*, *A. planiusculus*, *M. praeoxycona*, *M. kummi*, *F. viscida*, *V. excentrica*, *P. elata* and *C. gaultina* are documented in three bioprovinces (Fig. 6). The remaining recorded species were only observed in the Pacific and Atlantic bioprovinces (*V. schloenbachi*, *P. cylindroides*, *D. nana*, *M. linearis*, *L. subalata*, *P. subnodosa*, and *O. insigna*) except *G. nitida*, which is documented in the Pacific Ocean and Western Tethys (Fig. 6).

The existence of several cosmopolitan benthic foraminifera suggests the connection between the Pacific Ocean and one other or more bioprovinces. Assuming that many benthic foraminiferal species are widely distributed in different bioprovinces, the main question is: how was their dispersal achieved during the Early Cretaceous?

Indeed, the very large scale of geographic distribution of some benthic foraminifera implies prolonged migrations over large distances. According to different studies of modern benthic foraminifera, most species have excellent dispersive capacities, by means of microbe-sized propagules, which can remain viable for several years (Alve and Goldstein, 2010; Gooday and Jorissen, 2012). In turn, propagules of deep-water benthic foraminifera are optimal dispersers, characterized by a genetic homogeneity observed worldwide, that is not recorded in planktonic foraminifera and shallow-water benthic foraminifera (Pawlowski et al., 2007; LeCroq et al., 2009; Alve and Goldstein 2010). Species, either adults or juveniles or tiny propagules, are transported by thermohaline and other oceanic currents, which have the potential to genetically link distant populations. If individuals adapt to new environments and are able to reproduce, then the cycle continues (Berggren and Aubert, 1975; Alve, 1999, Murray, 2006; Pawlowski et al., 2007; Alve and Goldstein, 2010; Gooday and Jorissen, 2012).

From the Early Cretaceous (Hauterivian) until the Late Cenozoic (Pliocene), there was a relatively unrestricted flow between the Atlantic Ocean and the Pacific Ocean via the Straits of Panama, which could have generated a warm-water circum-equatorial current (Berggren and Hollister, 1977). Furthermore, the Arctic Ocean was connected to the Pacific Ocean through the South Anyui Ocean Gulf until the Albian, then this seaway closed and the Arctic Ocean became isolated (Mutterlose et al., 2003b; Hay, 2008). Surface waters along the South Pacific Antarctic suggest connections along the proto-Drake Passage during the Barremian to Albian time interval (Sewall et al., 2007; Eagles, 2016; Dummann et al., 2020). This connection between the South Atlantic and Southern Ocean is evidenced by the temporal evolution of seawater neodymium isotope, indicating a continuous water mass exchange between the Pacific and Southern Ocean (Dummann et al., 2020).

Many species found either at Shatsky Rise and in other bioprovinces show no preference for any particular ocean or paleo-latitude and may have benefited from the prevailing oceanic circulation in the Early Cretaceous by means of currents to populate the diverse bioprovinces. However, these cosmopolitan species showed a clear preference for deep-water settings as observed in different studies (e.g., Widmark and Malmgren, 1992; Bolli et al., 1994; Koutsoukos and Klasz, 2000; Holbourn et al., 2001a) and as evidenced by the benthic foraminiferal assemblages occurring at Shatsky Rise in the Early Cretaceous.

6. Conclusions

The study of the benthic foraminiferal assemblages in ODP holes 1207B, 1214A, 1213A and 1213B provided a good documentation of taxa occurring in the lower Hauterivian to the upper Albian interval of the Pacific Ocean.

- The thorough taxonomic revision of benthic foraminifera recorded at Shatsky Rise allows the verification of the stratigraphic ranges of several taxa including first and last appearance datums. On this basis, false endemism and stratigraphic ranges has been detected.
- The abundance and composition of the benthic foraminiferal assemblages recorded in the Shatsky Rise sedimentary record confirmed a progressive deepening of the Shirshov and Tamu Massif of the Shatsky Rise during the Early Cretaceous. In Hauterivian sediments, recovered only at ODP Site 1213, benthic foraminifera reveal an outer neritic setting (100 - 200 m). According to the benthic foraminiferal assemblages, an upper bathyal setting (200 - 500 m) is reconstructed for ODP Hole 1207B during the Barremian. A middle bathyal environment (500 - 1000 m) is interpreted for ODP holes 1207B, 1214A, 1213A, and 1213B during the Aptian. Finally, a deepening to a lower bathyal setting (1000 - 2000 m) is registered according to the composition of the benthic foraminiferal assemblages during the Albian.
- Variable affinity grades are evidenced between the cosmopolitan benthic foraminifera recorded at Shatsky Rise and the taxa documented worldwide in different bioprovinces in the Barremian - Albian interval. In particular, a strong faunal affinity between the taxa recorded at Shatsky Rise and in the Atlantic Ocean was observed. Differently, the Boreal and the Western Tethys bioprovinces display good and weak faunal affinity with the taxa recorded at Shatsky Rise, respectively. Finally, the benthic foraminiferal assemblages documented at Shatsky Rise show a minor relationship with the taxa reported from the Indian Ocean Bioprovince and have almost no correspondence with the Antarctic Bioprovince

- Differences between the benthic foraminiferal assemblages occurring at Shatsky Rise and those documented from other bioprovinces are mainly related to geographical distance and paleobathymetry. The cosmopolitan benthic foraminifera probably benefited from the ocean circulation patterns allowing them to populate different bioprovinces, without no preference for any particular ocean or paleo-latitudes.
- Data presented in this study demonstrate that the Pacific Ocean, as registered at Shatsky Rise, had full connections with other worldwide oceans, especially with the Atlantic Ocean, as proved by the presence of cosmopolitan taxa during the Early Cretaceous.

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Figures

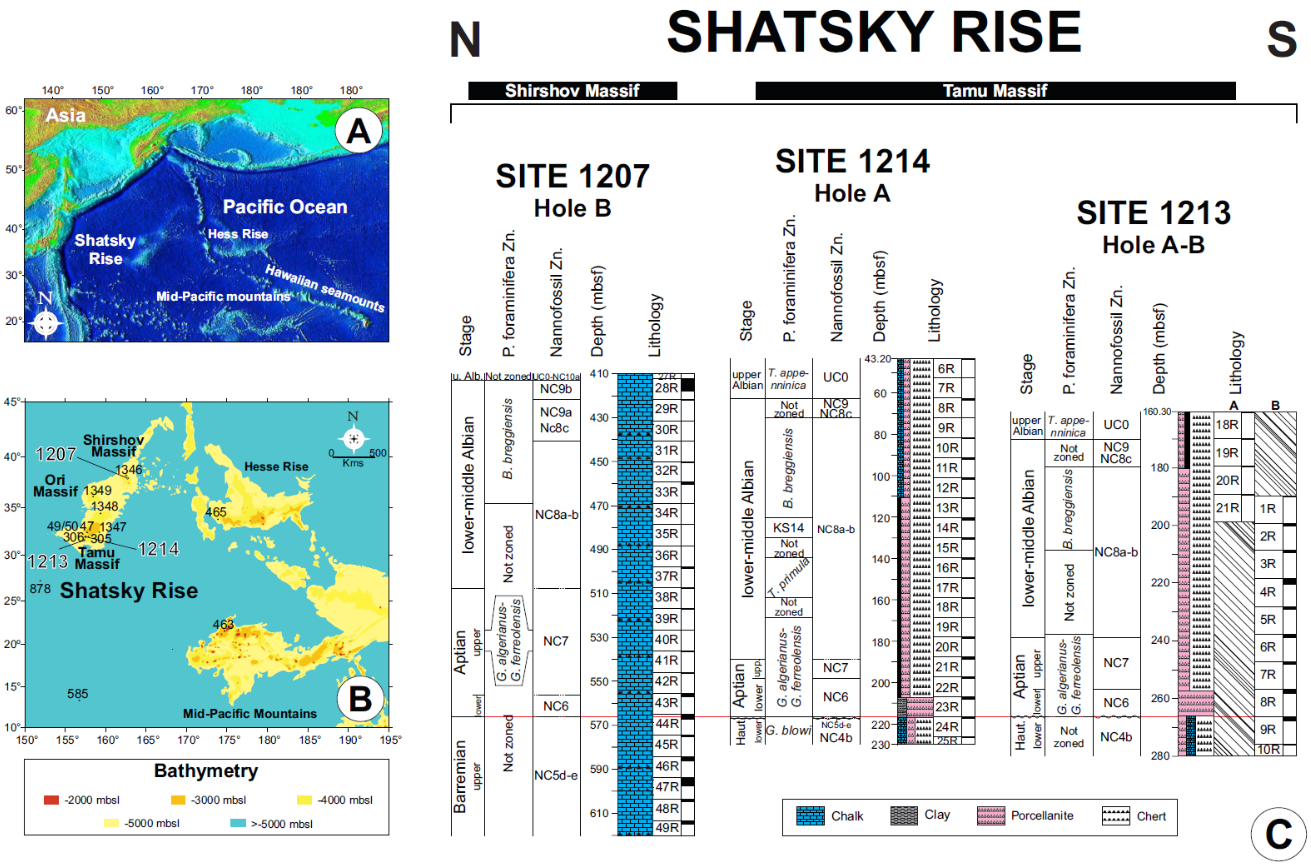


Fig 1. A. Location of Shatsky Rise in the central Pacific Ocean (modified from https://www.ngdc.noaa.gov/mgg/image/globalimages.html). **B.** Bathymetric map showing Shatsky Rise, Hesse Rise and the Mid-Pacific Mountains (modified from Rea and Vallier, 1983; Bralower, et al., 2002; Klaus and Sager, 2002). Location of ODP sites 1207, 1214 and 1213. **C.** Age, biostratigraphy, core recovery and lithology of ODP holes 1207B, 1214A, 1213A and 1213B (Shipboard Scientific Party, 2002a, b, c). Biostratigraphy of calcareous nannofossil according to Bown (2005), planktonic foraminifera from this study.

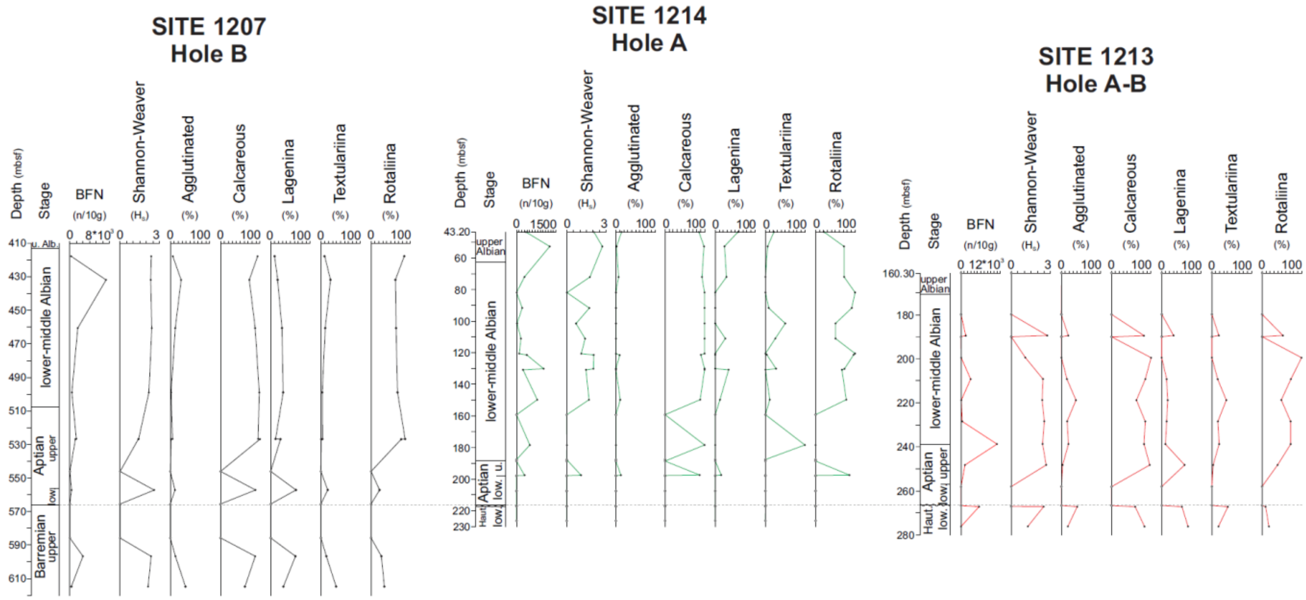
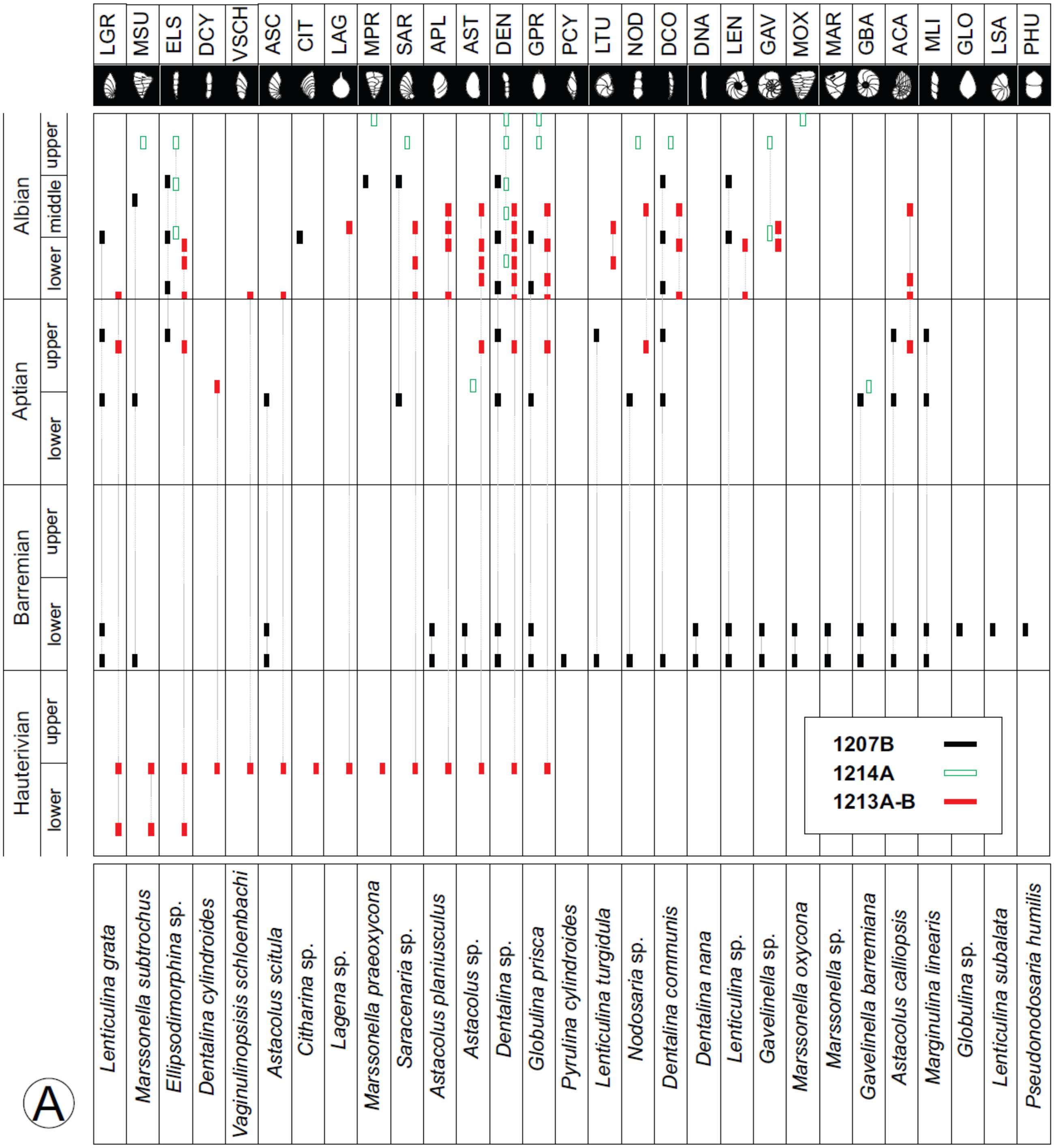


Fig. 2. Benthic foraminiferal distribution in the upper Hauterivian-Albian interval of the Shatsky Rise (ODP sites 1207, 1214 and 1213). Benthic foraminifera number (BFN: n/10g), Shannon-Weaver index (H_S), percentage of agglutinated and calcareous benthic foraminifera. Percentage of suborders of benthic foraminifera: Lagenina, Textulariina and Rotaliina.


A
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Barremian
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Lenticulina grata
Marssonella subtrochus
Ellipsodimorphina sp.
Dentalina cylindroides
Vaginulinopsisis schloenbachi
Astacolus scitula
Citharina sp.
Lagena sp.
Marssonella praeoxycona
Saracenaria sp.
Astacolus planiusculus
Astacolus sp.
Dentalina sp.
Globulina prisca
Pyrulina cylindroides
Lenticulina turgidula
Nodosaria sp.
Dentalina communis
Dentalina nana
Lenticulina sp.
Gavelinella sp.
Marssonella oxycona
Marssonella sp.
Gavelinella barremiana
Astacolus calliopsis
Marginulina linearis
Globulina sp.
Lenticulina subalata
Pseudonodosaria humilis
1207B
1214A
1213A-B

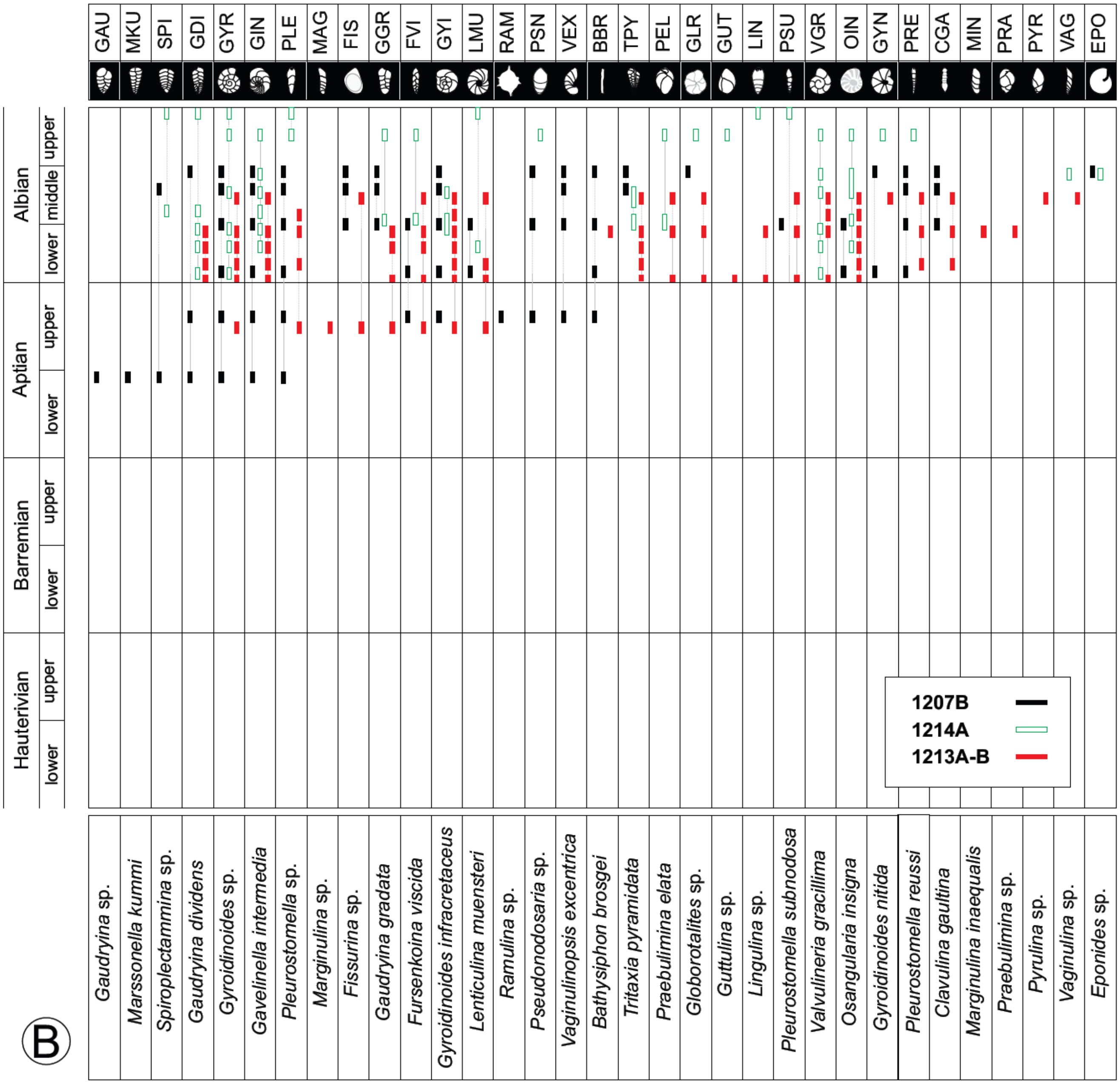

Fig. 3. A. Distribution and stratigraphic ranges of benthic foraminifera in ODP holes 1207B, 1214A, 1213A, and 1213B in the lower Hauterivian-lower Barremian interval at Shatsky Rise. **B.** Distribution and stratigraphical ranges of benthic foraminifera in ODP holes 1207B, 1214A, 1213A, and 1213B in the lower Aptian-upper Albian interval of Shatsky Rise.

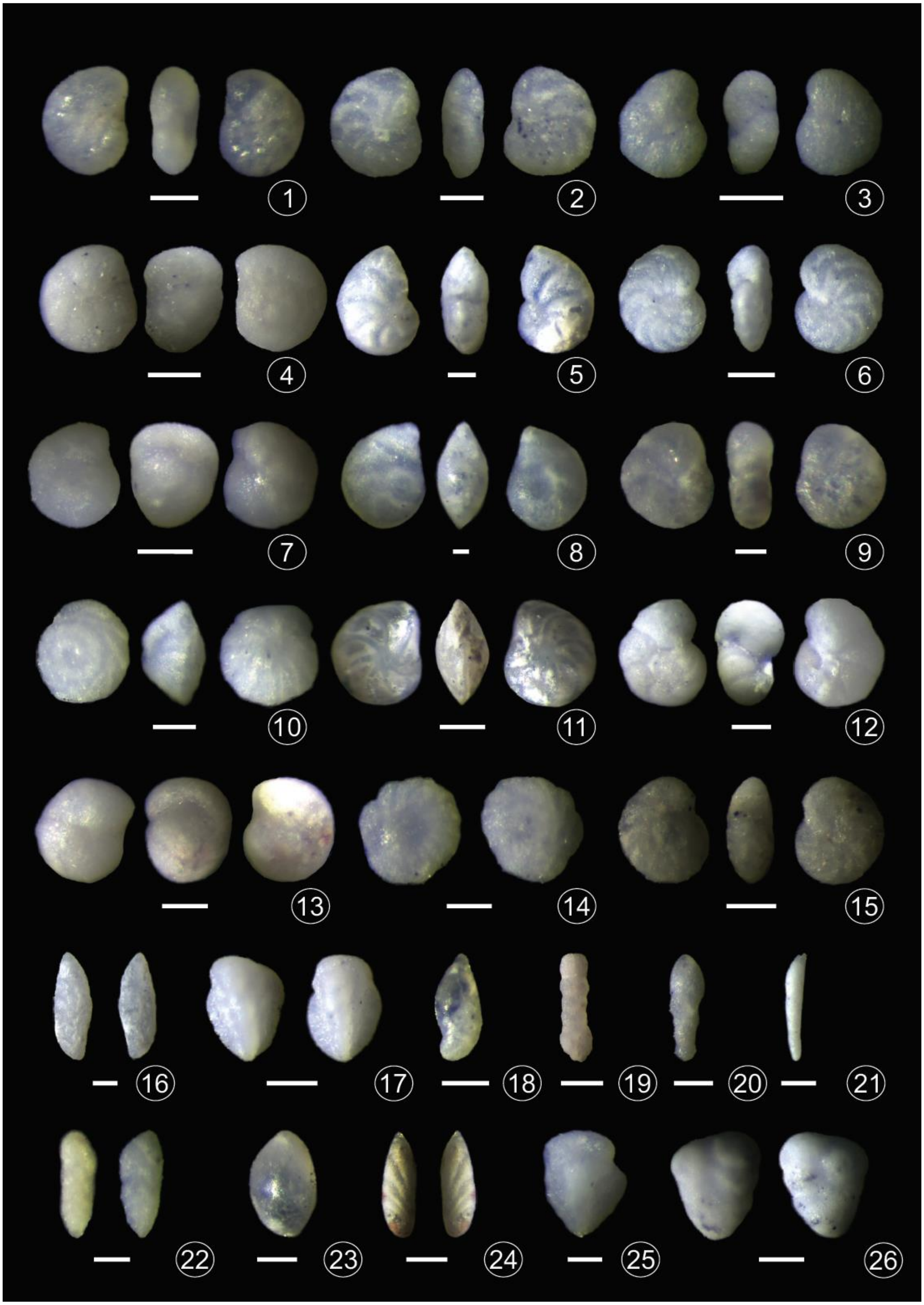
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Fig. 4A. Benthic foraminifera at ODP Site 1207. All scale-bars represent 100 μm. **1.** a/b/c *Gavelinella barremiana* (1207B-47R-CC; 596.59 mbsf); **2.** a/b/c *Gavelinella intermedia* (1207B-40R-CC, 15; 526.65 mbsf); **3.** a/b/c *Valvulineria gracillima* (1207B-33R-CC; 460.30 mbsf); **4.** a/b/c *Gyroidinoides* sp. (1207B-40R-CC, 15 cm; 526.65 mbsf); **5.** a/b/c *Lenticulina turgidula* (1207B-40R-CC, 15 cm; 526.65 mbsf); **6.** a/b/c *Gavelinella intermedia* (1207B-28R-CC; 417.34 mbsf); **7.** a/b/c *Gyroidinoides infracretaceus* (1207B-30R-CC; 431.49 mbsf); **8.** a/b/c *Lenticulina* sp. (1207B-28R-CC; 417.34 mbsf); **9.** a/b/c *Gavelinella barremiana* (1207B-47R-CC; 596.59 mbsf); **10.** a/b/c *Globorotalites* sp. (1207B-28R-CC; 417.34 mbsf); **11.** a/b/c *Lenticulina muensteri* (1207B-47R-CC; 596.59 mbsf); **12.** a/b/c *Gyroidinoides nitida* (1207B-28R-CC; 417.34 mbsf); **13.** a/b/c *Gyroidinoides infracretaceus* (1207B-40R-CC, 5 cm; 526.50 mbsf); **14.** a/b *Osangularia insigna* (1207B-33R-CC; 460.30 mbsf); **15.** a/b/c *Gavelinella* sp. (1207B-40R-CC, 15 cm; 526.65 mbsf); **16.** a/b *Astacolus calliopsis* (1207B-43R-CC; 557.02 mbsf); **17.** a/b *Tritaxia pyramidata* (1207B-33R-CC; 460.30 mbsf); **18.** *Vaginulinopsis excentrica* (1207B-47R-CC; 596.59 mbsf); **19.** *Clavulina gaultina* (1207B-33R-CC; 460.30 mbsf); **20.** *Pleurostomella reussi* (1207B-33R-CC; 460.30 mbsf); **21.** *Dentalina communis* (1207B-28R-CC; 417.34 mbsf); **22.** *Fursenkoina viscida* (1207B-40R-CC, 15 cm; 526.65 mbsf); **23.** *Globulina prisca* (1207B-47R-CC; 596.59 mbsf); **24.** *Astacolus* sp. (1207B-47R-CC; 596.59 mbsf); **25.** *Tritaxia pyramidata* (1207B-47R-CC; 431.49 mbsf); **26.** *Gaudryina gradata* (1207B-28R-CC; 417.34 mbsf).

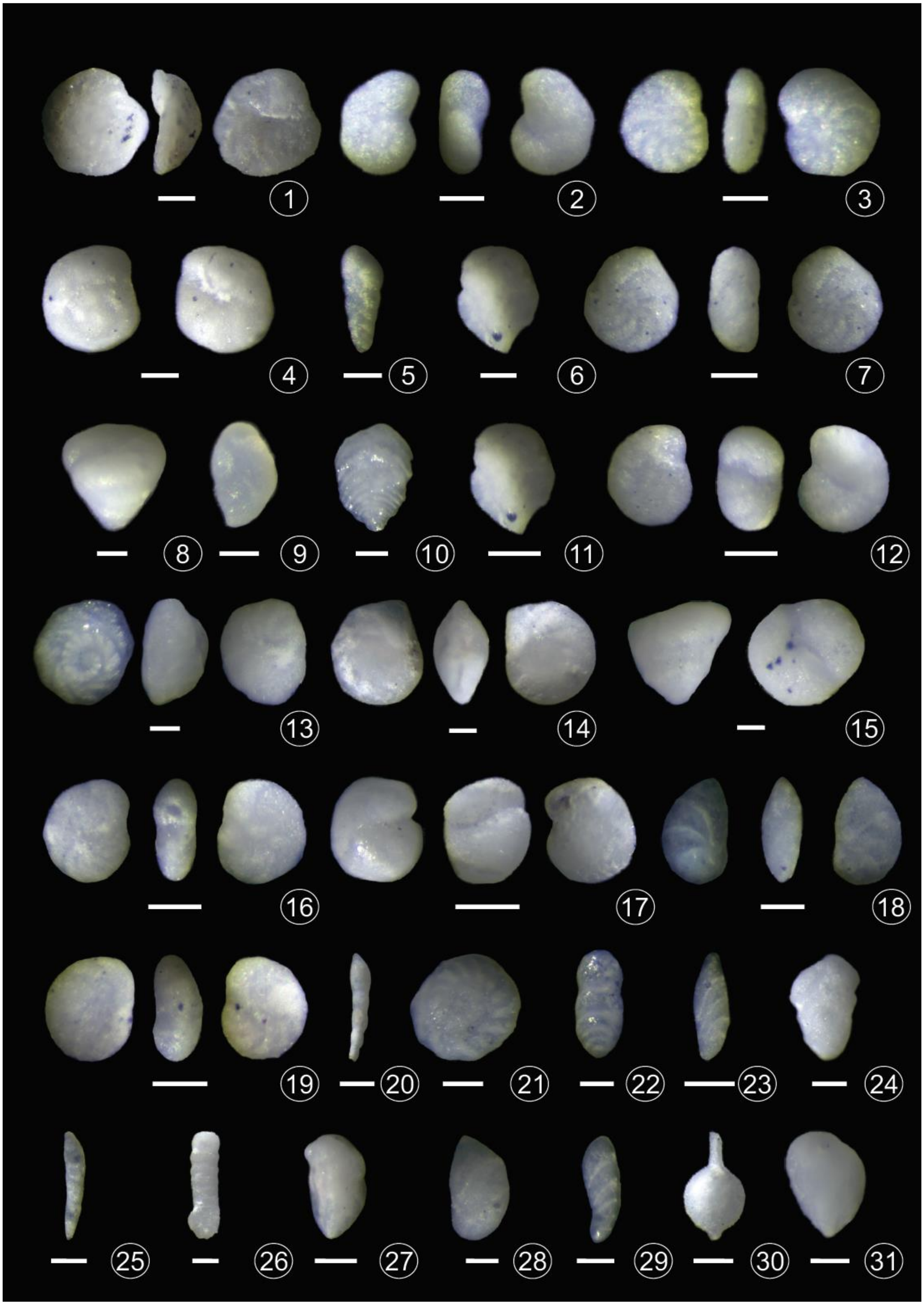
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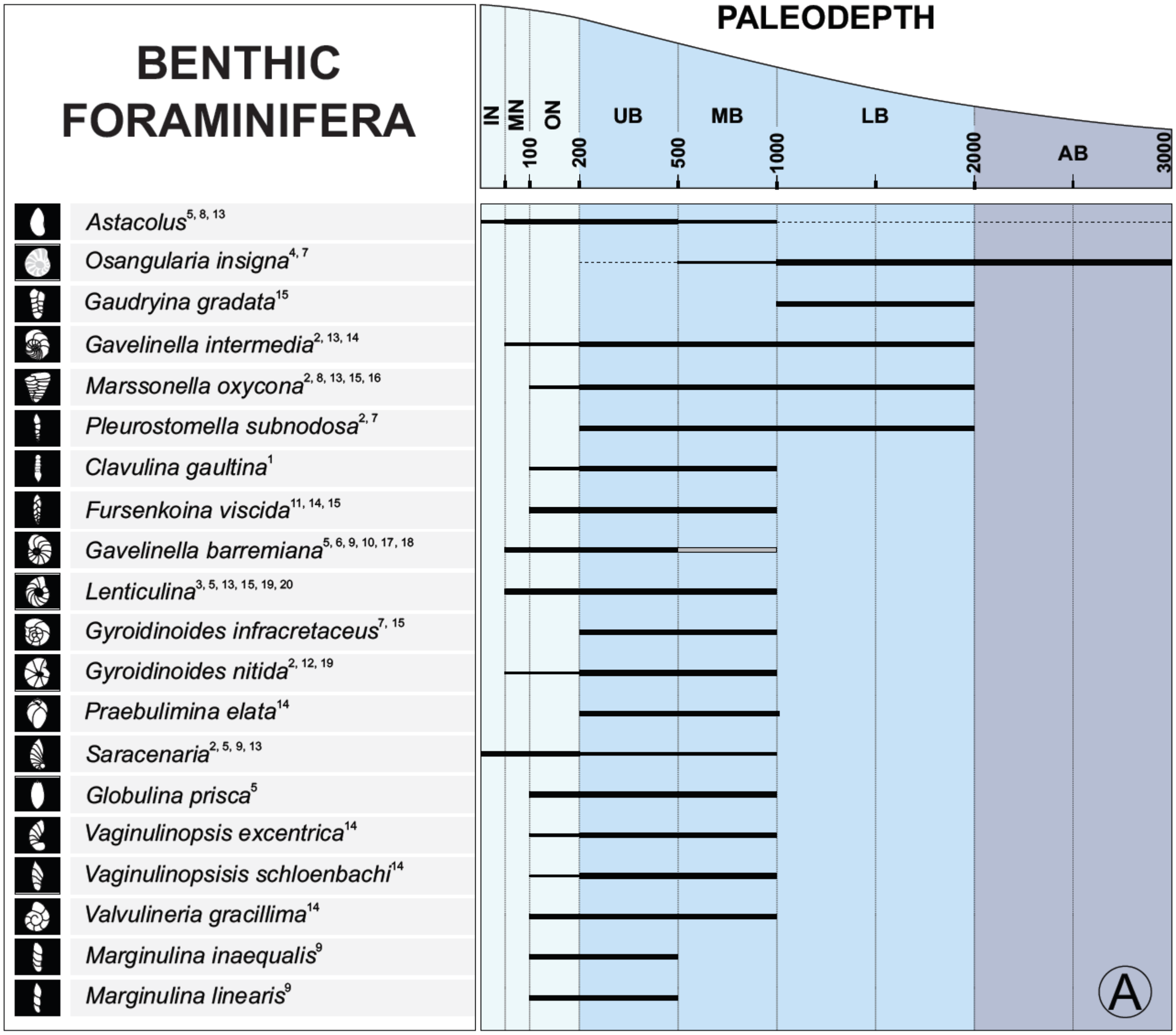
Fig. 4B. Benthic foraminifera at ODP sites 1214 and 1213 All scale-bars represent 100 µm. **1.** a/b/c *Osangularia insigna* (1214A-15R-1, 29-30 cm; 130.60 mbsf); **2.** a/b/c *Valvulineria gracillima* (1214A-9R-1, 8-11 cm; 72.09 mbsf); **3.** a/b/c *Gavelinella intermedia* (1214A-9R-1, 8-11 cm; 72.09 mbsf); **4.** a/b *Gyroidinoides* sp. (1214A-11R-1, 0-1 cm; 91.40 mbsf); **5.** *Fursenkoina viscida* (1214A-22R-1, 32-33 cm; 197.62 mbsf); **6.** *Tritaxia pyramidata* (1214A-22R-1, 32-33 cm; 197.62 mbsf); **7.** a/b/c *Gavelinella intermedia* (1214A-22R-1, 32-33 cm; 197.62 mbsf); **8.** *Marssonella subtrochus* sp. (1214A-6R-1, 4-5 cm; 43.20 mbsf); **9.** *Praebulimina* sp. (1214A-7R-1, 2-4 cm; 52.61 mbsf); **10.** *Spiroplectammina* sp. (1214A-7R-1, 2-4 cm; 52.51 mbsf); **11.** *Tritaxia pyramidata* (1214A-22R-1, 32-33 cm; 197.62 mbsf); **12.** a/b/c *Gyroidinoides infracretaceus* sp. (1213B-6R-1, 81-84 cm; 238.61 mbsf); **13.** a/b/c *Globorotalites* sp. (1213A-21R-CC; 189.33 mbsf); **14.** a/b/c *Lenticulina muensteri* (1213B-6R-1, 81-84 cm; 238.61 mbsf); **15.** a/b/ *Marssonella subtrochus* (1213B-9R-1, 70-71 cm; 276.11 mbsf); **16.** a/b/c *Gavelinella barremiana* (1213B-6R-1, 81-84 cm; 238.61 mbsf); **17.** a/b/c *Gyroidinoides infracretaceus* sp. (1213B-6R-1, 81-84 cm; 238.61 mbsf); **18.** a/b/c *Astacolus planiusculus* (1213A-21R-CC; 189.30 mbsf); **19.** a/b/c *Gavelinella barremiana* (1213B-6R-1, 81-84 cm; 238.61 mbsf); **20.** *Dentalina communis* (1213A-21R-CC; 189.30 mbsf); **21.** *Osangularia insigna* (1213B-2R-CC; 199.30 mbsf); **22.** *Lingulina* sp. (1213B-6R-1, 81-84 cm; 238.61 mbsf); **23.** *Astacolus* sp. (1213B-3R-1, 14-15 cm; 209.49 mbsf); **24.** *Gaudryina gradata* (1213B-6R-1, 81-84 cm; 238.61 mbsf); **25.** *Dentalina communis* (1213A-21R-CC; 189.30 mbsf); **26.** *Clavulina gaultina* (1213A-21R-CC; 189.30 mbsf); **27.** *Tritaxia pyramidata* (1213B-6R-1, 81-84 cm; 238.61 mbsf); **28.** *Astacolus planiusculus* (1213B-6R-1, 81-84 cm; 238.61 mbsf); **29.** *Vaginulinopsis schloenbachi* (1213B-6R-1, 81-84 cm; 238.61 mbsf); **30.** *Lagena* sp. (1213A-20R-CC; 179.6 mbsf); **31.** *Praebulimina* sp. (1213A-21R-CC; 189.30 mbsf).


BENTHIC FORAMINIFERA
PALEODEPTH
IN
MN
ON
UB
MB
LB
AB
100
200
500
1000
2000
3000
Astacolus[5, 8, 13]
Osangularia insigna[4, 7]
Gaudryina gradata[15]
Gavelinella intermedia[2, 13, 14]
Marssonella oxycona[2, 8, 13, 15, 16]
Pleurostomella subnodosa[2, 7]
Clavulina gaultina[1]
Fursenkoina viscida[11, 14, 15]
Gavelinella barremiana[5, 6, 9, 10, 17, 18]
Lenticulina[3, 5, 13, 15, 19, 20]
Gyroidinoides infracretaceus[7, 15]
Gyroidinoides nitida[2, 12, 19]
Praebulimina elata[14]
Saracenaria[2, 5, 9, 13]
Globulina prisca[5]
Vaginulinopsis excentrica[14]
Vaginulinopsisis schloenbachi[14]
Valvulineria gracillima[14]
Marginulina inaequalis[9]
Marginulina linearis[9]
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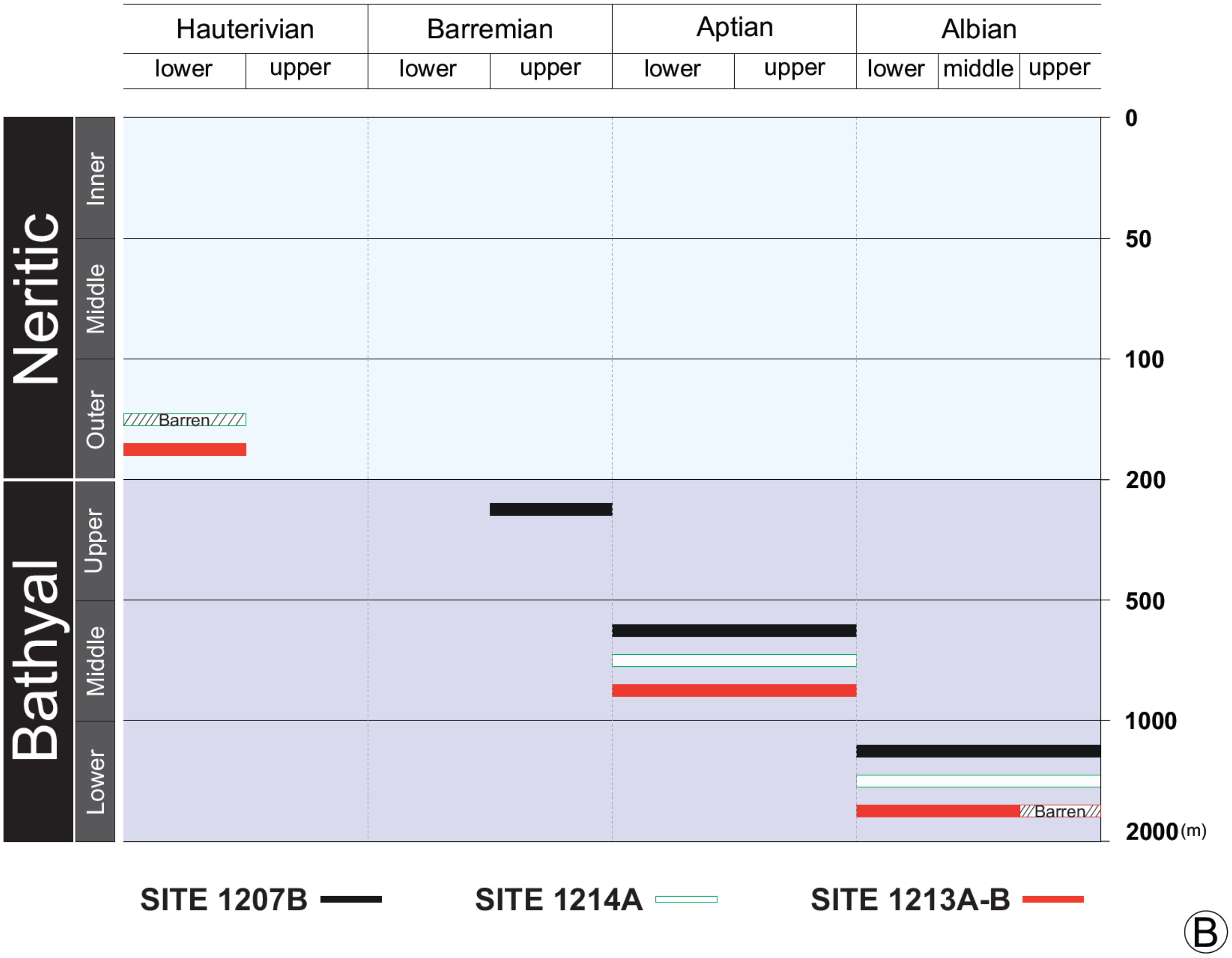


Fig. 5. A. Benthic foraminifera recorded in ODP holes 1207B, 1214A, 1213A, and 1213B showing the paleobathymetric preferences on the most important species, based on: Sliter (1977a)[1]; Nygon and Olson (1984)[2]; De Azevedo et al. (1987)[3]; Norris et al. (1988)[4]**;** Koutsoukos, (1989)[5]; Riegraf (1989)[6]; Sikora and Olsson (1991)[7]; Saint-Marc (1992)[8]; Holbourn and Kaminski (1995a)[9]; Moullade et al. (1998)[10]; Erbacher et al. (1999)[11]; Schnack (2000)[12]; Frenzel (2000)[13]; Holbourn and Kuhnt (2001)[14]; Holbourn et al. (2001a)[15]; Alegret et al. (2003)[16]; Tyszka (2006)[17]; Gradstein and Waters (2016)[18]; Aschckenazi-Polivoda et al. (2018)[19]; Giraldo-Gómez et al. (2018)[20]. We adopted in this study the paleobathymetric subdivision by Nyong and Olsson (1984) and van Morkhoven et al. (1986): inner-neritic (IN: 0–50 m), middle-neritic (MN: 50–100 m), outer-neritic (ON: 100–200 m), upper bathyal

(UB: 200–500 m), middle bathyal (MB: 500–1000 m), lower bathyal (LB: 1000–2000 m) and Abyssal (AB: > 2000 m). Black thick solid lines indicate a high abundance of species. Black thin solid lines mean less abundance of species. Dashed lines denote species that could be found with very low abundances. Grey thin solid lines indicate a non-studied depth range. **B.** Paleobathymetric reconstruction of ODP holes 1207B, 1214A, 1213A, and 1213B, based on benthic foraminifera showing the variation of the paleo-depths during the Lower Cretaceous.

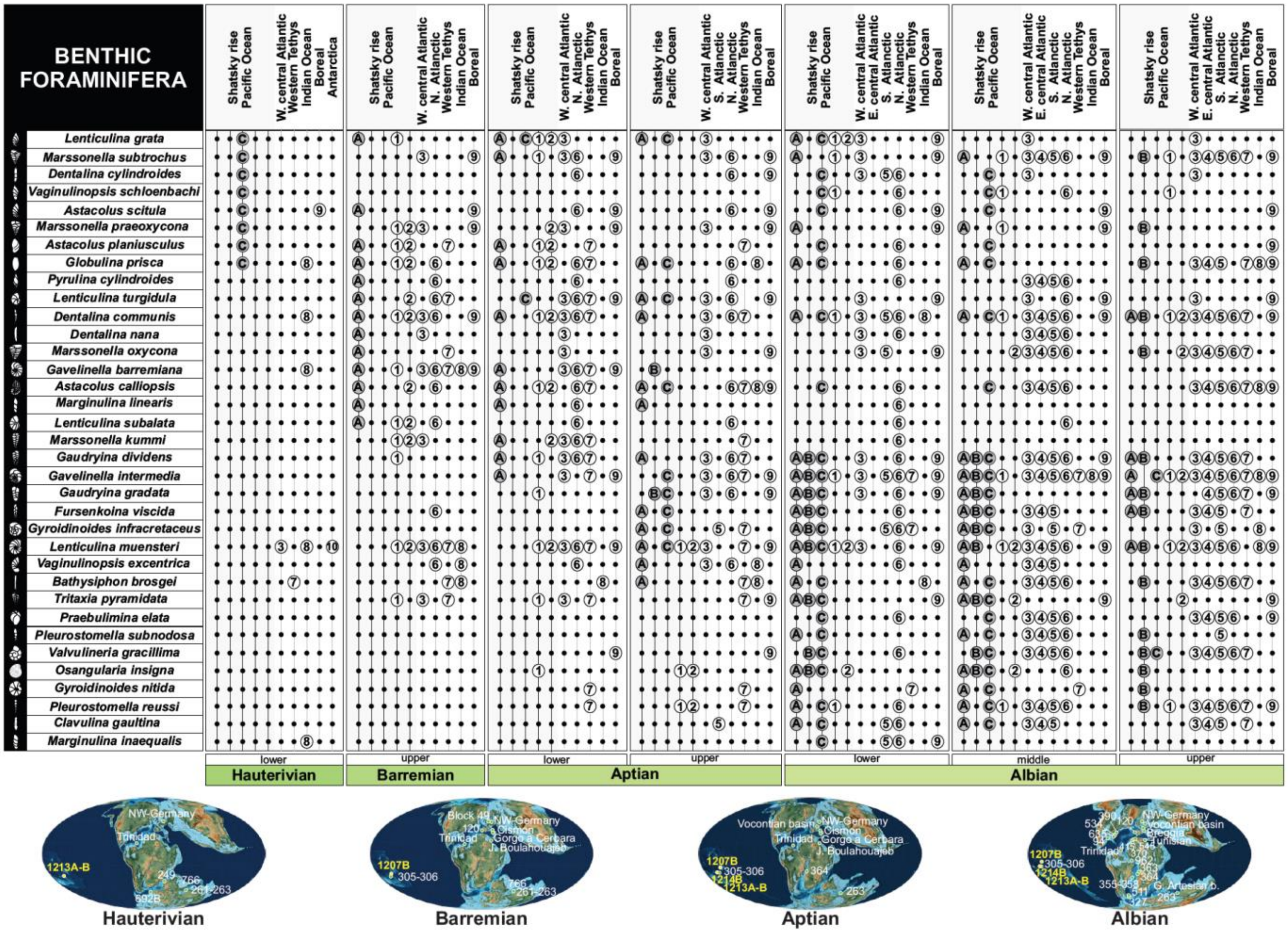
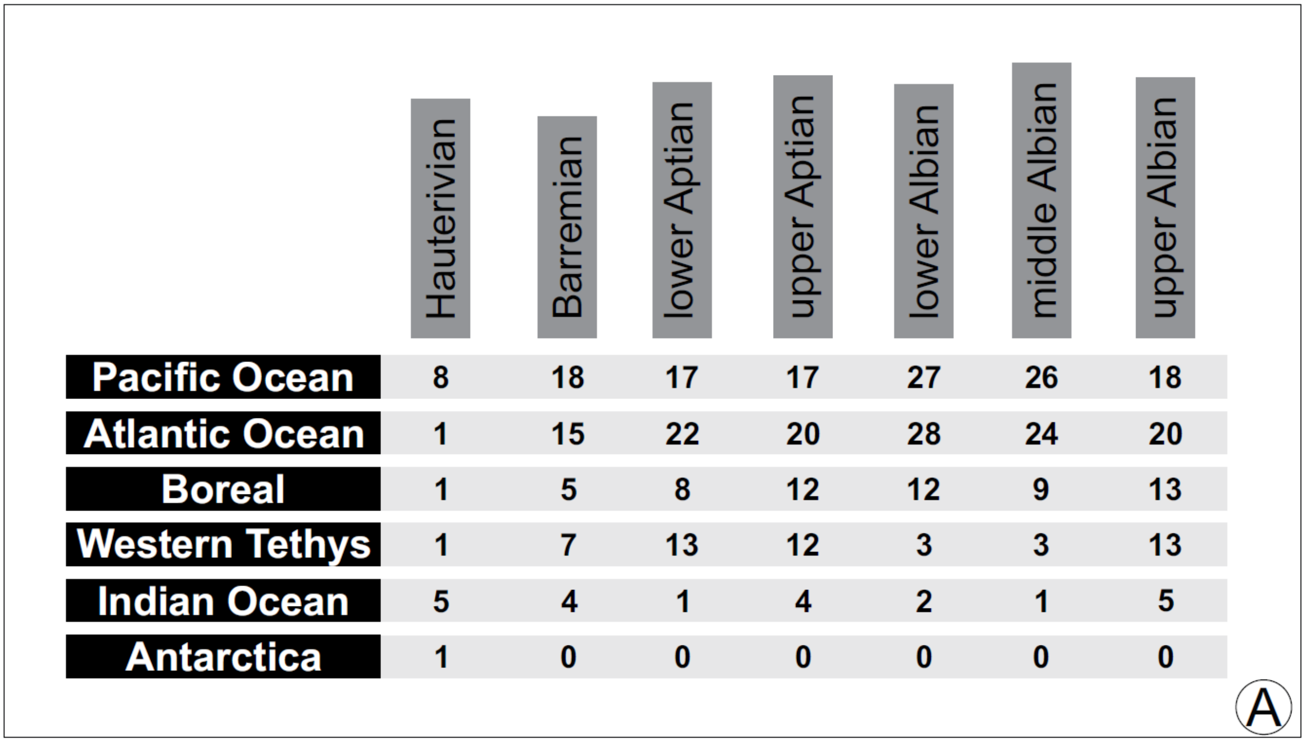


Fig. 6. Species of benthic foraminifera observed at Shatsky Rise ODP holes 1207B **(A)**, 1214B **(B)** and 1213A-1213B **(C)** during the Lower Cretaceous (Hauterivian, Barremian, Aptian and Albian) compared with the record of the same species reported from the **Pacific Ocean Bioprovince:** DSDP 305 **(1)** and 306 **(2)** (Shasky Rise): Luterbacher, 1975. The **Atlantic Ocean Bioprovince** comprises: **Western central Atlantic Ocean (3):** Trinidad: Bartenstein and Bolli, 1977; Bolli et al., 1994. DSDP 390-392 (Black Nose): Gradstein, 1978. DSDP 627 (southern Black Plateau) Holbourn et at., 2001a. DSDP 635 (Northeast Providence Channel): Holbourn et at., 2001a. DSDP 534 (Black Bahama Basin): Holbourn et at., 2001a. ODP 1049 (Black Plateau) Holbourn et al., 2001b; Holbourn, and Kuhnt, 2001; Erbacher, 2001. DSDP 94 (Yucatan): Holbourn et at., 2001a. **Eastern central Atlantic Ocean (4):** DSDP 369 (Cape Bojador): Kuznetsova, 1978. DSDP 370 (Morocco): Riegraf and Luterbacher, 1989;

Holbourn et at., 2001a. DSDP 547 (Mazagan Escarpment): Nederbragt et al., 2001; Holbourn et at., 2001a. DSDP 545 (Mazagan Escarpment): Holbourn et at., 2001a; Friedrich, 2005. **South Atlantic Ocean (5):** DSDP 364 (Angola offshore): Scheibnerová, 1978; Holbourn et at., 2001a; Kochhann et al., 2014. DSDP 355-358 (Rio Grande Rise): Sliter, 1977a. DSDP 962 (Côte d'Ivoire-Ghana): Holbourn and Moullade, 1998. DSDP 363 (Walvis Rise): Scheibnerová, 1978; Holbourn and Moullade, 1998. DSDP 356 (Sao Paulo Plateau): Slitter, 1977. DSDP 511 (Falkland Plateau): Basov and Krasheninnikov, 1983. DSDP 327 (East Falkland Plateau): Sliter, 1977b; Holbourn et at., 2001a. **North Atlantic Ocean (6):** DSDP 398 (Vigo Seamount -Spain): Holbourn et at., 2001a. DSDP 402-400 (North Biscay - France): Dupeuble, 1979; Holbourn et at., 2001a. DSDP 120 (Gorrige Bank -Portugal): Mayne, 1973. Speeton Clay (England): Hart et al., 1989, Mitchell and Underwood, 1999. Block 49 (England): Crittenden, 1986. The **Western Tethys Bioprovince (7):** Vocontian (France): Erbachen et al., 1998; Moullade et al., 1998; Moullade et al., 2015. Umbria-Marche (Italia): Patruno et al., 2015. Cismon (Italia): Giraldo-Gómez et al., (20XX). Tunisia: Melliti et al., 2019; Holbourn et at., 2001a. Breggia (Swiss): Holbourn et at., 2001a. **Indian Ocean Bioprovince (8)**: Southern Carnarvon Basin (Australia): Haig, 2005; DSDP 766 (Australia): Holbourn and Kaminski, 1995a; DSDP 263 (Australia): Holbourn and Kaminski, 1994, Holbourn and Kaminski, 1995b. Great Artesian Basin (Australia): Lambert and Scheibnerova, 1974. DSDP 249 (Madagascar): Riegraf, 1989. The **Boreal Bioprovince (9):** NW-Germany: Bartenstein et al., 1957; Bartenstein and Bolli, 1973; Neuss, 1979; Bartenstein and Bolli, 1986; Mutterlose, 1996; Prokoph, 1999; Mutterlose et al., 2003a; Löb and Mutterlose, 2012. NE-Germany: Szarek et al., 2000. The **Antarctica Bioprovince (10):** Giraldo-Gómez et al., 20XX. The paleogeographic maps of the Hauterivian, Barremian, Aptian and Albian (modified from Scotese, 2014) show the most important onshore sections and ODP-DSDP sites describes before.



	Hauterivian	Barremian	lower Aptian	upper Aptian	lower Albian	middle Albian	upper Albian
Pacific Ocean	8	18	17	17	27	26	18
Atlantic Ocean	1	15	22	20	28	24	20
Boreal	1	5	8	12	12	9	13
Western Tethys	1	7	13	12	3	3	13
Indian Ocean	5	4	1	4	2	1	5
Antarctica	1	0	0	0	0	0	0

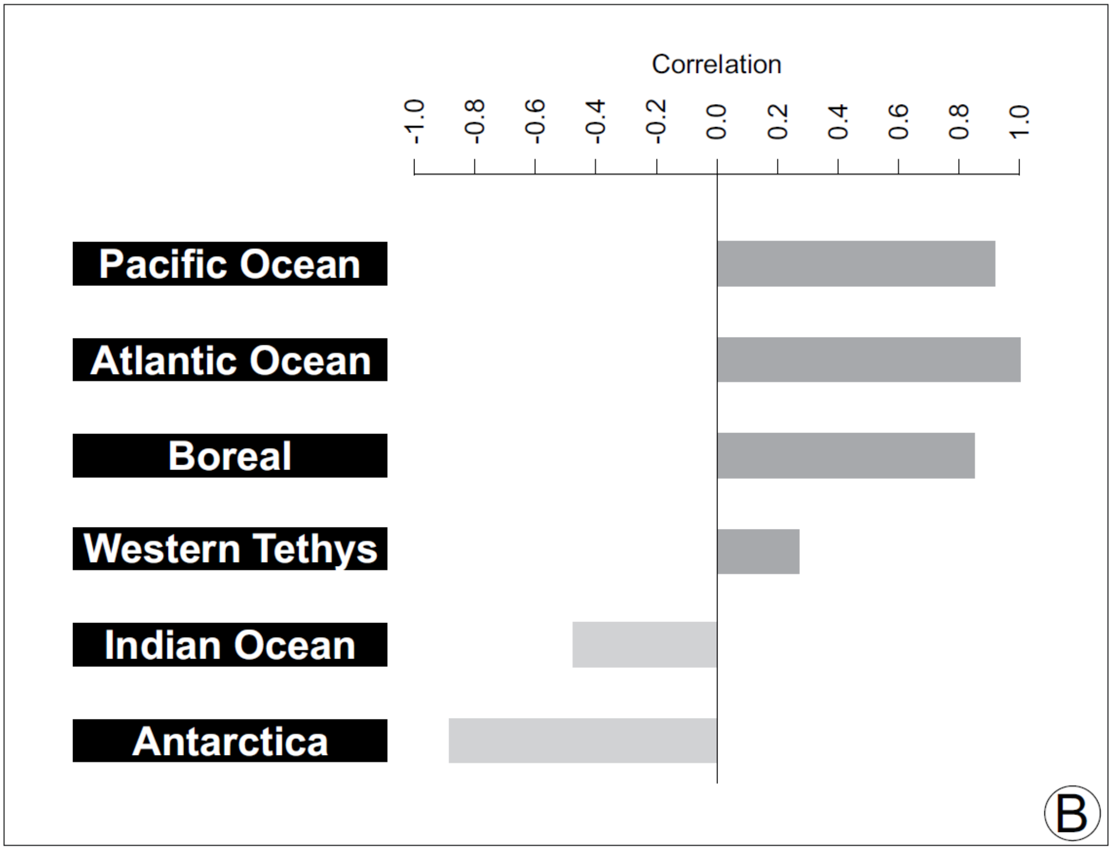
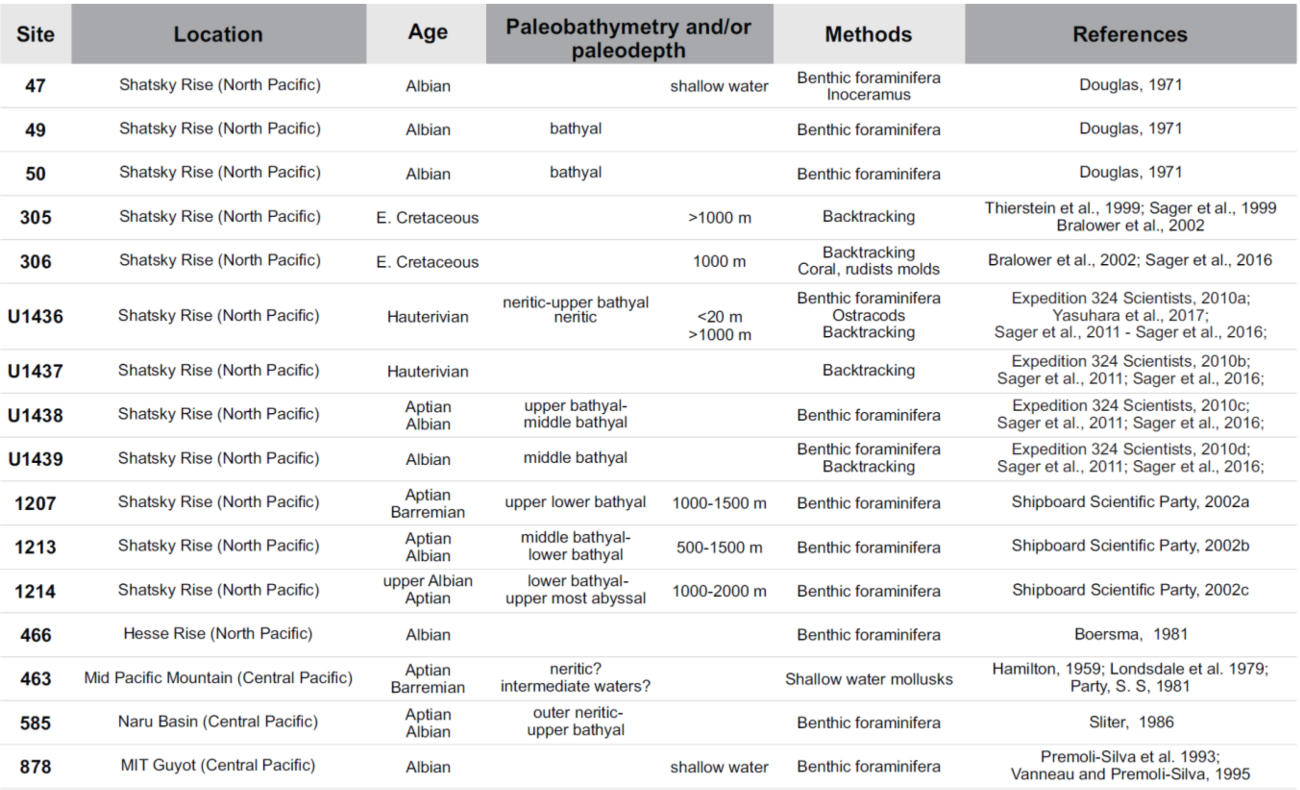


Fig. 7. A. Species richness of selected benthic foraminifera (see 35 species included in Fig. 6) from ODP holes 1207B, 1214A, 1213A and 1213B characteristics of the Pacific Ocean Bioprovince during the Lower Cretaceous, compared with the species documented from the bioprovinces of the Atlantic Ocean (western central Atlantic, eastern central Atlantic, south Atlantic, and north Atlantic), Western Tethys (France, Italia, and Swiss), Indian Ocean (Australia and Madagascar), Boreal (Germany) and Antarctica. **B.** Pearson correlation showing the affinity of benthic foraminifera recorded in the different bioprovinces (Positive values: high correlation= 0.5 – 1; moderate correlation= 0.30 – 0.49; low correlation= < 0.29; no correlation= 0. Negative values: high correlation= -0.5 – -1; moderate correlation= -0.30 – -0.49; low correlation= < -0.29; no correlation= 0).

Tables



Site	Location	Age	Paleobathymetry and/or paleodepth		Methods	References
47	Shatsky Rise (North Pacific)	Albian		shallow water	Benthic foraminifera Inoceramus	Douglas, 1971
49	Shatsky Rise (North Pacific)	Albian	bathyal		Benthic foraminifera	Douglas, 1971
50	Shatsky Rise (North Pacific)	Albian	bathyal		Benthic foraminifera	Douglas, 1971
305	Shatsky Rise (North Pacific)	E. Cretaceous		>1000 m	Backtracking	Thierstein et al., 1999; Sager et al., 1999 Bralower et al., 2002
306	Shatsky Rise (North Pacific)	E. Cretaceous		1000 m	Backtracking Coral, rudists molds	Bralower et al., 2002; Sager et al., 2016
U1436	Shatsky Rise (North Pacific)	Hauterivian	neritic-upper bathyal neritic	<20 m >1000 m	Benthic foraminifera Ostracods Backtracking	Expedition 324 Scientists, 2010a; Yasuhara et al., 2017; Sager et al., 2011 - Sager et al., 2016;
U1437	Shatsky Rise (North Pacific)	Hauterivian			Backtracking	Expedition 324 Scientists, 2010b; Sager et al., 2011; Sager et al., 2016;
U1438	Shatsky Rise (North Pacific)	Aptian Albian	upper bathyal- middle bathyal		Benthic foraminifera	Expedition 324 Scientists, 2010c; Sager et al., 2011; Sager et al., 2016;
U1439	Shatsky Rise (North Pacific)	Albian	middle bathyal		Benthic foraminifera Backtracking	Expedition 324 Scientists, 2010d; Sager et al., 2011; Sager et al., 2016;
1207	Shatsky Rise (North Pacific)	Aptian Barremian	upper lower bathyal	1000-1500 m	Benthic foraminifera	Shipboard Scientific Party, 2002a
1213	Shatsky Rise (North Pacific)	Aptian Albian	middle bathyal- lower bathyal	500-1500 m	Benthic foraminifera	Shipboard Scientific Party, 2002b
1214	Shatsky Rise (North Pacific)	upper Albian Aptian	lower bathyal- upper most abyssal	1000-2000 m	Benthic foraminifera	Shipboard Scientific Party, 2002c
466	Hesse Rise (North Pacific)	Albian			Benthic foraminifera	Boersma, 1981
463	Mid Pacific Mountain (Central Pacific)	Aptian Barremian	neritic? intermediate waters?		Shallow water mollusks	Hamilton, 1959; Londsdale et al. 1979; Party, S. S, 1981
585	Naru Basin (Central Pacific)	Aptian Albian	outer neritic- upper bathyal		Benthic foraminifera	Sliter, 1986
878	MIT Guyot (Central Pacific)	Albian		shallow water	Benthic foraminifera	Premoli-Silva et al. 1993; Vanneau and Premoli-Silva, 1995

Table 1. ODP-DSDP sites from the Pacific Ocean showing the paleobathymetric interpretations using different methodologies.

Taxonomic appendix

A detailed taxonomic description of the benthic foraminifera cited in the text, figures and tables is given by Ellis and Messina (1942-2015), Luterbacher (1975), Mjatliuk (1988), Weidich (1990), Meyn and Vespermann (1994), Holbourn, 1996; Holbourn and Kaminski (1997), Holbourn and Kuhnt (2001), Holbourn et al. (2001a).

Astacolus sp. Montfort, 1808
Astacolus calliopsis (Reuss, 1863)
Astacolus planiusculus (Reuss, 1863).
Astacolus scitula (Berthelin, 1880)
Bathysiphon sp. Sars, 1872
Bathysiphon brosgei Tappan, 1957
Citharina sp. d'Orbigny, 1839
Clavulina gaultina Morozova, 1948 = *Tritaxia gaultina* Morozova, 1948
Dentalina sp. Risso, 1826
Dentalina communis (d'Orbigny, 1826) = *Laevidentalina communis* (d'Orbigny, 1826)
Dentalina cylindroides Reuss, 1860 = *Laevidentalina cylindroides* Reuss, 1860
Dentalina nana Reuss, 1863 = *Laevidentalina nana* Reuss, 1863
Dorothia sp. Plummer, 1931
Ellipsodimorphina Silvestri, 1901 = *Nodosarella Rzehak*, 1895
Eponides Montfort, 1808
Fissurina Reuss, 1850
Fursenkoina viscida (Khan 1950)
Gaudryina sp. d'Orbigny, 1839
Gaudryina dividens Grabert, 1959
Gaudryina gradata Berthelin, 1880 = *Kadriayina gradata* (Berthelin, 1880)
Gavelinella sp. Brotzen, 1942
Gavelinella barremiana Bettenstaedt, 1952
Gavelinella intermedia (Berthelin, 1880) = *Berthelina intermedia* (Berthelin, 1880)

1216 *Globorotalites* sp. Brotzen, 1942

1217 *Globulina* sp. d'Orbigny, 1839

1218 *Globulina prisca* (Reuss, 1863)

1219 *Guttulina* sp. d'Orbigny, 1839

1220 *Gyroidinoides* Brotzen, 1942

1221 *Gyroidina nitida* (Reuss, 1850) = *Gyroidinoides nitida* (Reuss, 1844)

1222 *Gyroidina infracretacea* Morozova, 1948 = *Gyroidinoides infracretaceus* (Morozova, 1948)

1223 *Lagena* Walker & Jacob, 1798

1224 *Lenticulina* sp. Lamarck, 1804

1225 *Lenticulina acuta* (Reuss, 1860)

1226 *Lenticulina grata* (Reuss, 1863) = *Astacolus gratus* (Reuss, 1863)

1227 *Lenticulina muensteri* (Roemer, 1839)

1228 *Lenticulina turgidula* (Reuss, 1863)

1229 *Lenticulina subalata* (Reuss, 1854)

1230 *Lingulina* sp. d'Orbigny, 1826

1231 *Marginulina* sp. d'Orbigny, 1826

1232 *Marginulina inaequalis* Costa, 1855

1233 *Marginulina linearis* Reuss, 1863

1234 *Marssonella* Cushman, 1933

1235 *Marssonella kummi* Zedler, 1961

1236 *Marssonella oxycona* (Reuss, 1860)

1237 *Marssonella praeoxycona* (Moullade, 1966) = *Protomarssonella praeoxycona* (Moullade, 1966)

1238 *Marssonella subtrochus* Bartenstein, 1962

1239 *Nodosaria* sp. Lamarck, 1816

1240 *Osangularia insigna* Dailey, 1970

1241 *Pleurostomella* sp. Reuss, 1860

1242 *Pleurostomella reussi* Berthelin, 1880

1243 *Pleurostomella subnodosa* (Reuss, 1851)

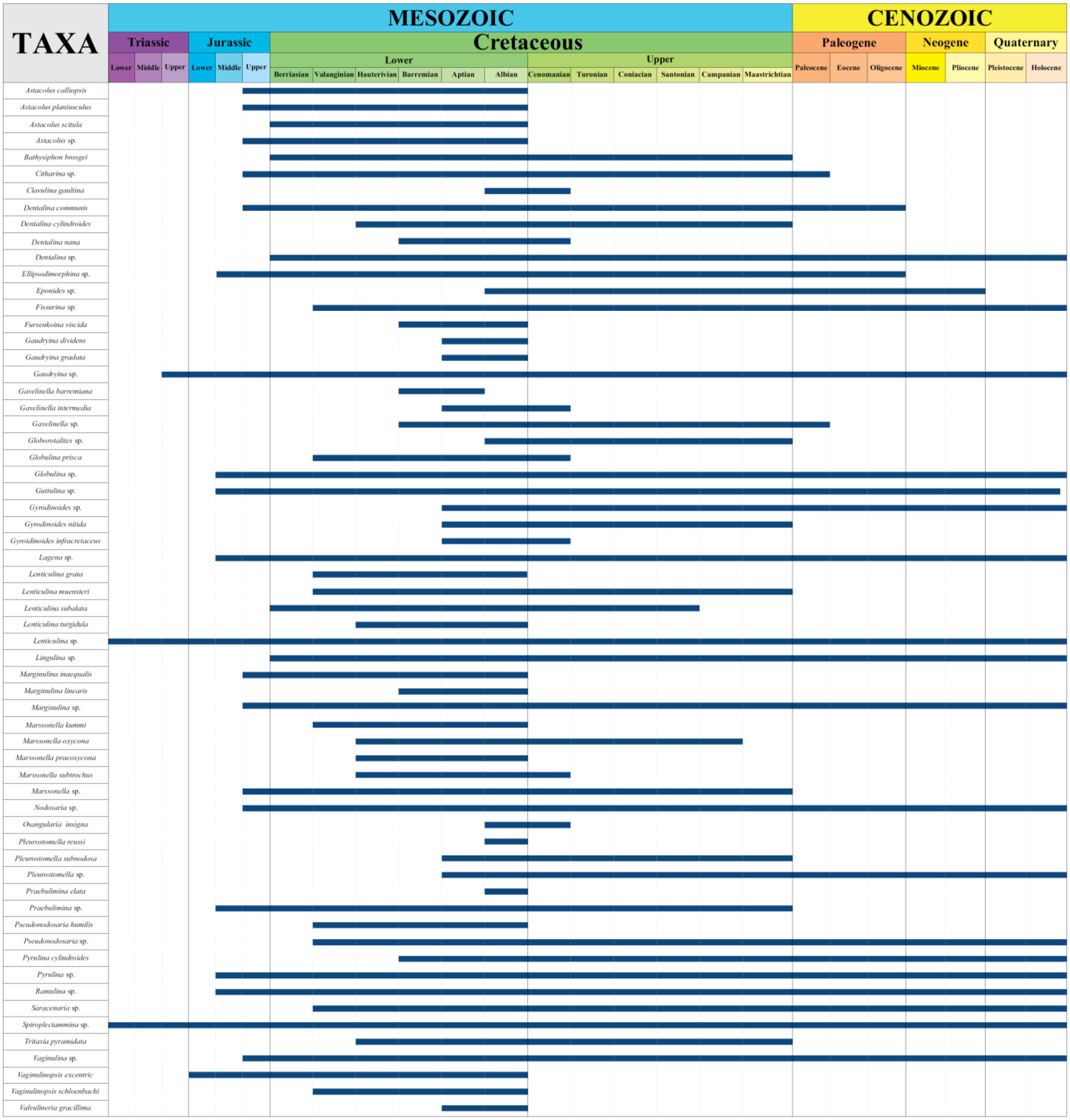
1244 *Praebulimina* sp. Hofker, 1953

1245 *Praebulimina elata* Magniez-Jannin, 1975

1246 *Pseudonodosaria* sp. Boomgaart, 1949

Pyrulina sp. d'Orbigny, 1839
Pyrulina cylindroides (Roemer, 1838)
Ramulina sp. T.R. Jones in Wright, 1875
Saracenaria sp. Defrance, 1824
Spiroplectammina Cushman, 1927
Tritxia pyramidata Reuss, 1863
Vaginulina sp. d'Orbigny, 1826
Vaginulinopsis sp. Silvestri, 1904
Vaginulinopsis excentrica (Cornuel, 1848)
Vaginulinopsis schloenbachi (Reuss, 1863) = *Astacolus schloenbachi* (Reuss, 1863)
Valvulineria gracillima Ten Dam, 1947

Supplementary data



Supplementary data, Figure S1. Stratigraphic ranges of all benthic foraminifera recorded at Shatsky Rise (ODP holes 1207B, 1214A, 1213A, and 1213B) according to Ellis and Messina (1942-2015), Loeblich and Tapan, (1987), and Holbourn (1996).

Ellis, B. E., Messina, A. R., 1942-2015. Catalogue of Foraminifera. Micropaleontology Press, American Museum of Natural History, New York. Catalogue online. http://www.micropress.org.

Loeblich, A. R.; Tappan, H., 1987. Foraminiferal genera and their classification. Van Nostrand Reinhold Company. New York. 970 pp.

Holbourn, A. E. L., 1996. Lower Cretaceous benthic foraminifera of the Indian Ocean. PhD. Thesis. University of London. 1-236.

Supplementary data, Table S1. Distribution chart of benthic foraminifera divided in suborders and families, showing the abundance expressed as benthic foraminiferal numbers (BFN).

Supplementary data, Table S2. Distribution chart of planktonic foraminifera.