

**Benthic foraminifera as proxies to infer  
paleoenvironmental conditions**

**Case studies from Western Siberia, and the Arabian and  
Mediterranean Sea**

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## Summary

Foraminifera are among the most important microfossils and invaluable tools for geosciences. They have an extensive fossil record their fossil record dates back to the Precambrian. and they are extensively distributed in all marine environments. Because of their small size and abundance, foraminifera are widely involved in applied studies where they are used for age-dating, correlation of sediments, and paleoenvironmental interpretations. Their mineralized shells record a wealth of information from the surrounding environment, including data on paleotemperatures, salinity, nutrient conditions, the extent of glaciation, current conditions and other paleogeographic features. In this thesis, examples, and case studies on modern and fossil foraminifera from different environments are provided to illustrate and document how this group of organisms can be applied to infer environmental conditions of the past. The studies presented here cover wide ranges of environmental conditions from low latitude, warm and tropical environments to high latitude temperate and cold-water settings. The material investigated here includes material from the Paleocene and Eocene of Western Siberia, and modern foraminifera from the Mediterranean coast of Tunisia and from the coast of Oman. The habitats differ fundamentally in their nature and surrounding environmental conditions, and as such provide a multitude of information to interpret the fossil record.

The study location in Western Siberia is situated in a complex geological structure where the Peri-Tethys and the Arctic Ocean basins were connected through marine corridors. Benthic foraminiferal assemblages are widespread in this area, occur in a variety of habitats, and are of fundamental importance for paleoecological reconstructions. Paleogene drill cores were studied to shed new light on the evolution of the West Siberian ecosystems. This has been accomplished by compiling benthic foraminiferal inventories from drill sites, through careful taxonomical analysis, and by studying the structure and numerical parameters of benthic foraminiferal assemblages in

relation to lithology, geochemical proxies, and paleoenvironmental indicators. To enable a detailed interpretation of past habitats, we applied actuopalaeontological approaches and compared the results with findings from modern marine ecosystems of the Arabian Sea and the Mediterranean Sea. (1) Analysis of the structural composition, species richness, diversity indices, and the oxygen index indicate that Early Paleocene sediments of the Arctic region of Western Siberia were deposited under variable but predominantly well-oxygenated environmental conditions. This feature that characterizes both deep- and shallow habitats. (2) In the Upper Eocene, the West Siberian Basin became increasingly isolated from the Peri-Tethys Ocean and shifted from normal marine to shallow subtidal and finally to brackish water conditions. (3) Paleogene sediments from Western Siberia revealed bioerosion structures on the test surfaces of benthic foraminifera, indicating that predation and/or epibionts were often associated with the foraminifera. (4) Studies on the modern foraminifera from Oman (Arabian Sea) and Mahrés Bay (Mediterranean Sea) showed that shallow water foraminiferal faunas are deposited in situ and preserve environmental information of their habitat. The structural composition of habitat-specific faunas can thus be transferred to fossil faunal communities and provide valuable to infer depositional settings and environmental conditions of the past.

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# Chapter 1

## **Introduction**

The research undertaken in this thesis includes the analysis of benthic foraminiferal assemblages as proxies for palaeoenvironmental assessment from Paleogene sediments in Western Siberia and a comparison to foraminiferal faunas from recent marine ecosystems, such as shallow water habitats along the coast of Oman in the Arabian Sea and Mahrés Bay in the Mediterranean Sea. To infer palaeoenvironmental conditions, we have analyzed the structure and composition of foraminiferal assemblages, species richness and diversity patterns, morphotypes, bioerosion structures, and applied actuopalaeontology approaches. The results of these studies were published in five papers (Trubin et al., 2022, 2023a, b, 2024; Kamoun et al., 2023).

In the first chapter, an introduction to the study localities is given, with a history of previous studies that were conducted in these areas. In the second part, a comprehensive survey of established benthic foraminiferal proxies is provided. The following chapters comprise the major findings of the published studies that constitute this cumulative doctoral thesis and a discussion of the results in light of the most recent publications.

### **1.1. Study localities**

#### **1.1.1. Western Siberia**

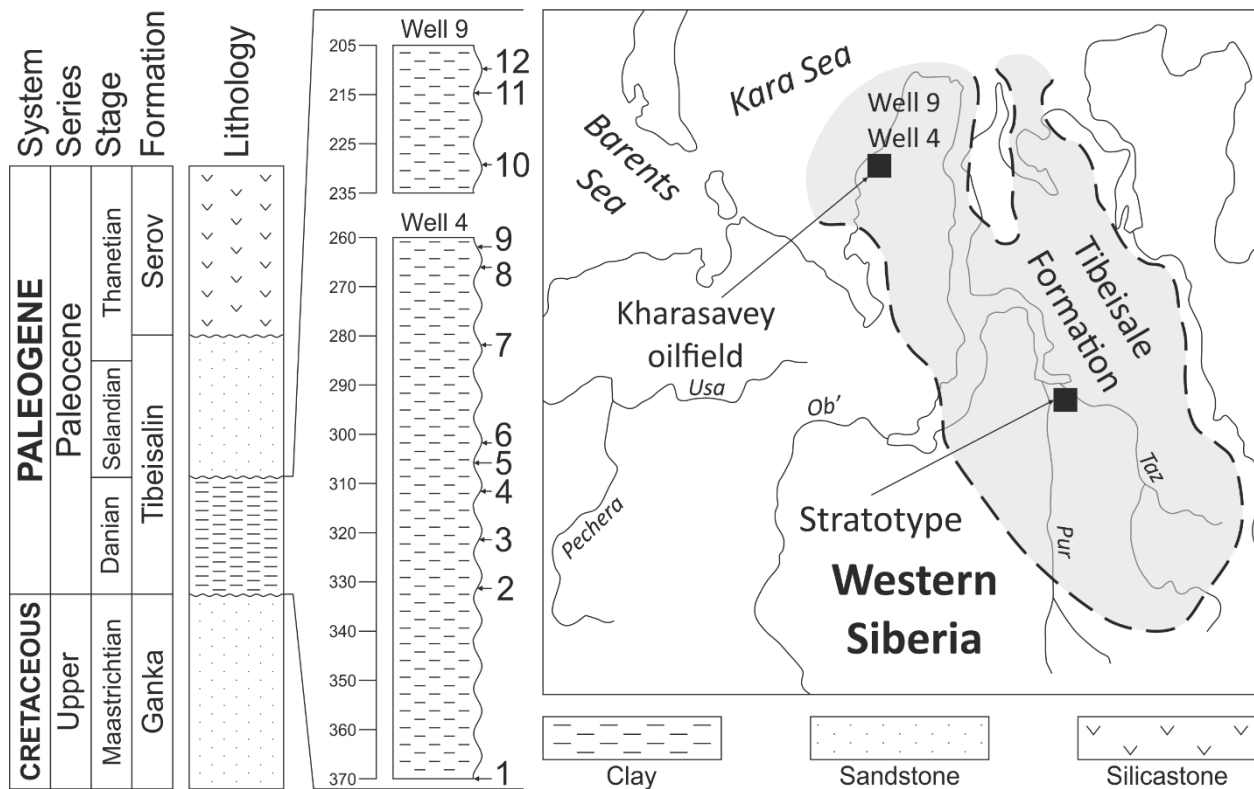
The West Siberian Basin formed after the collision of the Siberian and Kazakhstan continents with the Russian craton during the Late Carboniferous and Permian periods (Fedorov et al., 2004). It is bordered by the Eastern Slope of the Ural Mountains to the west, the Kazakh Highlands to the south, the Siberian platform to the east, and extends north into the Kara Sea. The sedimentary fillings of the basin started in the Early Triassic through rifting of the newly formed collision



structure and by deposition of predominantly basic and ultrabasic rocks. A north-south rift structure shaped the basin's elongated, intricate outline, allowing oceanic waters to enter from both the north and south and resulted in the accumulation of Middle Triassic to Middle Paleogene clastic rocks in marine sedimentary successions.

### **1.1.2 Tibeisale Formation (Lower Paleocene)**

The Tibeisale Formation has been attributed to belong to the Lower Paleocene based on palynological and foraminiferal data. The formation covers large areas in the Arctic Region in Western Siberia. In 1993, core sample material was collected from the formation during a drilling campaign. The material comprises 12 samples, including sedimentary samples from well 4 and well 9 at the Kharasavey oil and gas field (71°10'5"N, 67°2'52"E). Nine samples were retrieved from well 4 at depths between 263 and 372 m. Three samples were taken from the well 9 at a depth between 208 and 228 m (Fig. 1). The sedimentary core material examined comprise a blend of clay and siltstone and cover keystone phases of the marine evolution.



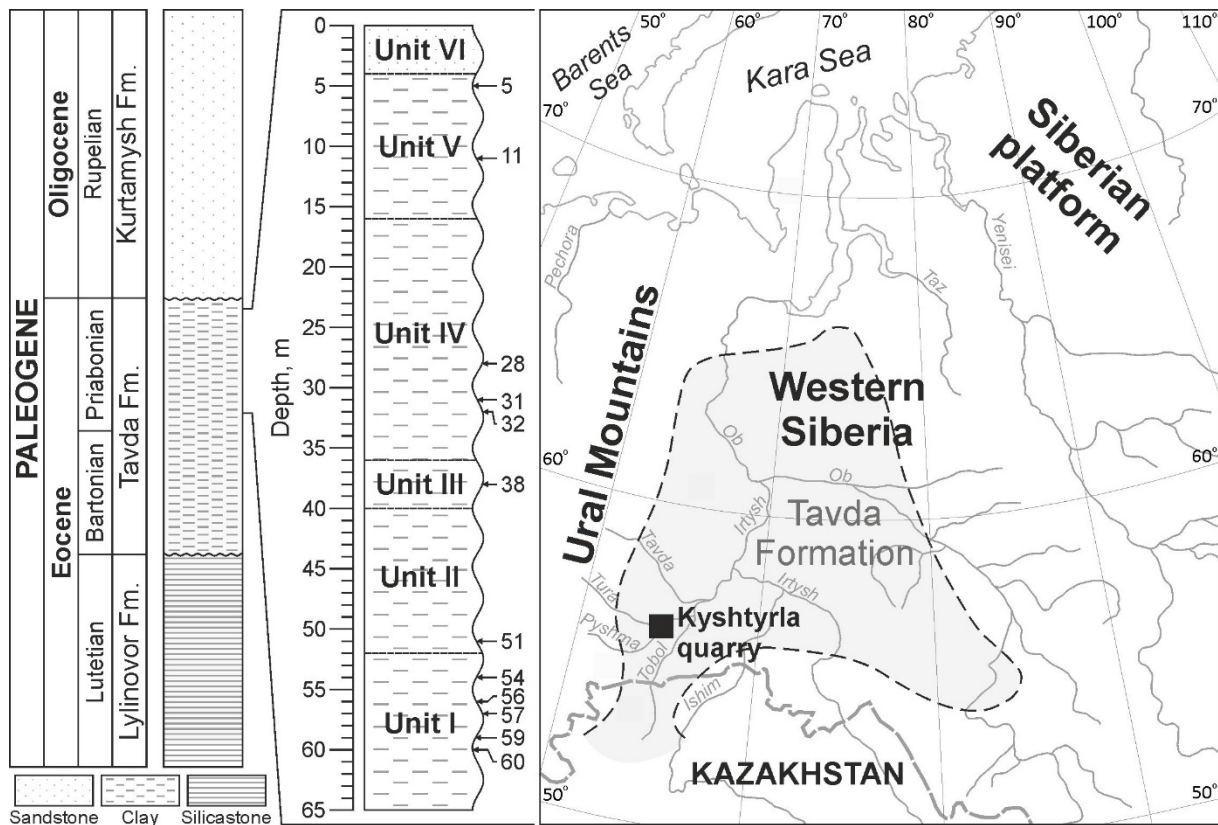
**Figure 1.** Location of well sites in the Arctic Region in Western Siberia and stratigraphic position of the Tibeisale Formation (modified after Lebedeva, 2006; Volkova, 2014).

### 1.1.3. Tavda Formation (Middle and Upper Eocene)

The Tavda Formation is considered to belong to the Middle and Upper Eocene based on palynological, foraminiferal, and magnetostratigraphic data. The formation is widely distributed in the southern and central region of Western Siberia. Research on this formation was conducted on a set of 65 core drill core samples extracted from the Kyshtyrla Quarry. The quarry is situated at the southwestern periphery of Western Siberia (Fig. 2; 55°55'15.50"N; 65°49'26.74"E). The drilling operation took place in the unexplored northeastern area of the quarry.

Drilling was carried out to a depth of 65 meters, with core samples extracted every meter. Six distinct facies units were observed through visual inspections and macroscopic analysis of the borehole samples. (1) The deepest facies unit comprises massive grey siltstone (52 – 65 m). At 57

m, a few small and poorly preserved mollusk shells along with rare shark teeth were found. (2) The unit is predominantly composed of massive grey siltstone, but it also contains thin interbedded layers of blue clay (40 –52 m). (3) The deposits comprise flat deposits of grey siltstone with intermittent layers of thin white sandstone (36 – 40 m). (4) The sediments are composed of blue clay (16 – 36 m). (5) Unit 5 mainly consists of brown and grey clay containing siderite concretions and small, infrequent gypsum crystals (4 – 16 m). (6) The highest unit comprises predominantly very coarse sand with incorporations of large, rounded rock fragments. This unit is most likely of Quaternary age (0 – 4 m).



**Figure 2.** Location of the well site and stratigraphic position of the Tavda Formation (modified after Gnibidenko et al., 2020; Kuzmina et al., 2021).

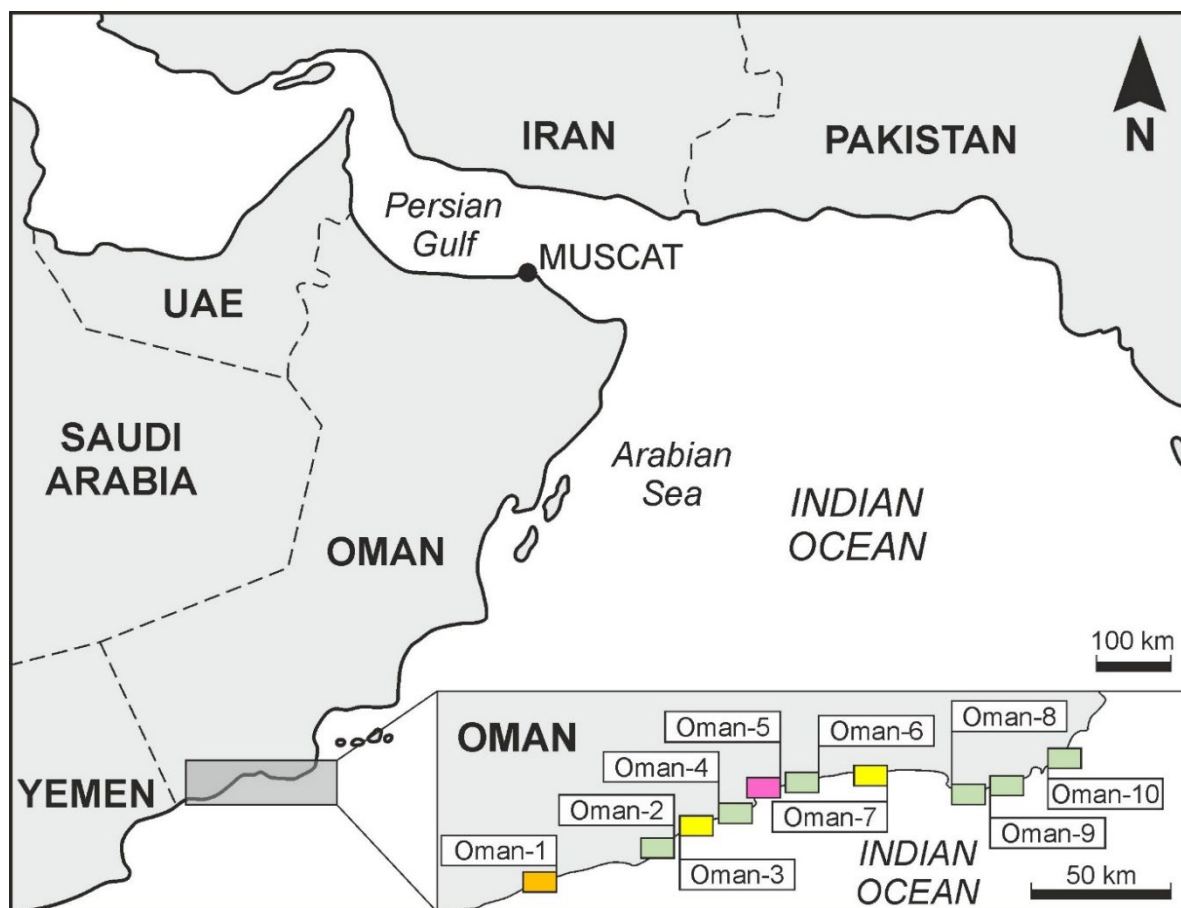
### 1.1.2. Oman coast

The southern region of the Sultanate of Oman is located on the southern tip of the Arabian Peninsula and falls within the monsoon belt. From mid-June to mid-September during the wet monsoon season, this area experiences the effect of cold upwelling waters that rapidly cool the humid winds against the steep escarpment facing the sea. This intense upwelling stimulates a high level of primary productivity that results in extensive phytoplankton blooms and fertilizes the coastal waters (Morrison et al., 1998). Most of the wadi systems in this area are deeply incised canyons that transport seasonal loads of freshwater, while a few serve as permanent water systems. Coastal environments in this region exhibit a remarkable variety, encompassing a mosaic of extensive sand bays, shallow-water embayments with patchy seagrass meadows, harbour inlets, muddy brackish-water inlets, and estuaries, as well as scattered mangrove forests with pure stands of *Avicennia marina*. Tides along the coastlines of Oman display a semidiurnal pattern, with an average daily range of 1.5-2 m and a maximum range of approximately 3 m (Al-Hatrushi et al., 2014; Hereher et al., 2020).

Ten sites were sampled and examined for benthic foraminifera (Fig. 3). The sites cover different shallow-water habitats and are ideally suited as modern counterparts to fossil ecosystems. The sites are located 20-80 m offshore and comprise of four types of shallow-water settings: (a) a muddy tidal-influenced harbor inlet (Dalkut Port = site 1); (b) vast sand bays devoid of phytal coverage (Mughsail Beach, Samharam Beach = sites 3, 7); (c) Sandy bays with associated patches of smaller or more extensive seagrass meadows. These habitats can be found at several locations along the southern coast of Oman, including Fazayat, Oasis, Alhafa, Eagles Bay Beach, and Sadah Port (sites 2, 4, 6, 8–10). In addition to this, muddy inlets lined with stands of *Avicennia marina* mangrove trees are also present at Khwar Al Qurm Al Kabir (site 5). Seagrasses in the region are

mainly patchy or in dense meadows, predominantly consisting of *Halodule universa* and *Thalassodendron ciliatum* (Jupp et al., 1996).

Samples of foraminifera from the southern region of Oman were collected in March 2019 by Martin R. Langer whilst snorkeling. This was achieved by filling small containers (300 ml) with sediment from the top 2 cm. The aim of this protocol was to gather samples of benthic foraminiferal assemblages from differing habitats to provide general environmental information that may be useful in paleoecology. Our samples are therefore time-averaged (total assemblages), presenting a proficient way of delineating habitats (Glenn-Sullivan and Evans, 2001; Langer and Lipps, 2003).



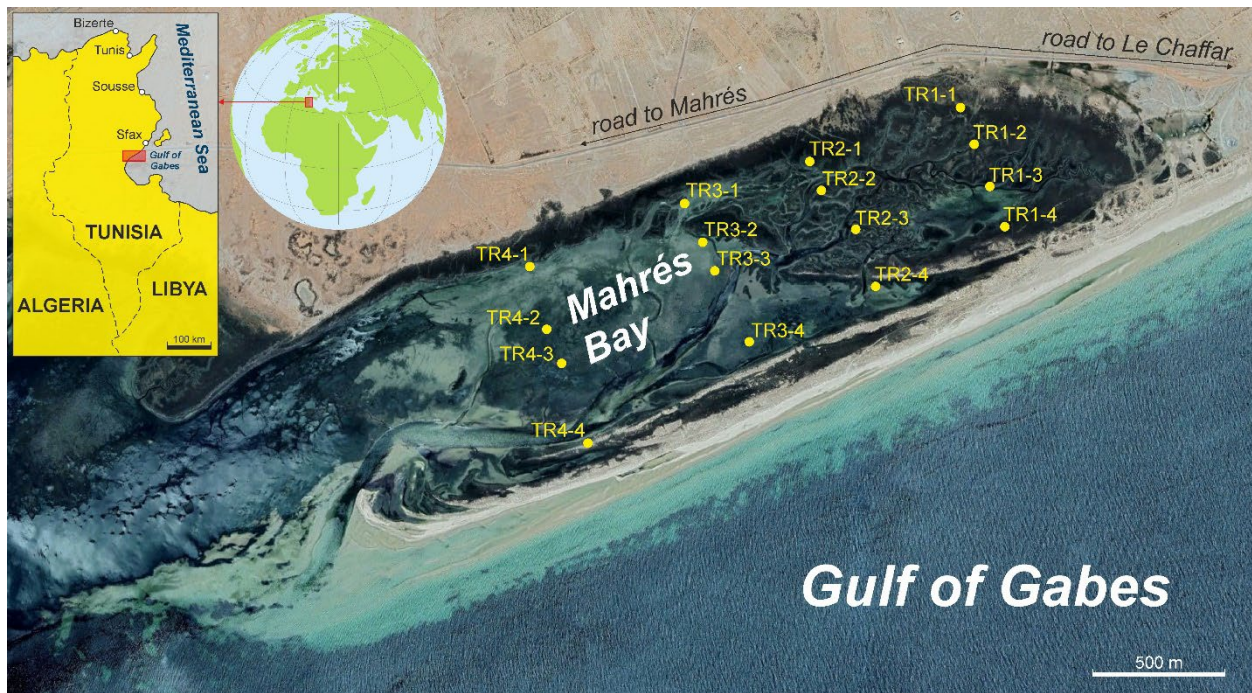
**Figure 3.** Sampling sites along the southern coast of Oman. Color legend: ocher – harbour, yellow – sand bay, green – phytal-associated habitats, and purple – mangrove inlet.

### 1.1.3. Mahrés Bay

Mahrés Lagoon is situated in the northern part of the Gulf of Gabes (Tunisia, Mediterranean Sea) between the towns of Le Chaffar and Mahrés (refer to Fig. 4). The lagoon covers an area of 1.75 km<sup>2</sup>, stretches over approximately 2.8 km in length and cones inward as it progresses. The lagoon's breadth fluctuates between 190 and 770 m. The average depth of water within the tidal channels is approximately 0.5 m at low tide and a maximum of 1.8 m at high tide. The partially enclosed lagoon is separated from the Mediterranean Sea by a long and vastly dynamic sandbank. Interaction between the ocean and lagoon takes place through an entrance nearly 450 meters in width, situated in the southern section, complemented by a smaller tidal channel. The sediments predominantly contain sand, silty sand, and silt, with sand being more prevalent in the southern section of the lagoon while the finer sediment components are found in the northern interior and the tidal channels.

The 16 surface sediment samples were obtained from four transects within the lagoon, oriented across its long axis and encompassing the peripheral high tide areas, inner lagoon, tidal channels, and sample stations along the opposite sandspit. Sampling was conducted in August 2019 using boats and snorkeling during high tide, with approximately 50 mL of sediment from the topmost layer of the seabed collected in 100 mL plastic containers. After allowing the excess water to settle, the remaining water was removed, and sample containers were filled with a solution of 90% ethanol and 2 g of Rose Bengal per liter to stain the cytoplasm of living foraminifera (Murray and Bowser, 2000).





**Figure 4.** Location of simple sites in Mahrés Bay (Gulf of Gabes, Mediterranean Sea).

## 1.2 Previous studies

### 1.2.1. Tibeisale Formation (Lower Paleocene) – previous studies

The Tibeisale Formation is located in the Arctic Region of Western Siberia, and it has been attributed to the Lower Paleocene (Lebedeva, 2006; Marinov and Urman, 2013; Volkova, 2014; Trubin et al., 2022). The formation is characterized by mainly clay deposits, and at its base, there are paleo-permafrost geomorphic features (Buddo et al., 2017). The clay deposits rest on top of marine Cretaceous sandstones (Lebedeva, 2006; Volkova, 2014) and are covered by terrestrial Paleocene sandstone. Gas hydrates sporadically occur within the deposits (Grace and Hart, 1986).

### 1.2.2. Tavda Formation (Upper Eocene) – previous studies

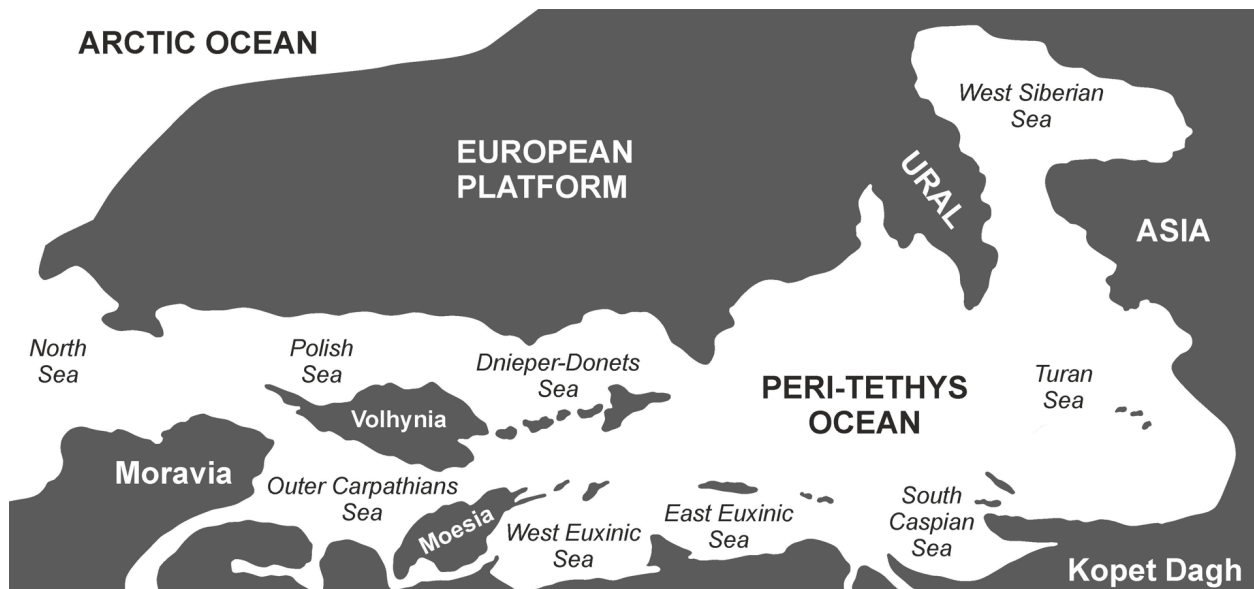
The Tavda Formation extensively covers Western Siberia and lies atop the Lyulinovor Formation, dominated by siliceous rocks comprising diatomite, opoka, and tripolite. This information is supported by multiple sources (Smirnov and Konstantinov, 2017; Trubin and Yan, 2019; Nesterov et al., 2021; Smirnov et al., 2022). Terrestrial sandstones of the Oligocene Kurtamysh Formation cover this formation (Aleksandrova et al., 2012; Kuzmina et al., 2021).

The Tavda Formation's lithology is primarily composed of marine polymineral illite-smectite and montmorillonite blue-green clays with pyrite, marcasite, siderite, and gypsum (Smirnov et al., 2019). The Tavda Formation has been attributed to the Middle and Upper Eocene based on pollen, dinoflagellate cysts, and magnetostratigraphy. This attribution is supported by the works of Akhmet'ev et al. (2004a, b, 2010, 2012), Iakovleva (2000, 2011), Iakovleva and Heilmann-Clausen (2010), Gnibidenko et al. (2020), and Kuzmina et al. (2021). Additional stratigraphic and paleoenvironmental data were obtained from the discovery of shark teeth (Malyskina, 2006, 2012, 2021), remains of teleost bones (Marrama et al., 2019), otoliths (Schwarzahns et al., 2021), mollusks (Trubin, 2018; Popov et al., 2019), and trace fossils (Nesterov et al., 2018). Research on the diversity and biostratigraphy of foraminiferal assemblages had been formerly supplied by Subbotina et al. (1964) and Podobina (1975, 1998, 2020).

During the Middle and Late Eocene, a barrier was established to the Arctic Ocean, causing the transformation of the Siberian Basin into a semi-enclosed basin (refer to Fig. 5). The basin is characterized by sand and clay sediments, incorporating proof of non-permanent Middle Eocene *Azolla* events (Akhmet'ev et al., 2010) as indicated by the presence of organic-rich beds of the freshwater fern *Azolla*. The constriction of the West Siberian Basin resulted in decreased vertical mixing and stratified waters, causing slight anoxia in its bottom waters. The basin gradually closed



around the Eocene-Oligocene boundary, resulting in vast rivers transforming it into an immense river-lake system, which experienced marine water invasions intermittently (Akhmet'ev et al., 2004a, b; Oreshkina et al., 2020; Palcu and Krijgsman, 2022).



**Figure 5.** Paleogeography of the Peri-Tethys region during the Late Eocene (modified after Akhmet'ev et al., 2012, and Palcu and Krijgsman, 2022).

### 1.2.3. Oman coast – previous studies

The Dhofar region, located on the southern coast of Oman, is at the center of one of the world's largest upwelling areas. This results in high primary productivity conditions extending along the coast and up to 300 km offshore (Currie et al., 1973; Locarnini et al., 2019). The shallow water areas provide diverse habitats, consisting of seagrass meadows, mangrove ecosystems, brackish water embayments, harbor inlets, and expansive sand bays, along with the distinctive interaction between coral reefs and macroalgal communities. Coastal regions are notably influenced by upwelling zones, as they shift oligotrophic water masses and influence the establishment and

dispersal of an array of tropical coral reefs and larger symbiont-bearing foraminifera (LBF). The combination of tropical oligotrophic and temperate eutrophic conditions creates species assemblages that are unique worldwide (Wilson, 2000; Schils and Coppejans, 2003; Förderer et al., 2018; Langer et al., 2022). The environmental conditions create the potential for unique foraminiferal faunal assemblages in Oman's modern coastal areas. However, there is a lack of detailed research on these foraminifera, despite extensive studies on tropical foraminifera.

Past research has revealed a clear biogeographic separation between the East-African-Red Sea and eastern Indian Ocean faunal provinces (Reiss and Hottinger, 1984; Langer and Hottinger, 2000; Förderer et al., 2018). Located at a vital position between the biologically diverse Coral Triangle and the tropical Red Sea/eastern African coast, the coastal waters of Oman play a dual role as a biogeographic link and as a cold-water barrier enriched with nutrients for reef-forming symbiotic-bearing taxa (Hood et al., 2017; Spreter et al., 2022).

The coast of Oman is one of the few tropical regions that has not been extensively researched, and where only a limited number of studies on modern benthic foraminifera have been published. These have mainly focused on identifying selective assemblages that indicate overwash/tsunami deposits (Pilarczyk et al., 2011, 2012; Pilarczyk and Reinhardt, 2012). In a previous study, Al-Sayigh et al. (2015) reported the identification of 27 taxa of benthic foraminifera from the northern and southern coastlines of Oman. The shallow-water areas have lower species richness compared to the much higher species numbers found in the inner Arabian Gulf and adjacent areas. However, it is important to note that these data include biotas from greater depth ranges and areas of the deep sea (Amao et al., 2022; see also Chapman, 1895; Stubbings, 1939; Cherif et al., 1997). Modern benthic foraminifera studies, sampled from the deeper regions of the Oman margin (~400-4000 m), have been carried out by Hermelin and Shimmield (1990) and Gooday et al. (2000). They provide data (~100 species) from the deep oxygen minimum zone (OMZ) and beneath.

Foraminiferal assemblages inhabiting extremely shallow-water habitats encounter challenging survival conditions leading to their poor preservation. Dead assemblages originate mainly from post-mortem processes, including out-of-habitat transport and test disintegration. Assemblages undergoing transport and destruction typically exhibit reduced species richness and are susceptible to substantial data loss due to taphonomic processes (Kidwell and Flessa, 1996; Goldstein and Watkins, 1999; Murray and Alve, 1999a, b; Martin et al., 2003).

#### **1.2.4. Mahrés Bay – previous studies**

Wetlands play a significant role in coastal environments in the Gulf of Gabes, Tunisia (Queslati 2022). Situated at the border of land and sea, they offer vital ecosystem services, acting as a shield against waves, floods, and storms, enhancing water quality and providing a habitat and nursery for diverse plant and animal species. Mahrés Bay, located thirty kilometers south of the city of Sfax, is a comparatively small lagoon that is semi-close and ensconced by intertidal saltmarsh vegetation. The lagoon is protected from the ocean by a sandspit barrier and linked to it by way of a shallow tidal conduit. At the rear of the sandspit barrier, an assemblage of vegetated wetland saltmarshes and sandy and muddy tidal flats has evolved, crossed through by an extensive network of tidal channels. The lagoon comprises a variety of habitats, including extensive meadows of the halophytic flowering plant *Salicornia* (*Sarcocornia fruticosa*), tidal channels, and sand and mud flats partially covered by microbial cyanobacteria mats. Along its fringes and some parts of the sandspit, the lagoon harbors species of halophile seepweeds (*Suaeda vermiculata* and *Suaeda maritima*). These areas can be found at the highest position where seawater covers the roots only during extreme tides. Habitats located in intertidal zones are stratified vertically due to tidal actions. The areas exhibit a range, starting from peripheral regions that are overgrown with *Suaeda*

seepweeds, to *Salicornia* marsh meadows which are somewhat deeper and densely populated in some places, followed by mud and sand flats situated towards the south, and deeper intertidal channels.

### **1.3. Methods and proxies**

#### **1.3.1. Preparation and identification fossil foraminifera**

Chemical preparations for the analysis of microbiota involved dissolving rock samples in hot water with NaCO<sub>3</sub> followed by wet-sieving them via freshwater over 63 µm mesh sieves. The residues obtained after sieving were then dried in an oven at 50°C. Dried sediments were subsequently investigated for foraminifera employing a microscope and Scanning Electron Microscopy (SEM) photography.

Individual foraminifera specimens were then picked and identified to species-level followed by recording of numerical abundances of each species. For consistency with existing literature, the list of taxa recorded from the Tibeisale Formation (Burgrova, 2008) and Tavda Formation (Akhmet'ev et al., 2004a, b; 2010; 2012) serves as the basis for identifying benthic foraminifera. Additional sources describing new species (Voloshinova and Dain, 1952; Vasilenko, 1954; Eremeeva and Belousova, 1961; Subbotina et al., 1964; Podobina, 1975, and 1998) were also consulted. This also includes SEM studies of foraminifera from Western Siberia (Amon and Marinov, 2011; Marinov, 2019), and recent updates and revisions (Kaminski, 2005; Anan, 2010, 2020, 2021; Holbourn et al., 2013; Mahfouz et al., 2018; Govindan and Vijayan, 2019; Besen et al., 2021).

### **1.3.2. Preparation techniques for recent foraminifera**

All samples were sieved using a 63- $\mu\text{m}$  mesh and dried. Subsequently, foraminifera were picked from each sample, identified to species level, and counted. To compare diverse samples, rarefaction was utilized according to Ludwig and Reynolds (1988), whereby foraminifera were picked from each sample until no new species were detected. This study entailed the careful selection and analysis of hundreds of specimens, apart from a limited number of samples that contained less than 200 specimens. All identified species were illustrated and documented through the utilization of SEM photography.

### **1.3.3. Structure and composition foraminiferal assemblages**

The investigation of foraminiferal biotas is based on assemblages comprising live and dead specimens, which in turn provide time-averaged data reflecting predominant long-term environmental conditions. These faunal accumulations eliminate short-term fluctuations (Martin et al., 2003) and serve as useful indicators in paleoenvironmental studies (Glenn-Sullivan and Evans, 2001). All statistical analyses were computed using the Paleontological Statistics software package for education and data analysis, ver. 3.18 (Hammer et al., 2001) or Microsoft Excel.

Recorded were the abundances of wall structural types (agglutinated, porcelaneous, and hyaline-perforate), and the percent abundances of each individual group were documented. The data was then plotted into a ternary diagram to determine wall type composition, as per the method introduced by Murray (1973). This technique is widely used in foraminiferal studies to differentiate major shallow-water environments and compare the structure of foraminiferal biotas from different habitat typologies.

To examine the structure and composition of foraminiferal faunas, we computed the relative abundances (RA) and frequencies of occurrence (FO) of diverse genera and species. To calculate the RA, we employed the formula:  $RA = n*(100/T)$ , where  $n$  represents the count of taxon individuals and  $T$  denotes the total number of benthic foraminiferal specimens in the sample. To establish the distribution of each taxon across the samples, the FO was computed using the formula  $FO = p*(100/P)$ , where  $p$  represents the number of samples containing the taxon and  $P$  is the total sample count. Stratigraphic occurrence and habitat distribution were given particular emphasis. The distribution and abundance of symbiotic-bearing larger benthic foraminifera (LBF) at various localities were assessed. The species abundances and distributions of the key LBF families, namely Amphisteginidae and Calcarinidae, were examined in detail.

#### **1.3.4. Species richness and diversity**

Species diversity was assessed using Fisher's alpha ( $\alpha$  or SFisher), Shannon's H (or H') and Equitability (J) indices. The logarithmic series model, developed by Fisher et al. (1943), mathematically describes the relationship between the total number of individual specimens and the number of species, assuming species abundance follows a log distribution. The Shannon H diversity index takes into consideration both the number of individuals and the number of species present. The range of equitability values varies from 0 for assemblages that comprise a single species to higher values for assemblages that contain multiple species. Equitability evaluates the evenness of the distribution of individuals among species in a community. The value of equitability ranges between 0 and 1, where a value of 1 indicates complete evenness of distribution.

### 1.3.5. Morphotype analysis

Based on prior morphotype analysis by Corliss (1985), Bernhard (1986), Corliss and Chen (1988), Jorissen et al., (1992), and Jones and Charnock (1985), we classified individual taxa based on their preferences for infaunal and epifaunal microhabitats to evaluate the oxygen conditions of the depositional environment. Epibenthic taxa exhibit high and low trochospiral, biconvex or planoconvex tests, whereas infaunal species display lenticular, ovate, spherical, tapered, elongate flattened, or cylindrical tests. These features are indicative of different species' adaptations to their environments.

To determine the oxygen content of the surrounding waters during deposition, we analyzed the ratio of oxic and dysoxic benthic foraminifera morphotypes. This analysis enabled us to estimate the foraminiferal dissolved oxygen index (FDOI) using the following equation:  $\{[O/(O + D)] \times 100\}$ , where O and D represent the number of oxic and dysoxic foraminifera specimens, respectively (Kaiho, 1994). Paleo-dissolved oxygen levels (OL) display variability from -55 to 100 and correspond to anoxic (OI = -55, OL=0.0-0.1 ml/L), dysoxic (OI = -50 - -40, OL = 0.1 - 0.3 ml/L), suboxic (OI = -40 - 0, OL = 0.3 -1.5 ml/L), low oxic (OI = 0 - 50, OL = 1.5 - 3.0 ml/L), and high oxic (OI = 50 - 100, OL = 3.0 - >6.0 ml/L) environments (Kaiho, 1994).

### 1.3.6. Bioerosion structures

The analysis of the bioerosion structures on the surface of foraminiferal tests originated in the early 20th century (Heron-Allen, 1915; Livan, 1937). Sliter (1971, 1975) pioneered the classification of holes in foraminiferal tests. The classification is based on objective features, such as the shape and orientation of structures in space. This enables the distinction of two groups: the

first comprises rounded and oval holes located at an angle to the surface, while the second is made up only of rounded holes-oriented perpendicular to the surface. As a result of further study, the ichnogenus *Oichnus* Bromley, 1981 was established, which is composed of two ichnospecies. *Oichnus simplex* Bromley, 1981 and *O. paraboloides* Bromley, 1981 are united under the ichnogenus, with the former being considered the type. This classification includes all subcircular and suboval small holes found on foraminiferal tests and mollusk shells. This information is based on Bromley's research from 1981, with additional information provided by Nielsen and Nielsen in 2001 (pp. 102-103) and Wisshak et al. in 2015 (pp. 448-449). The identification of ichnospecies involves assessing the shape of longitudinal and transverse sections, as well as the nature of the outer contour of the holes (Bromley, 1981; 1993; 2004; Kowalewski, 1993; Wisshak et al., 2015). Since Brett's (1985) proposal of the new ichnogenus *Tremichnus*, which features similar but non-penetrating small pits on the shell surface, a series of ongoing discussions have been ignited (Brett, 1985; Nielsen and Nielsen, 2001; Zonneveld and Gingras, 2014; Wisshak et al., 2015; 2019). During further investigation, Wisshak et al. (2019) established five additional ichnospecies that are presently accepted. These are *Oichnus ovalis* Bromley, 1993, *O. cornatus* Nielsen et Nielsen, 2001, *O. asperus* Nielsen et Nielsen, 2001, *O. gradatus* Nielsen et Nielsen, 2001, and *O. solus* (Nielsen et al., 2003). According to Wisshak et al. (2019), we allocate the ichnogenus *Oichnus* to the ichnofamily Oichnidae and to either Praedichnia (predation traces) or Fixichnia (attachment traces) based on the ethological category. Studies on bioerosion structures provide information about potential predators, the structure of associated faunal assemblages, the preservation of foraminiferal shells and the surrounding habitat. This information is vital for paleoenvironmental inferences and useful for paleoecological reconstructions.



### 1.3.7. Preservation status

To investigate the impact of wave action on the resilience of foraminiferal tests in very shallow coastal habitats, we conducted a systematic analysis of the tests and applied a grading system for preservation. This method has proved valuable for recording alterations to the environment (Weinmann and Langer, 2017; Pavlopoulos et al., 2018). Previous research has indicated that well-preserved foraminiferal tests are reliable proxies for the living or in situ fauna, while poorly preserved tests may originate from an allochthonous source or have been reworked (Yordanova and Hohenegger, 2002). Our classification system for foraminiferal tests aligns with the work of Yordanova & Hohenegger (2002) and Weinmann and Langer (2017) and categorizes them into four groups. (1) Specimens classified as «well preserved» show no signs or only minor instances of microscopic damage. (2) «Moderately preserved» tests display slight abrasion and/or breakage. (3) For «abraded and broken» specimens, distinct features of abrasion, depressions, pits, or scratches are visible on the overall shape and outline of the test, often accompanied by breakage of chambers and spines, as described by Cottey and Hallock (1988). Peebles and Lewis (1991) found that fully damaged, broken, and abraded tests show clear signs of transport or reworking, which alter the overall shape and outline of the test. The tests exhibit damages, breakages, strong abrasions, and polished surfaces where most of the test ornaments are fully abraded (Peebles and Lewis, 1991; Yordanova and Hohenegger, 2002; Weinmann and Langer, 2017). Identification of species in this state of preservation is based on the few remaining morphological details, requiring substantial expertise, and causing frustration for many morphologists (Kidwell and Flessa, 1996). Percentages of each category were calculated by site and habitat and presented in diagrams. Studies on the preservation of foraminiferal test allow inferences about past energy systems and

current conditions and can be used to assess whether faunas were deposited in situ or transported out-of-habitat.

### 1.3.8. Geochemical proxies

Geochemical sediment analysis involved measurements on the relative abundance of 14 elements (Si, Al, Cu, Mo, Ti, K, Zn, V, Sr, Ba, Ca, Na, Th, and U). The measurements were taken on powdered material for all 65 samples at micrometer size, where the powder was stacked in capsules and covered by plastic membrane. The levels of biogenic-fractionated elements (Cu, Mo, and V) and terrigenous associated elements (Si, Ti, K, Zn; Chagué-Gof et al., 2002; Affouri et al., 2017; Judd et al., 2017) were standardized to Al (Martinez-Ruiz et al., 2015), with the aim of identifying the origin of the terrigenous sediment (Engel et al., 2016). Due to variable proportions of biogenic and detrital minerals, bulk element concentrations may fluctuate significantly. To serve as paleoenvironmental proxies, we utilized the normalized concentrations of Al rather than major bulk concentrations. The characteristics of the terrigenous fraction provide information about the origin and source of detrital input into the basin. The indices of Si/Al, Ti/Al and Zr/Al were utilized to evaluate aeolian detrital and the K/Al index for riverine detrital influx (Tribovillard et al., 2006; Soua, 2011; Natalicchio et al., 2019). The V/Cr index acted as a proxy for paleoxygenation and redox conditions, U/Th for paleoproductivity, and Sr/Ba for salinity (Brumsack, 1986, 2006; Jones and Manning, 1994; Calvert and Pedersen, 2007; Martinez-Ruiz et al., 2015; Zhang et al., 2021). The Chemical Index of Alteration (CIA) was employed to evaluate the degree of feldspar transformation to clay, influenced by distinct climatic circumstances. It is computed utilizing molar proportions as  $CIA = 100 (Al_2O_3 / (Al_2O_3 + CaO^* + Na_2O + K_2O))$ , where CaO\* denotes the volume of CaO incorporated in the silicate fraction of the rock.

To evaluate the TOC concentration, specimens were subjected to a high temperature of 450°C for 16 hours to break down the organic components. By taking away the TIC from the Total Carbon (TC), the TOC values were computed. The inorganic carbon content (TIC) was then measured by means of a EL vario cube element analyzer. Prior to this, the TC amount was determined using the vario EL cube. The loss on ignition at 450°C was established twice (duplicate determination). Variations in major geochemical element ratios, sediment texture and structure, paleontological and organic matter richness data were utilized to characterize facies types across all cores and to infer changes to the environment.

#### **1.4. Aim and outline of this study**

Benthic foraminifera widely occur in recent and ancient marine sediment basins and are well-known as excellent proxies and sensitive bioindicators of environmental disturbances. However, the ecosystems which were studied through benthic foraminifera were situated under variable conditions. Therefore, the need for comprehensive studies and independent lines of evidence on the structure, distribution, diversity of benthic foraminifera was employed to infer paleoenvironmental conditions.

## Chapter 2

**Published in *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen***

Title: Lower Paleocene foraminiferal assemblages from the Tibeisale Formation in the Arctic region of Western Siberia

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Authors: **Yaroslav S. Trubin**, Vladimir A. Marinov, Pavel V. Smirnov, Andrey A. Novoselov, Martin R. Langer

Contributions: M.R.L. and Y.S.T. designed the study including the methodology and performed the investigation. Y.S.T. and M.R.L. wrote the original manuscript. All authors discussed the results and contributed to the final manuscript. P.V.S. and M.R.L. acquired the funding.

### Summary

The Tibeisale Formation's marine clay deposits are expansive on the Yamal Peninsula in western Siberia and overlie Cretaceous sandstones. According to biostratigraphic research the deposits have been attributed to the Lower Paleocene. However, their age remains uncertain due to the absence of zonal index markers. The composition, structure, and diversity of benthic foraminiferal assemblages from core material collected at the Kharasavey drill site on the Yamal Peninsula were studied to determine the biostratigraphic age, reconstruct the depositional environment of the Tibeisale Formation, and infer the response of benthic foraminifera to changes in oxygen content in the surrounding waters. Based on biostratigraphical marker species, analysis of foraminifera assemblages, and lithological successions, a Danian age can be inferred for the time of deposition. The composition and numerical analysis of the foraminiferal faunas suggest that the deposit occurred in well-oxygenated waters from deep to shallow shelf areas.

## Chapter 3

**Accepted in *Micropaleontology***

Title: Upper Eocene benthic foraminiferal assemblages from the Western Siberia (Trans-Ural Region): a multi-proxy approach to infer environmental changes

Authors: **Yaroslav S. Trubin**, Vladimir A. Marinov, Pavel V. Smirnov, Andrey A. Novoselov, Martin R. Langer

Contributions: M.R.L. and Y.S.T. designed the study including the methodology and performed the investigation. Y.S.T. and M.R.L. wrote the original manuscript. All authors discussed the results and contributed to the final manuscript. P.V.S. and M.R.L. acquired the funding.

## Summary

During the Late Eocene, the West Siberian Basin experienced a gradual isolation from the Peri-Tethys Ocean. No subjective evaluations have been included. The Tavda Formation sediments, deposited during the Bartonian and Priabonian epochs, signify the final stage of this marine connection. The analysis of benthic foraminiferal assemblages in core material from the Kyshtyrla Quarry, situated in the southwest of Western Siberia, enabled us to reconstruct the depositional environment during the concluding phase of marine sedimentation in the West Siberian Basin (Upper Tavda Subformation). Herein, we examined the composition, structure, and diversity of these assemblages. The chronology of events that led to the complete closure of the basin was inferred by utilizing the foraminiferal record along with lithological and geochemical multi-proxy data. The Upper Tavda Subformation sediments are suggested to be of Priabonian age based on stratigraphic index markers. From the base to the summit of the core, the foraminiferal biotas gradually transition from shallow subtidal to intertidal assemblages that are low in diversity and

stress tolerant. This suggests a growing isolation of the West Siberian Basin. The gradual shallowing of the marine basin is concurrent with a change in grain size. The continuous presence of benthic foraminifera, as well as ratios of geochemical proxies (Sr/Ba, Si/Al, Ti/Al, Zr/Al, K/Al, and U/Th), suggests that predominantly marine to brackish water conditions were prevalent.

## Chapter 4

### **Published in *Paleontological Journal***

Title: Bioerosion Structures on Benthic foraminiferal tests from the Upper Cretaceous and Paleogene of Western Siberia

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Authors: **Yaroslav S. Trubin**, Vladimir A. Marinov, Igor N. Kosenko, Pavel V. Smirnov, Andrey A. Novoselov

Contributions: Y.S.T. and V.A.M. designed the study including the methodology and performed the investigation. Y.S.T., V.A.M., I.N.K., P.V.S., and A.A.N. wrote the original manuscript. All authors discussed the results and contributed to the final manuscript. P.V.S. acquired the funding.

### Summary

Bioerosion structures, such as holes, pits, and grooves, found on the surface of benthic foraminiferal tests from the Upper Cretaceous and Paleogene of Western Siberia have been analysed. The morphology is examined, their potential origin and the paleogeographic and stratigraphic distribution within sections illustrating marine basins of Western Siberia are discussed. The assemblage of ichnospecies under examination comprises *Oichnus simplex* Bromley, 1981, *O. paraboloides* Bromley, 1981, *O. gradatus* Nielsen and Nielsen, 2001, and *O. ovalis* Bromley, 1993.

## Chapter 5

**Published in *The Journal of Foraminiferal Research***

Title: Environmental signatures preserved in extremely shallow-water benthic foraminifera assemblages from Oman, Arabian Sea

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Contributions: M.R.L. and Y.S.T. designed the study including the methodology, performed the investigation and wrote the original manuscript. All authors discussed the results and contributed to the final manuscript. M.R.L. acquired the funding.

## Summary

The composition and preservation of testate foraminiferal assemblages are of paramount importance for palaeoenvironmental and palaeoclimatic reconstructions. However, coastal nearshore areas are often subject to harsh conditions, being shaped by continuous wave action and exposed to turbulence, erosion, and dynamic processes of sediment reworking. Located at the interface between land and water, the environmental signatures preserved in coastal benthic foraminiferal assemblages are therefore prone to taphonomic changes that can potentially bias the fossil record and compromise accurate reconstructions. In this study, we analyzed the composition and preservation of benthic foraminifera from a range of extremely shallow-water habitats along the Dhofar coast (Oman) to document assemblage structure and illustrate species richness. Our analyses show that extremely shallow-water foraminiferal assemblages from the southern coast of Oman retain the environmental signatures of their habitats despite intense environmental processes, making them useful for paleoenvironmental studies. Characteristics of these signatures



are recorded in the structural composition, species richness, dominance, and diversity indices of foraminiferal communities, in addition to the numerical abundances of shell preservation groups.

## Chapter 6

**Published in *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen***

Title: Distribution patterns of living benthic foraminifera in Mahrés Bay (Gulf of Gabes, Tunisia):

Linking habitats and faunal components

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Authors: Mohamed Kamoun, **Yaroslav S. Trubin**, Khawla Ben Khalifa, Chahira Zaibi, and Martin R. Langer

Contributions: M.K., K.B.K., and M.R.L. designed the study including the methodology and performed the investigation. C.Z performed the laboratory analyses. M.K. and Y.S.T. prepared the graphics. M.R.L., M.K., and Y.S.T. wrote the manuscript.

## Summary

Living benthic foraminifera from Mahrés Bay (Gulf of Gabes, Tunisia) were analysed to document the spatial distribution of species and to relate assemblage composition to habitat characteristics and environmental conditions. Mahrés Bay is a shallow, semi-enclosed coastal lagoon characterised by a variety of habitats including tidal channels, mudflats, sandflats, algae, and seagrass beds, salicornia and suaeva salt marshes, and has been gradually formed by the formation of a sand spit south of Le Chaffar promontory. Analysis of the foraminiferal fauna shows that the bay is characterised by a low diversity fauna, but individual habitats are characterised by distinct faunal communities and the dominance of a few indicator species. On the high intertidal inner margins, the dense *Salicornia* salt marshes are dominated by the agglutinated foraminifer *Trochammina inflata*. The less dense *Salicornia* meadows, the central inner part of the lagoon and the areas along the tidal channels are predominantly colonised by *Ammonia* species. Milioids and

other associated species are mainly found in the southern part of the lagoon facing the sea and in the deeper tidal channels near the entrance channel but may also be distributed in patches.

The areas colonised by *Trochammina* and *Ammonia* show a clear spatial separation. The spatial partitioning is evident in both cluster and ternary diagram analysis, indicating minimal lateral exchange of faunas or transport outside their habitat. The highest abundances of living benthic foraminifera were found in the innermost northern areas covered by *Salicornia* meadows. Benthic diversity and species richness are generally low, increasing slightly towards the open entrance of the lagoon and peaking in the algal-covered southern part near the deepest tidal channel. Throughout the lagoon, dominance indices are generally high, with maximum values at the highest tidal levels along the inner sandbank and in the innermost northernmost part. The individual composition of habitat-specific faunas, the observed patterns of diversity and abundance, and the presence of indicator species are of interest for reconstructing the evolution of coastal bays and for interpreting past coastal habitats.

## Chapter 7

### **Discussion and Conclusions**

Studies of foraminiferal assemblages from the Paleogene of Western Siberia have provided new information on the paleoenvironmental conditions of ancient marine basins and on the biodiversity and biostratigraphy. In this chapter, these are discussed in comparison with previous studies.

During the Early Paleocene, western Siberia was covered by an epicontinental sea connecting the high Arctic Ocean and the remnants of the northern Tethys Ocean via the Turgay Strait. As expected for high latitude regions, species richness (25 taxa) and diversity (Fisher  $\alpha = 0.3-4.0$ ) of foraminiferal assemblages were generally low, but higher than in time-equivalent strata where species richness is strongly restricted to agglutinated and endemic taxa (Young and McNeil, 1984; McNeil, 1990; Backman and Moran, 2009; Akmet'ev et al., 2010). Whether calcareous plankton groups were excluded from the High Arctic Ocean due to unfavorable palaeoecological conditions or whether their absence reflects a preservation bias (level of carbonate compensation depth (CCD): low pH and alkalinity) is still under debate (Backman and Moran, 2009). To date, there is no consensus to explain the overall decline in diversity with increasing latitude, but it is most likely due to a variety of complex interactions, including less available energy and light in area at high latitudes, extreme seasonality, short time spans for diversification, and the comparatively young age of the ecosystem.

In contrast to the High Arctic Ocean, the new Yamal core material from Western Siberia consists mainly of hyaline perforated forms. Agglutinated foraminifers are rare and planktonic foraminifers are completely absent (see also Bugrova, 2008). This finding agrees with studies by Podobina (2003), who reported abundant calcareous benthic foraminifers from the southwestern part of the basin in the Omsk Depression (Maastrichtian to Lower Danian) and agglutinated taxa from

shallow Danian deposits of the Ust-Tym Depression (Bathysiphon, Glomospira, Ammodiscus), and the Selandian and Thanetian. In addition, the faunal assemblages recorded by Podobina (1998) indicate a fall in sea level during the Early Paleocene (Early Danian), a transgression during the Selandian, and again a shallow rise during the Thanetian.

Bernhard (1986) reported that fossil anaerobic and low-oxygen foraminifera (anoxic and dysoxic) are characterized by flattened test forms, whereas foraminifers from aerobic (oxygenated) environments have more spherical test morphologies (Table 2). Anaerobic and low-oxygen species are represented by *Bolivina?* sp, *Bulimina* sp, *Glodocassidulina* sp, *Guttulina communis* and *Guttulina* sp, in addition to species of *Ammodiscus* and *Cibicidoides* that can survive in areas close to anoxic conditions (Kaiho, 1991; Alve, 1995). True anaerobic taxa were rare in our assemblages. Accordingly, the foraminiferal dissolved oxygen indices (FDOI) of the assemblages were relatively high, ranging between ~70-90. The monospecific assemblages (Samples 8 and 9) and Sample 11 (dominated by *Cibicidoides* and Gavelinellinae) are composed of oxic species only and the FDOI is 100. Therefore, according to Kaiho (1994), the environment can be considered as well oxygenated. However, the percent abundances of infaunal morphotypes varied along the core, suggesting that oxygen concentrations and/or carbon flux rates to the sediments varied over time. The presence of monospecific assemblages is unusual (*Cibicidoides proprius*) and suggests that selective preservation mechanisms were involved. A reliable and detailed reconstruction of the prevailing environmental conditions is therefore limited.

The dominant faunal assemblages (*Cibicidoides*, Gavelinellinae, and Pulleniinae) occur over a wide bathymetric range and typical shallow water indicator taxa are largely absent. In addition, rare but well-preserved smaller miliolids indicate that allochthonous species were occasionally introduced into deeper habitats from nearby shallow water areas. A deep-water shelf environment extending from a deeper shelf environment towards the slope is therefore conceivable and may

include deep-water canyons that may have facilitated the downward transport of shallow-water taxa. Reconstructions of environmental conditions are further complicated by documented phases of transgression and regression during the Danian and Selandian time intervals (Iakovleva, 2000; Volkova, 2014). A distinct shallow upward trend towards the top of the core is indicated by the presence of abundant Elphidiidae (*Elphidium* and *Criboelphidium*), genera that are common in shallow (inner shelf), well-oxygenated environments of the Paleocene photic zone. The foraminiferal faunal composition along the cores thus traces an evolution from a steeply sloping shelf to a shallow inner shelf environment, consistent with the palaeogeographic position of Western Siberia, which connects the High Arctic with the northern remnants of the Tethys Ocean through a shallow basin.

During the Late Eocene, the West Siberian Basin was a shallow epicontinental sea connected to the Peri-Tethys by the narrow Turgay Strait (Akhmet'ev et al., 2010). As the West Siberian Basin became increasingly isolated from the Tethys Ocean (Akhmet'ev et al., 2010, 2012; Palcu and Krijgsman, 2022), the inflow of marine waters was further reduced, and conditions changed to a system where rivers became dominant. The chronology of the basins' increasing isolation and limited exchange with the Peri-Tethys Ocean waters is reflected in (1) the composition and diversity of the benthic foraminiferal fauna, (2) geochemical proxies, and (3) grain size distributions.

As mentioned above, the foraminiferal assemblages recorded in the core material include typical stratigraphic indicator taxa for the Priabonian Upper part of Tavda Subformation (Akhmet'ev et al., 2010). The benthic foraminiferal assemblages recovered are characterized by low indices of species richness and diversity and consist mainly of taxa indicative of shallow-water subtidal and intertidal conditions (Murray, 2006). However, abundance, species richness and diversity values decrease significantly from the bottom to the top of the section, suggesting an increase in

environmental stressors. The lowermost units (Units 1-3 and the lower part of Unit 4; 60-33 m core depth) comprise an assemblage of moderately low diversity subtidal and intertidal taxa (*Miliolinella*, *Cibicides*, *Criboelphidium*, *Porosononion*, *Ammonia*, *Trochammina*) with Fisher  $\alpha$  values up to 5. The upper core units are almost exclusively composed of monospecific, typically intertidal and stress tolerant species (e.g. *Ammonia*, *Trochammina*; Murray, 2006; Debenay, 2000; Scott, 2001; Fajemila et al., 2020; Langer et al., 2016a, b; Hayward et al., 2021). The pronounced decline in diversity and species richness towards the top of the section is accompanied by a marked decline in the abundance of individual taxa and associated diversity indices. The degradation of environmental conditions is also evident in the composition of wall structural types, which show a three-stage change from a fauna dominated by miliolids and hyaline perforated taxa, to a predominantly hyaline perforated fauna, and finally to a purely agglutinated foraminiferal fauna. The faunal changes recorded from the bottom to the top of the core are considered to indicate a transition from a shallow subtidal to a tidally influenced habitat, a scenario consistent with (1) the findings of Akhmet'ev et al. (2010), who noted a regression at the end of the Priabonian, and (2) increasing SC values from the bottom to the top of the core. In the upper part, gypsum crystals are abundant on pyrite sand aggregates. Their occurrence is probably related to the oxidation of the sulphidic primary sediments (Pirlet et al., 2010).

The geochemical background throughout the core interval in terms of Si/Al, Ti/Al, Zr/Al, K/Al, V/Cr and U/Th ratios, as well as the CIA index, remains comparatively stable, except for a few low amplitude fluctuations at about 15 and 33 m core depth. These proxies are commonly used to infer weathering rates, salinity changes, oxygenation conditions, and redox states (Jones and Manning, 1994; Martinez-Ruiz et al., 2015; Zhang et al., 2021). The ratio values of the redox-sensitive markers V/Cr remained low ( $<2$ ) throughout the core, indicating oxic environmental conditions at the time of deposition (Jones and Manning, 1994; Ferriday and Montenari, 2016).

The CIA index has been widely used as a proxy for chemical weathering, with higher CIA values indicating increased conversion of feldspars to clays and higher chemical weathering rates (Nesbitt and Young, 1982, Li and Yang, 2010). The record of a strong negative amplitude at about 33 m may indicate a short pulse of higher physical than chemical weathering rates, consistent with a peak in U/Th and lower Si/Al, Ti/Al, Zr/Al, K/Al indices in this core interval.

Low Sr/Ba values ( $<1.0$ ) were recorded throughout the core. In theory, values below 1.0 are typical of terrestrial sediments, as Ba is typically enriched in terrestrial and freshwater sediments and Sr is poor compared to marine deposits (Zwolsman and van Eck, 1999; Wang et al., 2021; Dashtgard et al., 2022). However, the continuous presence of shallow marine benthic foraminifera clearly indicates marine or brackish water conditions (Iglukowska and Pawłowska, 2015), which is consistent with very low Sr/Ba records ( $< 1$ ) from marine sediments (Ross and Bustin, 2009; Wei and Algeo, 2020; Wang et al., 2021). Remnants, traces or deposits of the freshwater fern *Azolla*, an indicator of freshwater pulses, were not found throughout the core. The prevalence of predominantly marine conditions is underlined by the full suite of geochemical proxies (Sr/Ba as a proxy for salinity, accompanied by low detrital indices of Si/Al, Ti/Al, Zr/Al, K/Al and U/Th as proxies for weathering and chemical alteration) and the continued presence of benthic foraminifers. Consistently higher levels of copper and molybdenum, elements that perform vital metabolic functions in biological systems, also suggest that marine conditions were more conducive to life in the lower core area, consistent with a scenario of increasing isolation of the West Siberian Basin. The analysis of litho-geochemical and micropaleontological multiproxy data from the core material of the Kyshtyrla quarry in Western Siberia thus provides a basis for reconstructing the environmental conditions that document the transition from an open to an increasingly isolated basin.



The study of bioerosion structures on foraminiferal specimens has provided new information on palaeoecological relationships between foraminifera and predators and epibionts from the Paleogene West Siberian seas. Investigated *Oichnus* holes are mainly interpreted as evidence of predation to obtain nutrients from cell cytoplasm (Douglas, 1973; Arnold et al., 1985). Some foraminiferal assemblages may have been posthumously colonized and their chambers were used as a habitata or shelter for other organisms (Sliter, 1971, 1975; Culver and Lipps, 2003). Evidence for this may be the frequent occurrence of nematodes in partially emptied chambers of living or completely empty chambers of dead benthic foraminifers in laboratory cultures (Sliter, 1965), although this behavior is rare in the natural population (Sliter, 1971). Therefore, the formation of such holes on living foraminifera by epibionts cannot be excluded (Lipps, 1988; Todd, 1965; Banner, 1971; Alexander and DeLaca, 1987; Cherchi and Schroeder, 1991; Wisshak et al., 2019). By analogy with similar large structures, the perforation holes in *Oichnus* could have been made by predatory gastropods, especially their juvenile forms (Shonman and Nybakken, 1978; Arnold et al., 1985). However, this assumption is questionable (Sliter, 1971) because gastropods, even juveniles, make larger holes than those observed on foraminiferal shells (Arnold et al., 1985). These holes were more likely made by smaller, soft-bodied organisms, most likely nematodes or polychaetas (Sliter, 1971, 1975; Douglas, 1973). Scaphopods (Bilyard, 1974; Langer et al., 1995), some sipunculids (Heeger, 1990) or isopods (Svavarsson et al., 1991) are also sometimes considered to be borers in *Oichnus*.

Studies on recent foraminiferal assemblages have provided a better understanding of the occurrence of biota in different habitats using actuopalaeontological approaches. Within the frame of this study I provided the first faunal inventory and environmental analysis of recent benthic foraminifera from extremely shallow-water habitats along the upwelling-influenced coast of southern Oman. As expected for extremely shallow-water benthic foraminiferal assemblages,

species richness and Fisher  $\alpha$  diversity values of individual samples were generally low (16-34 species, Fisher  $\alpha$  = 4.5-6.8), but showed a clear trend towards higher values in habitats with patches of phytal cover, reaching the highest values at the sampling site within a dense seagrass meadow (Site 9, Eagles Bay). In contrast, monotonous sandy bays (sites 3 and 7) showed significantly lower values (16-20 species, Fisher  $\alpha$  = 3.5-4.9). Moderate species richness and Fisher  $\alpha$  values were recorded from the semi-enclosed harbor and muddy mangrove bay habitats (18-22 species, Fisher  $\alpha$  = 5.0-5.8; Table 2). Species richness and Fisher  $\alpha$  trends are reflected in both Shannon H' and SID values, supporting the conclusion that habitats with plant coverage contain more diverse and heterogeneous foraminiferal biotas than sandy bays.

The low-diversity biotas are consistent with previous shallow-water studies from Oman (Pilarczyk et al., 2011; Pilarczyk and Reinhardt, 2012; Al-Sayigh et al., 2015), with shallow-water faunal data from the African coast (Langer et al., 2013, 2016a, b; Thissen and Langer, 2017; Weinmann and Langer, 2017), and the Oman assemblages can be classified as low-diversity faunas according to the diversity categories established by Langer and Lipps (2003) and Förderer and Langer (2018; with Fisher  $\alpha$  indices <10). The low species richness is undoubtedly due to the shallow depths studied at our sites, where rough, turbulent and dynamic processes of sediment transport and reworking occur, and where the record is further filtered by intense taphonomic processes that particularly affect thin-shelled and fragile taxa and favor the preservation of robust, large and thick-shelled specimens (Goldstein and Watkins, 1999; Murray and Alve, 1999a, b; Martin et al., 2003).

As outlined above and summarized in Table 4, a variety of features characterize foraminiferal assemblages from different shallow water habitats along the southern coast of Oman. These include the composition, species richness, diversity, dominance, and preservation of the benthic foraminiferal biotas. Assemblages from phytal-associated habitats contained mainly

amphisteginids, variable amounts of smaller miliolids, elphidiids and *Pararotalia calcariformata*, and numerous species of heterotrophic foraminifera. Typical indicator taxa for phytal hard substrates (cibicidiids; Langer, 1988, 1993) are on average twice as abundant in phytal-associated habitats as in sand bays without phytal cover (5.5% versus 2.7%). Sand bay habitats are dominated by *P. calcariformata* (site 7), elphidiids and *Amphistegina* (site 3) and show significantly lower species richness and diversity but higher dominance. Samples from the mangrove bay inlet and the harbor were dominated by smaller miliolids and elphidiids, respectively.

Computational analysis of wall structure groups revealed that hyaline-perforate rotaliids dominate the foraminiferal biotas along the southern coast of Oman. The dominance of perforate-hyaline taxa is mainly driven by the abundance of larger rotaliids, in particular amphisteginids and *P. calcariformata*. In terms of absolute abundance, robust, thick-shelled amphisteginids are among the most abundant taxa, although their abundance and shell accumulation may well be the result of selective preservation processes. Amphisteginid foraminifers exhibit the highest environmental tolerance of all LBF, are prolific carbonate producers in tropical reef environments (Langer et al., 1997; Langer, 2008), often act as ecosystem engineers, and contribute to the formation and stabilization of coastal environments (Langer and Hottinger, 2000; Langer et al., 2012, 2013; Weinmann et al., 2013; Langer and Mouanga, 2016). Hyaline calcareous rotaliids were also found to dominate the stained fauna within the 412 m OMZ (Gooday et al., 2000), but the OMZ foraminiferal biotas differs significantly from our shallow-water assemblages and from predominantly soft-shelled and agglutinated deep-water assemblages below the 3350 m OMZ (allogromiids, saccaminids, hormosinaceans, bathysiphonids, hippocrepinaceans; Gooday et al., 2000).

Symbiont-bearing taxa, represented by six species, play a prominent role in the composition of Oman's foraminiferal assemblages, accounting for more than 40% of all foraminifera in eight out

of ten samples. In the sheltered harbor environments, they make up 25%, and in the mangrove environment they contribute only 8% to the total assemblage. The low number of only six LBF species is well below the estimated 20 species predicted by the species distribution modelling of Förderer et al. (2018) but is certainly an artefact of the extremely shallow water depth range analysed (1-3 m).

The LBF recorded in our material include two orders (Rotaliida and Miliolida), five different families, five genera and six species. Among the LBF identified are two species of *Amphistegina*: *A. radiata* and *A. lessonii*. Amphisteginids are characteristic of shallow, well-lit habitats and are mostly associated with phytal substrates (Langer, 1993; Murray, 2006; Mateu-Vicens et al., 2014). Among the LBF, *Pararotalia calcariformata* was found to be the dominant taxon in the monotonous sandy bay with no phytal cover (Samaharam Beach). The high percentage of damaged and abraded calcarinids in this assemblage indicates a current-exposed environment and suggests frequent reworking of the sediments. According to Hohenegger (1994), calcarinids preferentially live in highly turbulent waters, an observation consistent with the function of tubular spines as anchors in turbulent waters (Röttger and Krüger, 1990) and consistent with the current-exposed environment of the sandy bay at Samharam Beach. All other symbiont-bearing LBF (*Peneroplis pertusus*, *Sorites orbiculus*, *Borelis schlumbergeri*) are rare and rather randomly distributed between habitats.

Our records of substantial compositional differences are strongly supported by cluster analysis, where seagrass-associated habitats are clearly distinguishable from sandy bays, harbor and mangrove assemblages. Furthermore, seagrass-associated, harbor and mangrove faunas showed lower test damage rates than sandy bay faunas, indicating that destructive and taphonomic forces acting on foraminiferal shell preservation are more pronounced in sandy bays than in any other habitat. The dynamic processes under extreme shallow water conditions, including constant wave

action, turbulence, and sediment movement, are reflected in the large number of poorly preserved foraminiferal shells, indicating that the faunas were not deposited in situ. However, our detailed analyses of the structural composition, diversity and preservation of the foraminifera show that the faunas were not deposited out of habitat, but retain the characteristics of their habitat, record many ecological details, and provide useful information for palaeoecological and environmental studies. The Gulf of Gabes and its associated coastal wetlands are considered highly productive areas, contributing about 40% of Tunisia's total fish production (DGPA 2015). Numerous recent studies on modern shallow-water benthic foraminifera have provided essential contributions and information on the species richness, habitat structures and evolution of coastal environments along the Tunisian coast (Ben Hamad et al., 2018, 2019; Ben Khalifa et al., 2019; Blanc-Vernet et al., 1979; Damak et al., 2019; Kamoun et al., 2019, 2020, 2022a, b; Zaïbi et al., 2011, 2016). This work has contributed to a better understanding of the evolution of the Tunisian coast, a coastal environment that has undergone significant changes over the last 6000 years due to tectonic, climatic, and anthropogenic forcing (Jedoui et al., 1998; Morhange and Pirazzoli, 2005; Marquer et al., 2008; Anzidei et al., 2011; Zaïbi et al., 2016; Béjaoui et al., 2019). Our study on living benthic foraminifera from the relatively small Mahrés Lagoon provides further insights into the structuring of foraminiferal faunas, the distribution and abundance of indicator species, and their dependence on habitats. Analysis of numerical abundance, species richness and dominance of individual taxa revealed relatively low diversity assemblages of living benthic foraminifera. In general, the Mahrés Lagoon assemblages can be divided into two groups: (1) The first group is located at the margin and extreme distal end of the lagoon and is characterized by a high concentration of foraminifera and assemblages with low diversity on sandy and muddy substrates covered by *Salicornia* meadows. This group is strongly dominated by the agglutinated foraminifer *Trochammina inflata*. (2) The second group is found in the inner central parts of the lagoon and at

sampling stations oriented towards the mouth of the lagoon and is dominated by *Ammonia* species. The foraminiferal faunas within this group contain much fewer living specimens but are relatively more diverse. They are found in deeper tidal channels, on sandy substrates and in partially vegetated areas.

Low species richness and diversity indices (1-18 species, Fisher  $\alpha = 0.1$  and 4.3, Shannon H values = 0.0 and 2.4) typically define foraminiferal faunas at individual lagoon sites with high dominance values (max  $p_i = 0.2$  and 1.0). The peripheral and distal lagoon stations show the lowest diversity values. These stations, located at the highest tidal range, are subject to significant fluctuations in salinity and temperature. Lagoon areas that do not experience extreme fluctuations or that remain submerged during low tide show slightly higher diversity, although still low.

*Trochammina* and other agglutinated faunas are known to dominate areas with extreme tidal conditions, as demonstrated by numerous studies (Culver, 1990; Fajemila et al., 2020; 2022; Fiorini et al., 2019; Hayward and Triggs, 1994; Horton, 1999; Langer et al., 2016; Langer and Lipps, 2006; Patterson, 1990; Woodroffe et al., 2005; Sariaslan and Langer, 2021). These findings have proved invaluable in interpreting past environments.

While the peripheral higher areas of the lagoon are dominated by *Trochammina*, the central inner areas and those towards the opening of the lagoon are dominated by *Ammonia*. These areas are also affected by the tides, although to a lesser extent. In the tidal channels, the inflowing seawater is permanently retained, but the associated habitats are also subject to evaporation and the associated fluctuations in temperature and salinity. Some of these areas (sandbanks) actually dry out completely at extremely low tide and are thus different from the lagoon areas covered by *Salicornia*, which retain a residual moisture around their dense root systems. Like *Trochammina*, several ammonoid species cope well with such stress conditions (Langer, 1993; Koukousioura et al., 2011, 2012; Hayward et al., 2021).

However, when studying the living fauna of the Mahrés Lagoon, it is noticeable that the distribution of *Trochammina inflata* remains restricted to the very narrow area of the higher edges of the lagoon, and that they are either not transported at all or only in very small proportions from their habitats. The restricted distribution of *Trochammina* is probably influenced by the abundant and extensive colonization of dense *Salicornia* meadows and the low tidal range in the lagoon. Spatial dispersal and transport out of the habitat are probably hindered by both factors. In the Mahrés Lagoon, *Trochammina* maintains its distribution and remains within its restricted habitat, allowing the fauna to document important ecological information applicable to paleoecological and environmental studies.

A lateral and out-of-habitat distribution is more likely for the tidal channels and sampling stations located at the lagoon entrance. This conclusion is supported by the increased diversity, changes in the proportions of wall structural groups and the presence of characteristic marine species (e.g. *Lobatula lobatula*, *Nonion* sp. 1 and *Peneroplis pertusus*). However, the dominant presence of the *Ammonia* genus in the foraminiferal fauna indicates typical intertidal and shallow water conditions.

The introduction of fully marine foraminiferal species is probably mainly via the wide opening of the lagoon in the south. As the wetlands of Tunisia are frequently visited by migratory birds (Hamza and Selmi, 2015), avian transport via bird feet cannot be excluded (Lipps, 1982; Culver and Lipps, 2003). Apart from a single individual of *Peneroplis pertusus*, no other symbiont-bearing foraminifera were found in the material examined. Specimens of the genus *Amphistegina*, a taxon of large foraminifera that rapidly spread from the eastern to the central Mediterranean after the opening of the Suez Canal (Langer, 2008; Langer and Mouanga, 2016; Langer et al., 2012, 2013; Langer and Hottinger, 2000; Guastella et al., 2019, 2021, 2023; Raposo et al., 2023), were also absent. However, this species in particular spread deep into the Gulf of Gabes at a very early

stage and subsequently established large and permanent populations throughout the region (Blanc-Vernet et al., 1979, El Kateb et al., 2018; Stulpinaite et al., 2020). It is likely that the extreme conditions of the lagoon, combined with the absence of extensive seagrass beds or algal turf, have successfully prevented this species from invading the lagoon. At the same time, this may indicate that the sandspit effectively prevents the invasion of fully marine species into the lagoon.



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# **APPENDIX**

## Chapter 2: Publication

## Lower Paleocene foraminiferal assemblages from the Tibeisale Formation in the Arctic region of Western Siberia

Yaroslav S. Trubin, Vladimir A. Marinov, Pavel V. Smirnov, Andrey A. Novoselov, and Martin R. Langer

With 6 figures and 2 tables

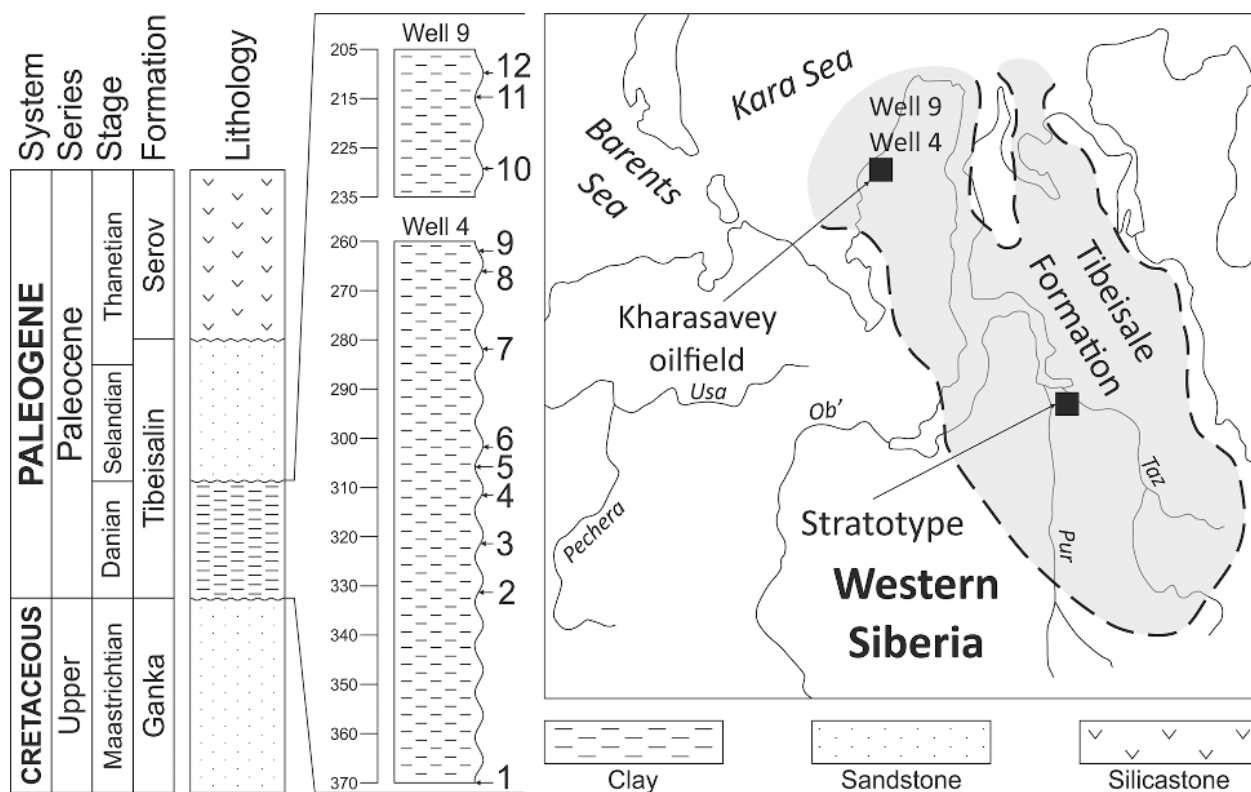
**Abstract:** The marine clay deposits of the Tibeisale Formation cover large parts of the Yamal Peninsula in Western Siberia and overlie Cretaceous sandstones, clays and siltstones. Previous biostratigraphic studies have placed them in the lower Paleocene, but due to the lack of zonal index markers, their age has not been fully elucidated. We have analyzed the composition, structure and diversity of benthic foraminiferal assemblages from core material of the Kharasavey drill site on the Yamal Peninsula, with the aim to constrain the biostratigraphic age, to reconstruct the depositional environment of the Tibeisale Formation, and to infer the response of benthic foraminifera to changes in the oxygen content of the surrounding waters. Based on biostratigraphic marker species, the composition of foraminiferal assemblages and lithological successions, we infer a Danian age for the time of deposition. The composition and numerical analyses of the foraminiferal faunas indicate deposition in well-oxygenated waters from deep to shallow shelf areas.

**Key words:** Yamal Peninsula, Western Siberia, Tibeisale Formation, benthic foraminifera, biostratigraphy.

### 1. Introduction

The West Siberian Basin is among the world's largest oil and gas producing regions, contains several giant and supergiant oil and gas fields, and has a total estimated ultimate recovery of about 200 billion barrels of oil and 1942 trillion cubic feet of gas (PETROCONSULTANTS 1996; ULMISHEK 2003; VYSSOTSKI et al. 2006). The basin is flanked by the Ural Mountains to the west, the Kazakh highlands to the south, the Siberian platform to the east and extends north into the Kara Sea. The basin has formed after the Late Carboniferous and Permian collision of the Siberian and Kazakhstan continents with the Russian Craton (SENGOR & NATAL'IN 1996; VYSSOTSKI et al. 2006; PETERSON & CLARKE 1991; SURKOV & ZHERO 1981; KONTOROVICH et al. 1975). The basins filling started in the Early Triassic when the newly formed collision structure underwent

rifting, with the deposition of mainly basic and ultrabasic rocks. The rift structure, running north-south, shaped the basin's outline, a complicated elongated structure where oceanic water entered from both the north and south, and led to the deposition of marine sedimentary successions comprising Middle Triassic through Middle Eocene clastic rocks. The largest oil and gas reservoirs are in Jurassic and Cretaceous strata (Bazhenov-Neocomian System) and were subject to detailed geophysical and stratigraphic studies (KONTOROVICH et al. 1975; PETERSON & CLARKE 1991; ROVENSKAYA & NEMCHENKO 1992; PETERS et al. 1993; PETERS et al. 1994; NIKITIN et al. 1999; NIKITIN & ROVNIN 2000; VYSSOTSKI et al. 2006). Younger deposits, however, have received little attention and their stratigraphy is compromised by the absence of time equivalent zonal markers from other northern hemisphere locations (IAKOVLEVA 2000; IAKOVLEVA &



**Fig. 1.** Location of the Kharasavey oil field on the Yamal Peninsula (Russian Federation), extent of the Tibeisale Formation (shaded in light gray), and location of the stratotype section of the Tibeisale Formation (modified after [LEBEDEVA 2006](#); [VOLKOVA 2014](#)).

[KULKOVA 2003](#); [AKHMET'EV et al. 2010](#)). This includes the Paleocene Tibeisale Formation in the Arctic portion of Western Siberia ([LEBEDEVA 2006](#); [MARINOV & URMAN 2013](#); [VOLKOVA 2014](#)), a formation of mainly clay deposits that is marked by palaeo-permafrost geomorphic features at its base ([BUDDO et al. 2017](#)). The clay deposits directly overlie marine Cretaceous strata ([LEBEDEVA 2006](#); [VOLKOVA 2014](#)), are capped by terrestrial Paleocene sandstone, and occasionally contain gas hydrates ([GRACE & HART 1986](#)). Based on the presence of a hiatus, [BUGROVA \(2008\)](#) assigned the clay deposits to the Selandian and considered the Danian likely to be missing (see also [Unified Regional Stratigraphic Chart 2001](#)).

We have studied the benthic foraminiferal assemblages from a suite of core samples obtained from the Kharasavey oilfield in Western Siberia (Yamal Peninsula), to provide a better understanding of the Tibeisale depositional environment by analyzing the composition, structure, and diversity of foraminiferal biotas. The Kharasavey drill site is situated in a hard-to-reach

northern area of Western Siberia and holds important clues to reconstruct the connection between the high Arctic and northern boreal Atlantic. Based on a modern taxonomic revision, we illustrate the entire benthic foraminiferal fauna and to place the assemblages in a biostratigraphic and palaeoecologic concept.

## 2. Material and methods

Core sample material was collected by geologists of the Glavtyumengeology association in 1993. The material includes a total of 12 samples and includes sedimentary samples from two cores (Well 4 and Well 9) of the Kharasavey oilfield (71° 10' 5" N, 67° 2' 52" E). Nine samples were taken from Well 4 at depths between 263 and 372 m and three samples were obtained from Well 9 at depth between 208 and 228 m (Fig. 1). The sedimentary core material analyzed included a mixture of clay and siltstone.

Rock samples were dissolved in hot water with  $\text{NaCO}_3$  and residues were then wet-sieved with fresh-water using a 63  $\mu\text{m}$  mesh sieve and later oven-dried at 50 °C. Foraminifera were then picked from each sample, inspected by using a Zeiss Stemi 508 microscope, and photographed via scanning electron microscopy (Hitachi TM3000, SEM). All specimens are archived in the micropalaeontological collection of the Laboratory of Sedimentology and Paleobiosphere Evolution at the University of Tyumen.

Picked foraminifera were then identified to species-level and numerical abundances of individual species were recorded. For the identification of benthic foraminifera and for reasons of consistency with the existing literature, we mainly follow the list of taxa recorded from the Tibeisale Formation (BUGROVA 2008), other literature with first descriptions of new species (VOLOSHINOVA & DAIN 1952; VASSILENKO 1954; EREMEEVA & BELOUSOVA 1961; SUBBOTINA *et al.* 1964; PODOBINA 1975, PODOBINA 1998), SEM illustrated foraminifera studies from Western Siberia (AMON & MARINOV 2011; MARINOV 2019), and modern updates and revisions (KAMINSKI & GRADSTEIN 2005; ANAN 2010; HOLBOURN *et al.* 2013; MAHFOUZ *et al.* 2018; GOVINDAN & VIJAYAN 2019; ANAN 2020; ANAN 2021; BESEN *et al.* 2021).

Abundances wall structural types (agglutinated, porcelaneous, and hyaline-perforate) were recorded, and percentages of individual groups documented. To analyze the structure and composition of foraminiferal assemblages, relative abundances (RA) and the frequency of occurrence (FO) of different orders, genera, and species were calculated. RA was calculated by using the following equation:  $\text{RA} = n * (100/T)$ , where  $n$  is the number of individuals of a taxon and  $T$  is the number of all benthic foraminiferal specimens in the sample. To determine the distribution of each taxon along the core interval, the FO was calculated as  $\text{FO} = p * (100/P)$ , where  $p$  is the number of samples containing the taxon and  $P$  is the total number of samples. Special attention was paid to the stratigraphic distribution of species belonging to the Pulleniinae, Cibicidinae, Parrelloidea, Heterolepoidae, Gavelinellinae, Elphidiinae, and Ceratobulimininae.

The number of species was recorded for each sample and Fisher's  $\alpha$ , Shannon H ( $H'$ ), and Equitability (or  $J$ ) indices were calculated. The logarithmic series model of FISHER, CORBET and WILLIAMS (1943) mathematically describes the relationship between the number of species and the total number of individual specimens and assumes that species abundance fol-

lows a log distribution. The Shannon H diversity index considers both the number of individuals and the number of species. It varies from 0 for assemblages that contain a single species to higher values for species-rich assemblages. Equitability or evenness measures how equally distributed the individuals in the community are among the species. The value ranges between 0 and 1, with a value of 1 for complete evenness.

Hierarchical cluster analysis was performed using the Paired group (UPGMA) algorithm with correlation similarity index. Cluster analysis is a multivariate analytical technique to detect structural entities in complex faunal data (taxa, samples) and reveals environmental signatures embedded in hierarchical cluster groups. Prior to cluster analysis, the abundance data set was converted using a logarithmical transformation (for details see PARKER & ARNOLD 1999).

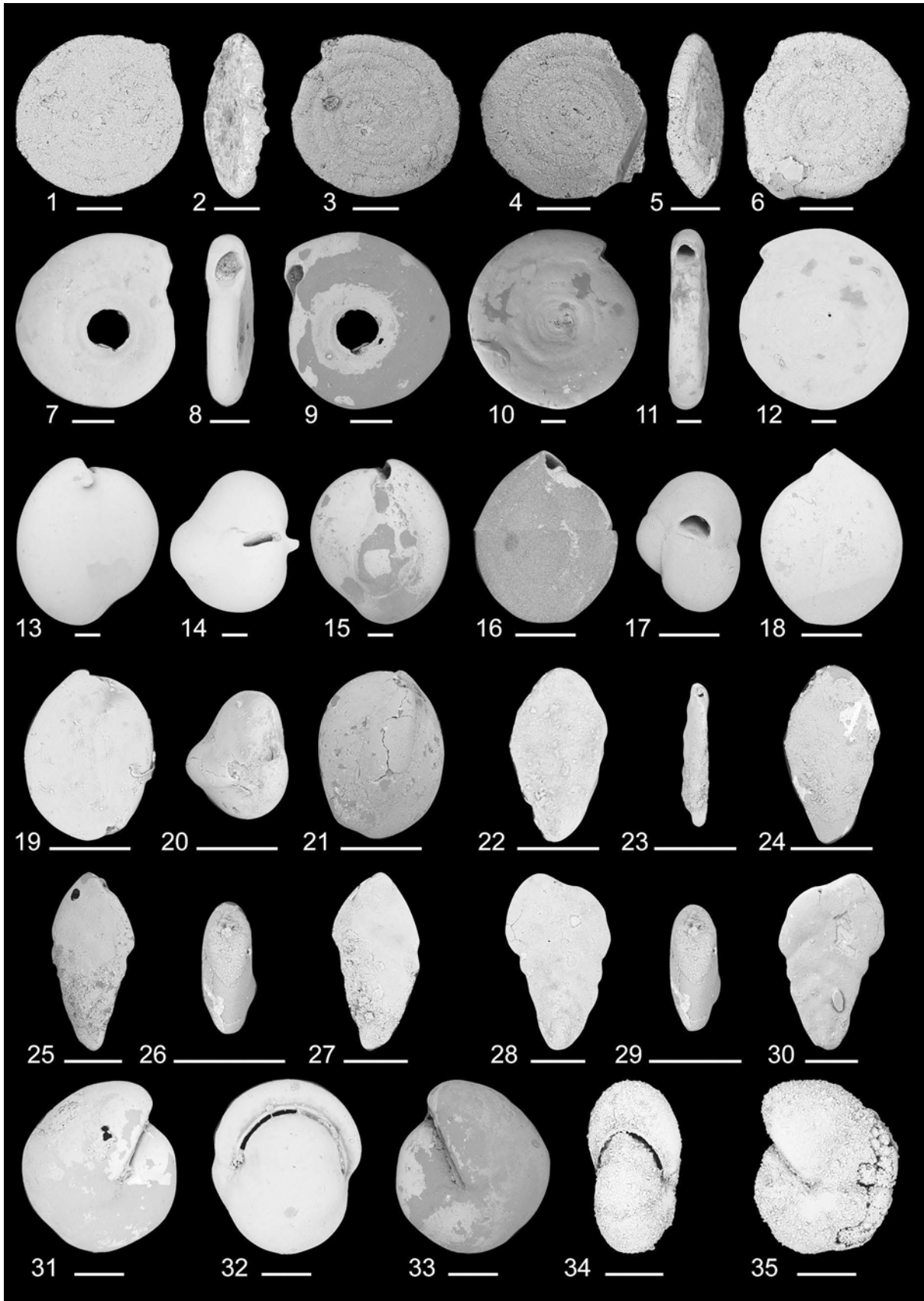
Numerical abundance analyses, calculations of diversity indices, and cluster analyses were conducted via PAST (Paleontological Statistics software package for education and data analysis) ver. 3.18 (HAMMER *et al.* 2001) and Microsoft Excel.

To assess the oxygen content of the surrounding waters at the time of deposition, we computed the relation of oxic and dysoxic morphotypes of benthic foraminifera. On the basis of this relation, the foraminiferal dissolved oxygen index (FDOI) can be estimated (KAIHO 1994) by using the following equation:  $\{[O/(O + D)] \times -100\}$ , where  $O$  and  $D$  are the numbers of specimens of oxic and dysoxic foraminifera. Palaeo-dissolved oxygen levels (OL) may vary between  $-55$  and  $100$  and equate to anoxic ( $\text{OI} = -55$ ,  $\text{OL} = 0.0-0.1$  ml/L), dysoxic ( $\text{OI} = -50$ – $-40$ ,  $\text{OL} = 0.1-0.3$  ml/L), sub-oxic ( $\text{OI} = -40$ – $0$ ,  $\text{OL} = 0.3-1.5$  ml/L), low oxic ( $\text{OI} = 0-50$ ,  $\text{OL} = 1.5-3.0$  ml/L), and high oxic ( $\text{OI} = 50-100$ ,  $\text{OL} = 3.0->6.0$  ml/L) conditions (KAIHO 1994).

### 3. Results

#### 3.1. Structure and composition of foraminiferal assemblages

A total of 25 species of benthic foraminifera were identified from 992 picked specimens (Figs. 2–4). This includes 21 perforate-hyaline, 3 porcelaneous and 1 agglutinated species. Individuals of perforate-hyaline species are dominant and constitute 98.5 % of the total assemblages. Porcelaneous taxa and agglutinated tests



**Table 1.** Foraminiferal faunal characteristics of cluster groups and outliers

Clusters groups and outliers	Dominant faunal constituents	Diversity indices
Cluster A Sample 7	Assemblages dominated by <i>Cibicidoides</i> and <i>Cibicides</i> , Pulleniinae and Gavelinellinae	Fisher $\alpha$ = 2.6 Shannon H (H') = 1.5 Simpson 1-D = 0.6
Samples 8, 9	Monospecific assemblage composed of <i>Cibicidoides proprius</i>	Fisher $\alpha$ = 0.3 Shannon H (H') = 0.0 Simpson 1-D = 0.0
Cluster B Samples 2, 4, 5, 6	Assemblages dominated by <i>Cibicidoides</i> and <i>Cibicides</i> , with low abundances of Pulleniinae and Gavelinellinae	Fisher $\alpha$ = 1.4–3.6 Shannon H (H') = 1.2–2.1 Simpson 1-D = 0.6–0.9
Cluster C Samples 1, 10, 11	Assemblages dominated by <i>Cibicidoides</i> and <i>Cibicides</i> and Gavelinellinae, with low abundances of Pulleniinae, Polymorphininae, and Miliolina	Fisher $\alpha$ = 2.1–4.0 Shannon H (H') = 1.3–2.1 Simpson 1-D = 0.6–0.8
Outlier sample 12	Assemblage dominated by Elphidiinae, Gavelinellinae, and Polymorphininae	Fisher $\alpha$ = 2.9 Shannon H (H') = 1.8 Simpson 1-D = 0.8
Outlier sample 3	Assemblage dominated by <i>Cibicidoides</i> and <i>Cibicides</i> and Pulleniinae	Fisher $\alpha$ = 2.2 Shannon H (H') = 1.5 Simpson 1-D = 0.7

are rare and contribute between 0.7% and 0.8% to the foraminiferal biotas. The number of picked foraminifera from individual samples varied and ranged between 10 and 246. Larger numbers of individuals were obtained from 7 samples (samples 1, 2, 4, 5, 7, 10, 12).

Five different orders of foraminifera were recorded among the total fauna including the Allogromiida, the porcelaneous Miliolina, and the hyaline-perforate Rotaliina, Robertinina, and Lagenina. Individuals of the Rotaliina constitute the highest percent abundances of the total number of taxa (93.9%) and also represent the most species-rich group (17 species). They are followed by the Lagenina (4.5%, 4 species), Miliolina (0.8%, 3 species), and Allogromiida (0.7%, 1 species).

### 3.2. Cluster analysis

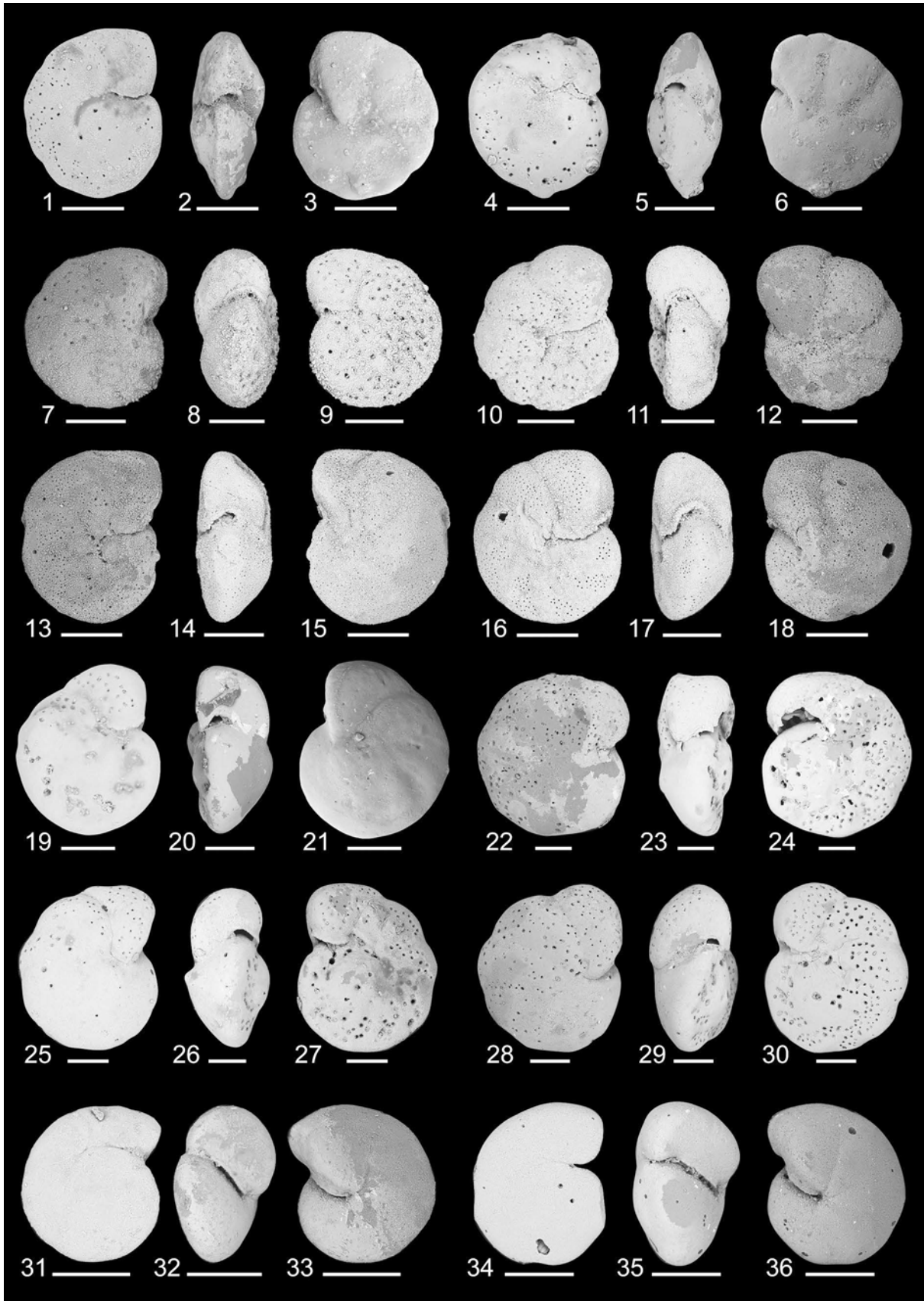
Cluster analysis resulted in three major clusters (A, B, and C; Fig. 5) and two outliers (samples 3 and 12; Fig. 5). Cluster A comprises the monospecific assemblages of samples 8 and 9 (*Cibicidoides proprius*

us BROTZEN, 1948) and sample 7 which contains low amounts of Pulleniinae and Gavelinellinae. Cluster B includes samples 2, 4–5, and 6, representing assemblages with mostly *Cibicidoides* and *Cibicides* and variable amounts of Pulleniinae and Gavelinellinae. Cluster C includes assemblages with *Cibicidoides* and *Cibicides* and Gavelinellinae (samples 1, 10, and 11). The two outliers (sample 3, 12) flank clusters A, B, and C, and comprise assemblages composed of Gavelinellinae and Pulleniinae (sample 3) and Elphidiinae, Gavelinellinae, and Polymorphininae (sample 12; Table 1).

Percent analyses data are provided in Table 2 and resulted in the following values for some cluster-typical samples. Sample 1 (cluster C) is composed of *Cibicidoides* and *Cibicides* (44.9%), Gavelinellinae (25.5%), Pulleniinae (5.1%), Polymorphininae (3.1%), and Miliolina (3.1%). Samples 2, 4, 5, 6, (Cluster B) comprises variable amounts of *Cibicidoides* and *Cibicides* (46.7–81.8%) Pulleniinae (8.1–20.0%) and Gavelinellinae (0–17.1% sample 2, 4, 5, 6). Sample 3 is dominated by Pulleniinae (46%) and *Cibicidoides* and *Cibicides* (42%). Only a few individuals were found in samples 8 and 9 (cluster A) and the assem-

**Fig. 2.** 1–6 – *Ammodiscus glabratus* CUSHMAN & JARVIS, 1928 (sample 25, 283 m); 7–12 – *Cornuspira sibirica* (PODOBINA, 1975) (sample 31, 333 m); 13–18 – *Triloculinella* sp. 1 (sample 60, 208 m); 19–21 – *Triloculinella* sp. 2 (sample 36, 372 m); 22–30 – *Bolivina* (?) sp. (sample 27, 303 m); 31–33 – *Pullenia cretacea* CUSHMAN, 1936 (sample 9, 313 m); 34–35 – *Pullenia* aff. *quinqueloba* (REUSS, 1851) (sample 25, 283 m). Scale bar = 100  $\mu$ m.





blages of both were monospecific. Samples 10 and 11 (Cluster C) is dominated by *Cibicidoides* and *Cibicides* (45.3–74.3%) and Gavelinellinae (20.0–27.4%) and sample 12 (outlier) is composed of Elphidiinae (30.2%), Gavelinellinae (30.2%), and Polymorphininae (24.4%).

### 3.3. Species richness and diversity

The species richness in the samples varies from sample to sample and is generally very low and in samples 8 and 9 only one species was found (*Cibicidoides proprius* BROTZEN, 1948, Table 2). Diversity Fisher  $\alpha$  index computations (Fig. 6, Table 2) revealed a range between 1.4 and 4.0, except for the monospecific samples 8 and 9, where the value is only 0.3. Shannon H values range between 1.2 and 2.1 (0 in sample 8 and 9), and for the Simpson index between 0.6 and 0.9 (0 in sample 8 and 9). The highest value was recorded in sample 1 (Fisher  $\alpha$  index 4.0) and the lowest value (0.3) in samples 8 and 9. This trend is generally followed by the Shannon H and Simpson1-D indices (Table 2).

### 3.4. Frequency and abundances

The species with the highest relative abundance (RA) are the *Cibicidoides* with *Cibicidoides proprius* (27.6%), *Cibicidoides spiropunctatus* (GALLOWAY & MORREY, 1931; 26.7%), Gavelinellinae (*Gyroidina* sp.; 10.9%), and Pulleniinae (*Pullenia cretacea* CUSHMAN, 1936; 9.6%). All of them belong to the hyaline-perforate Rotaliina. The agglutinated taxon *Ammodiscus glabratus* CUSHMAN & JARVIS, 1928 is rare and occurs only sporadically (0.7%). Among the porcelaneous Miliolina, *Triloculinella* sp. 2 (0.4%) was found to be the most common species, followed by *Triloculinella* sp. 1 (0.3%), and *Cornuspira sibirica* (PODOBINA, 1975; 0.1%). On a generic level, *Cibi-*

*cidoides* shows the highest RA (54.2), followed by *Gyroidina* (10.9%), *Pullenia* (10%), *Bagginoides* (?) *quadrilobus* (6.5%), and *Guttulina* (3.8%).

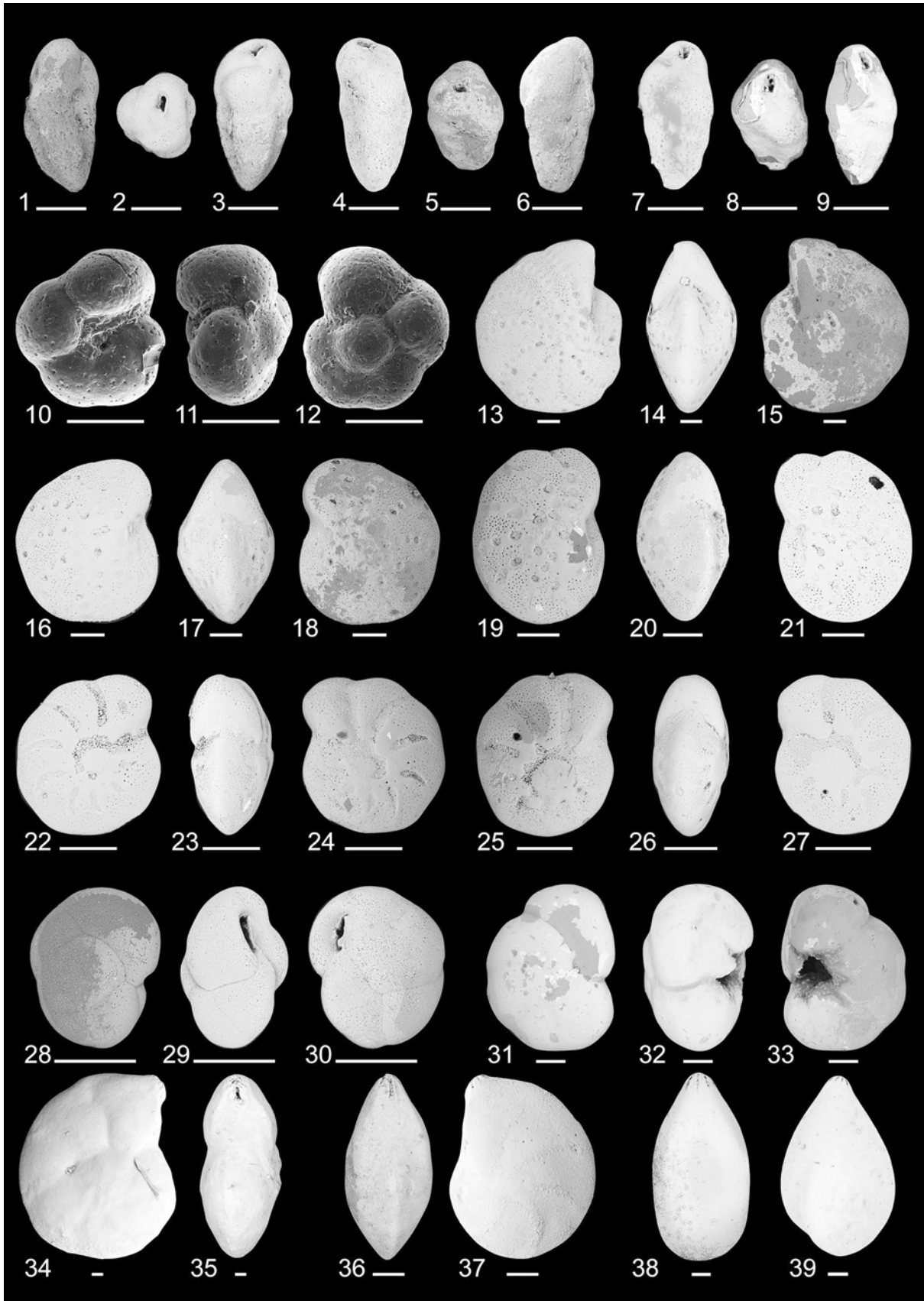
Based on the frequency of occurrence (FO), *Cibicidoides proprius* (91.7%), *C. spiropunctatus* (75%), *Pullenia cretacea* (75%), and *Bagginoides* (?) *quadrilobus* (66.7%) were found to be the most ubiquitous and occurred in the 8–11 samples analyzed (FO > 50%). Among the 25 species identified, 4 are common (FO > 25%), and 7 occur only occasionally (FO > 10%). The remaining 10 species are rare (FO > 10%) and their occurrence was recorded in a single sample. A total of 4 species (0.4% of the fauna) is represented by a single individual only.

### 3.5. Infaunal and epifaunal taxa

Based on previous morphotype analysis of CORLISS (1985), BERNHARD (1986), CORLISS & CHEN (1988), JORISSEN et al. (1992) and JONES & CHARNOCK (1985), we categorized individual taxa according to their infaunal and epifaunal microhabitat preferences to assess oxygen conditions of the depositional environment. Epibenthic taxa are characterized by high and low trochospiral, biconvex or planoconvex tests and infaunal species are characterized by lenticular, ovate and spherical, tapered, elongate flattened, or cylindrical test (Table 2). Percent abundance computations of infaunal taxa across the cores (Table 2 and Fig. 6) varies between 0 and 50%, with moderate amounts in deeper core parts (5.7–27.9%, samples 10–12), and moderate to high amounts in the top portion (9.8–50%; samples 1–7). Sample 9 and 8 are barren of infaunal taxa and comprise monospecific assemblages of epibenthic *Cibicidoides proprius* only. Other assemblages with the high amounts of epibenthic species were dominated by *Cibicidoides* and Gavelinellinae (~70–90%, samples 1, 10, 12), *Cibicidoides* with variable amounts of Pulleniinae and Gavelinellinae (~70–90%, samples 2, 4–7), or Elphidiinae, Gavelinellinae, and Polymorphininae (~70%, sample 12).

**Fig. 3.** 1–6 – *Cibicidoides proprius* BROTZEN, 1948 (sample 31, 333 m); 7–9 – *Gavellinella danica* (BROTZEN, 1940) (sample 25, 283 m); 10–12 – *Anomalinulla* sp (sample 25, 283 m); 13–15 – *Cibicidoides* aff. *favorabilis* (VASSILENKO, 1953) (sample 36, 372 m); 16–18 – *Cibicides* sp. 1 (sample 36, 372 m); 19–21 – *Cibicides* sp. 2 (sample 9, 313 m); 22–30 – *Cibicidoides spiropunctatus* (GALLOWAY & MORREY, 1931) (sample 31, 333 m); 31–36 – *Gyroidina* sp. (sample 9, 313 m). Scale bar = 100  $\mu$ m.





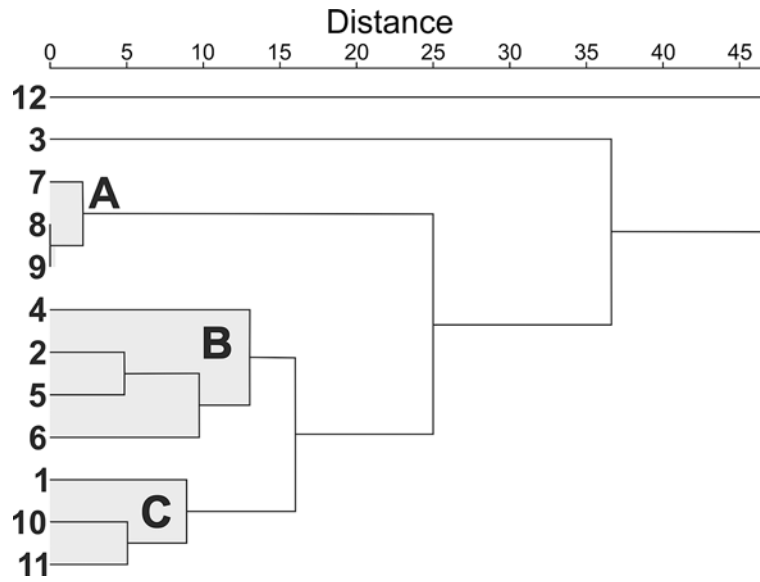


Fig. 5. Cluster dendrogram showing Cluster A, B, and C flanked by two outliers.

#### 4. Discussion

During the Early Paleocene, Western Siberia was covered by an epicontinental sea, connecting the high Arctic Ocean and the remnants of the northern Tethys Ocean via the Turgay Strait. As expected for high latitude regions, species richness (25 taxa) and diversity (Fisher  $\alpha = 0.3\text{--}4.0$ ) of foraminiferal assemblages was found to be generally low, but higher than in time-equivalent strata where species richness is severely limited to agglutinated and endemic taxa (YOUNG & McNEIL 1984; McNEIL 1990; BACKMAN & MORAN 2009; AKMET'EV *et al.* 2010). Whether calcareous plankton groups were excluded from the high Arctic Ocean because of unfavorable palaeoecological conditions or their absence reflects a preservation bias (level of carbonate compensation depth (CCD): low pH and alkalinity) is still under debate (BACKMAN & MORAN 2009). To date, no consensus has been reached to explain the overall diversity decline with increasing latitude, but most likely result from a multitude of com-

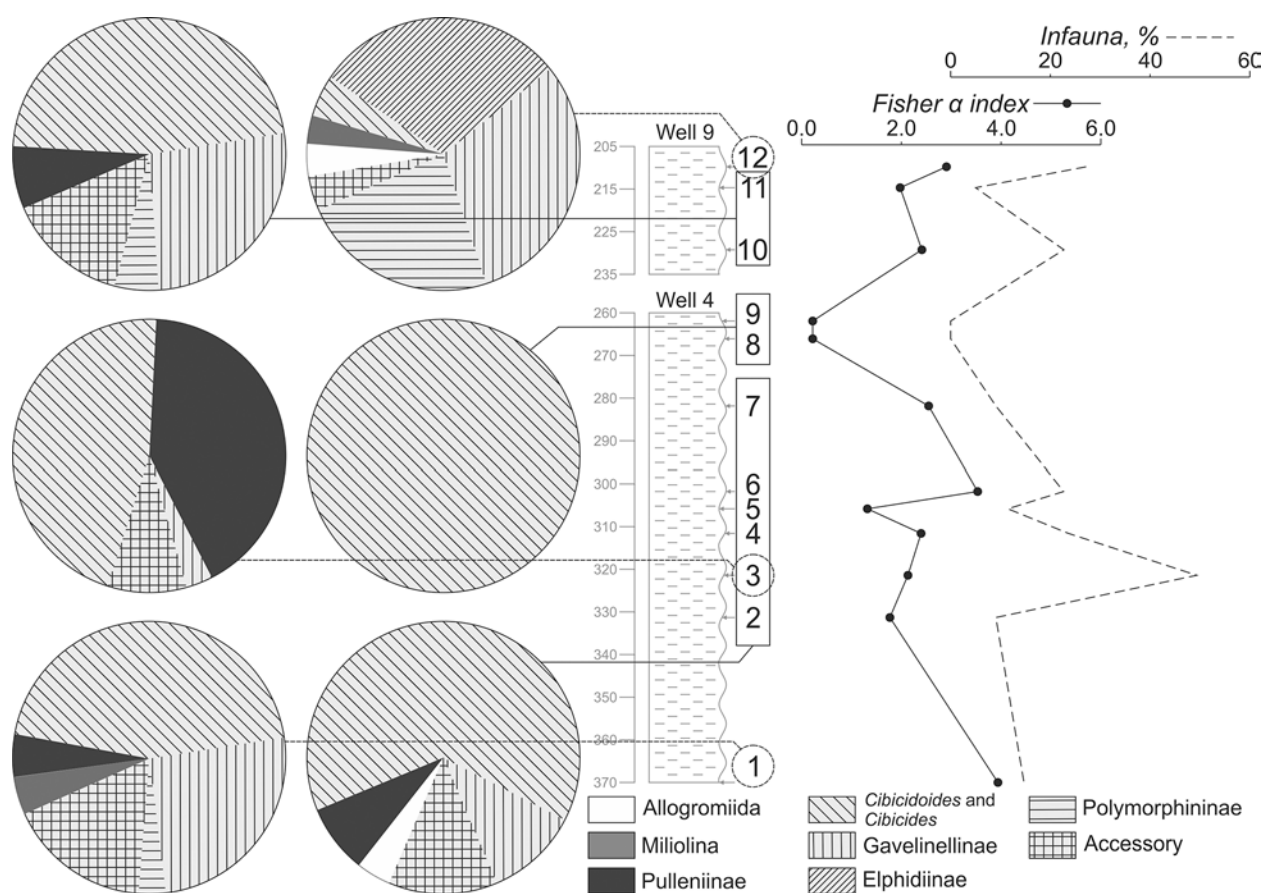
plex interactions, including lower available energy and area at high latitudes, extreme seasonality, short time spans for diversification, and the comparatively young age of the ecosystem.

Unlike the high Arctic Ocean, the new Yamal core material from Western Siberia comprises predominantly hyaline-perforated forms. Agglutinated foraminifera were rare and planktonic foraminifera are completely missing (see also BUGROVA 2008). This finding is in line with studies by PODOBINA (2003), who recorded abundant calcareous benthic foraminifera from the southwestern part of the basin in the Omsk depression (Maastrichtian to lowermost Danian), and agglutinated taxa from shallow Danian deposits of the Ust-Tym depression (*Bathysiphon*, *Glomospira*, *Ammodiscus*) and the Selandian and Thanetian. In addition, the faunal assemblages recorded by PODOBINA indicated a sea-level fall during the early Paleocene (earliest Danian), a transgression during the Selandian, and again a shallowing upward trend in the Thanetian.

Fig. 4. 1–9 – *Bulimina* sp. (sample 65, 228 m); 10–12 – *Bagginoides* (?) *quadrilobus* (MELLO, 1969) (sample 31, 333 m); 13–21 – *Elphidium* sp. (sample 60, 208 m); 22–27 – *Criboelphidium* sp. (sample 60, 208 m); 28–30 – *Glodocassidulina* sp. (sample 60, 208 m); 31–33 – *Ceratolamarckina tuberculata* (BROTZEN, 1948) (sample 36, 372 m); 34, 35 – *Lenticulina grauli* (PUTRJA, 1963) (sample 36, 372 m); 36, 37. *Lenticulina* sp. (sample 36, 372 m); 38 – *Guttulina* sp. (sample 60, 208 m); 39 – *Guttulina communis* (D'ORBIGNY, 1826) (sample 60, 208 m). Scale bar = 100  $\mu\text{m}$ .

**Table 2.** Quantitative faunal data including number of individuals per species, percentages of wall structural types, dominant families and genera, and diversity and dominance index values. Infaunal taxa are marked by a \*.

Core Depth (m)	208	213	228	263	267	283	303	307	313	323	333	372
Sample number	12	11	10	9	8	7	6	5	4	3	2	1
<i>Ammodiscus glabratus</i>	3	0	0	0	0	1	1	2	0	0	0	0
<i>Anomalinulla</i> sp.	0	2	5	0	0	4	3	0	0	0	6	0
<i>Bagginoides</i> (?) <i>quadrilobus</i>	0	0	4	0	0	11	5	4	13	4	14	10
<i>Bolivina</i> (?) sp.*	0	0	0	0	0	0	1	2	9	0	0	0
<i>Bulimina</i> sp.*	0	0	10	0	0	0	0	0	5	0	0	3
<i>Ceratolamarckina tuberculata</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Cibicides</i> aff. <i>favirabilis</i>	0	0	0	0	0	0	0	0	8	6	0	11
<i>Cibicides</i> sp. 1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Cibicides</i> sp. 2	2	0	0	0	0	0	0	0	8	6	0	0
<i>Cibicoides proprius</i>	2	6	12	10	11	46	5	52	38	0	84	8
<i>Cibicoides spiropunctatus</i>	0	20	31	0	0	6	9	29	22	9	115	24
<i>Cornuspira sibirica</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Criboelphidium</i> sp.	5	0	0	0	0	0	0	0	0	0	0	0
<i>Elphidium</i> sp.	21	0	0	0	0	0	0	0	0	0	0	0
<i>Gavellinella danica</i>	0	0	0	0	0	1	0	0	0	0	0	0
<i>Glodocassidulina</i> sp.*	3	0	0	0	0	0	0	0	0	0	0	0
<i>Guttulina communis</i> *	3	0	0	0	0	0	0	0	0	0	0	0
<i>Guttulina</i> sp.*	18	0	5	0	0	0	0	0	4	1	4	3
<i>Gyroidina</i> sp.	26	5	21	0	0	5	0	0	26	0	0	25
<i>Lenticulina grauli</i> *	0	0	0	0	0	0	0	0	0	1	0	2
<i>Lenticulina</i> sp.*	0	1	0	0	0	0	0	0	0	0	1	2
<i>Pullenia</i> aff. <i>quinqueloba</i> *	0	0	1	0	0	2	1	0	0	0	0	0
<i>Pullenia cretacea</i> *	0	1	6	0	0	6	5	10	19	23	20	5
<i>Triloculinella</i> sp. 1	3	0	0	0	0	0	0	0	0	0	0	0
<i>Triloculinella</i> sp. 2	0	0	0	0	0	0	0	0	0	0	1	3
<b>Total number of individuals</b>	<b>86</b>	<b>35</b>	<b>95</b>	<b>10</b>	<b>11</b>	<b>82</b>	<b>30</b>	<b>99</b>	<b>152</b>	<b>50</b>	<b>246</b>	<b>98</b>
Number of species	11	6	9	1	1	9	8	6	10	7	9	13
Allogromiida %	3.5	0.0	0.0	0.0	0.0	1.2	3.3	2.0	0.0	0.0	0.0	0.0
Miliolina %	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	3.1
Perforate-hyaline %	93.0	100	100	100	100	98.8	96.7	98.0	100	100	99.2	96.9
Pulleniinae %	0.0	2.9	7.4	0.0	0.0	9.8	20.0	10.1	12.5	46.0	8.1	5.1
<i>Cibicoides</i> and <i>Cibicides</i> %	4.7	74.3	45.3	100	100	63.4	46.7	81.8	50.0	42.0	80.9	44.9
Elphidiinae %	30.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gavellinellinae %	30.2	20.0	27.4	0.0	0.0	11.0	10.0	0.0	17.1	0.0	2.4	25.5
Polymorphininae %	24.4	0.0	5.3	0.0	0.0	0.0	0.0	0.0	2.6	2.0	1.6	3.1
Accessory taxa %	3.5	2.9	14.7	0.0	0.0	14.6	20.0	6.1	17.8	10.0	6.1	18.4
Fisher a values	2.9	2.1	2.4	0.3	0.3	2.6	3.6	1.4	2.4	2.2	1.8	4.0
Shannon's H'	1.8	1.3	1.9	0.0	0.0	1.5	1.8	1.2	2.1	1.5	1.3	2.1
Simpson 1-D	0.8	0.6	0.8	0.0	0.0	0.6	0.8	0.6	0.9	0.7	0.7	0.8
Dominance (SID)	0.2	0.4	0.2	1.0	1.0	0.4	0.2	0.4	0.1	0.3	0.3	0.2
Infauna %	27.9	5.7	23.2	0.0	0.0	9.8	23.3	12.1	24.3	50.0	10.2	15.3
Epifauna %	72.1	94.3	76.8	100	100	90.2	76.7	87.9	75.7	50.0	89.8	84.7
Oxic taxa %	72.1	100	84.2	100	100	100	96.7	98.0	88.2	98.0	98.4	93.9
Dysoxic taxa %	27.9	0.0	15.8	0.0	0.0	0.0	3.3	2.0	11.8	2.0	1.6	6.1
FDOI	72.1	100	84.2	100	100	100	96.7	98.0	88.2	98.0	98.4	93.9



**Fig. 6.** Depth and position of samples across the cores and percent abundance analyses of foraminiferal groups of cluster-typical samples.

#### 4.1. Biostratigraphy

During the Paleocene, the Arctic Ocean was a severely restricted marine basin (BACKMAN & MORAN 2009). Because of the wide absence of nannoplankton and planktonic foraminifera standard index markers, high Arctic Paleocene biostratigraphy has remained a fundamental problem and the relatively poor record comprises mainly agglutinated and endemic taxa (YOUNG & McNEIL 1984; McNEIL 1990; AKMET'EV & BENIAMOVSKI 2006; AKMET'EV et al. 2010).

Previous biostratigraphic studies on Western Siberian Paleocene foraminifera include the works of FREIMANN (1960), SUBBOTINA & KISELMAN (1961), PODOBINA (1998, 2000, 2003), BUGROVA (2008) and MARINOV (2020). Based on the absence of *Brotzenella praeacuta* and planktonic foraminifera, BUGROVA

(2008) referred the clay deposits from Western Siberia to the Selandian, and considered the presence of *Ceratolamarckina tuberculata* and *Ceratobulimina perplexa* to be indicative for the Selandian lower boundary. However, both taxa have been reported from older Danian strata (FUCHS 1975; FENNER 1976) and their stratigraphic value requires further study.

Our biostratigraphic assignment is based on multiple lines of evidence: lithology, benthic foraminifera index markers, and the composition of the foraminiferal biotas: (1) the clay deposits of the Tibeisale Formation directly overlie the Cretaceous sandstones (LEBEDEVA 2006; VOLKOVA 2014) and commonly contain foraminiferal assemblages dominated by *Cibicidoides proprius*, *Gavellinella danica*, *Ceratolamarckina tuberculata*, *Pullenia* aff. *quinqueloba*, and *Cibicidoides spiropunctatus*. Some of these taxa (e.g., *Cibicidoides*

*proprius* and *Gavellinella danica*) are abundant and typical constituents in the West Siberian plain (Vasyugan River) and to the east of the Ural Mountains, and are considered to be indicative for both the Danian and Selandian (PODOBINA 2003; BUGROVA 2008). However, faunal communities comparable to those from the Yamal Peninsula have been described from the basal sands of Clayton, Alabama (*Cibicidoides*, *Gavellinellinae*, and *Pulleniinae*), and these have been unambiguously assigned to the early Danian (OLSSON et al. 1996). (2) Typical West Siberian and low Arctic Danian and Selandian assemblages also include numerous agglutinated and calcareous species that survived the late Maastrichtian and are widely distributed in the southern region of West Siberia (e.g., *Heterostomella foveolata* (*Siphogaudryina stephensoni*), *Valvulineria imitata*, *Valvulinoides umovi*, *Gyroidinoides turgidus*, *Cibicides gankinoensis*, *Anomalinoides pinguis*, *Pullenia americana*; *Bulimina rozenkrantzi*, *Reussella minuta*, *Bolivina plaita*; PODOBINA 2000). (3) Lower Paleocene assemblages of foraminifera are characterized by a distinct increase in infaunal, «rounded planispiral» and «spherical» morphotypes (e.g., *Pullenia*; ALEGRET & THOMAS 2007), a finding that is in line with the numerical recordings in our sample material. Younger Paleocene strata of the Upper Selandian and Thanetian in Western Siberia are characterized by siliceous sediments (SMIRNOV & KONSTANTINOV 2017), and are frequently dominated by agglutinated species (PODOBINA 2003; PODOBINA 2015). Neither Cretaceous sandstones nor siliceous Upper Selandian–Thanetian sediments and abundant agglutinated taxa were recorded here and we therefore infer a Danian age for the core material examined here. The stratigraphic placement is supported by studies of VOLKOVA (2014) and VOLKOVA et al. (2002), who also inferred a Danian age for the gray clays of the Upper Tibeisale Formation based on pollen and dinoflagellate cysts.

#### 4.2. Palaeoenvironment

BERNHARD (1986) reported that fossil anaerobic (anoxic and dysoxic) are characterized by flattened test shapes and foraminifera from aerobic (oxygenated) environments had more spherical test morphologies (Table 2). Anaerobic species are represented by *Bolivina* (?) sp., *Bulimina* sp., *Glodocassidulina* sp., *Guttulina communis*, and *Guttulina* sp., in addition

to species of *Ammodiscus* and *Cibicidoides* that may survive in areas near anoxic conditions (KAIHO 1991; ALVE 1995). True anaerobic taxa were found to be rare in our assemblages. Accordingly, the foraminiferal dissolved-oxygen indexes (FDOI) of the assemblages were comparatively high and ranges between ~70–90. The monospecific assemblages (sample 8 and 9) and sample 11 (dominated by *Cibicidoides* and *Gavellinellinae*) are composed of oxic species only and the FDOI is 100. According to KAIHO (1994), the environmental setting can therefore be considered to be well oxygenated. However, percent abundance infaunal morphotypes varied along the core, suggesting that oxygen concentrations and/or carbon flux rates to the sediments varied over time. The presence of monospecific assemblages is unusual (*Cibicidoides proprius*) and suggests that mechanisms of selective preservation processes were involved. A detailed reconstruction of the prevailing environmental conditions is therefore only possible to a limited extent.

The dominant faunal constituents (*Cibicidoides*, *Gavellinellinae*, and *Pulleniinae*) occur over a wide bathymetric range, and typical shallow water indicator taxa are largely lacking. In addition, rare but well-preserved smaller miliolids indicate that allochthonous species were occasionally introduced from nearby shallow water areas into deeper habitats. BERGGREN (1974a, 1974b) considered Paleocene faunal assemblages composed of *Cibicidoides* and *Gavellinella danica* to be indicative for a middle to outer shelf environment (30–200 m water depth). A deep-water shelf environment, extending from a deeper shelf setting toward slope, is therefore conceivable and may include deep-water canyons that may have facilitated the downward transport of shallow-water taxa. The reconstruction of the environmental conditions is additionally complicated by documented phases of transgression and regression during the Danian and Selandian time interval (IAKOVLEVA 2000; VOLKOVA 2014). A distinct shallowing upward trend toward the top of the core is indicated by the presence of abundant Elphidiidae (*Elphidium* and *Criboelphidium*), genera that are common in Paleocene shallow (inner shelf), well-oxygenated environments of the photic zone (BERGGREN 1974b). The foraminiferal faunal composition along the cores thus traces an evolution from a steeply sloping shelf to a shallow inner-shelf setting, in line with the palaeogeographic position of Western Siberia, connecting the high Arctic with the northern remnants of the Tethys Ocean through a shallow basin.



## 5. Conclusions

A total of 25 species of benthic foraminifera were recovered from clayish core material of the Tibeisale Formation from the Kharasavey oilfield in Western Siberia (Yamal Peninsula). The foraminiferal assemblages are dominated by hyaline-perforate taxa (*Cibicidoides*, Gavelinellinae, and Pulleniinae), and characterized by rare occurrences of agglutinated and porcelaneous species. The presence of atypical, mono-specific assemblages of *Cibicidoides proprius* in the middle part of the core indicates a preservation bias, suggesting that actual species richness may have been higher, limiting reconstruction of prevailing environmental conditions. Foraminiferal assemblage composition and structure, as well as diversity and oxygen index calculations indicate slightly variable but predominantly well-oxygenated environmental conditions. The succession of foraminiferal communities indicates a transition from a relatively deep shelf to a shallow-water inner shelf environment, consistent with a deep passage (Turgay Strait) connecting the northern part of the boreal Atlantic with the high Arctic Ocean. Based on the composition of foraminiferal assemblages, successions of lithological sequences, and index markers, the Kharasavey sediments of the Tibeisale Formation were probably deposited during the Early Paleocene (Danian).

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## Chapter 3: Publication

**Upper Eocene benthic foraminiferal assemblages from the Western Siberia (Trans-Ural Region): a multi-proxy approach to infer environmental changes. *Micropaleontology* (in press)**

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**ABSTRACT:** During the Late Eocene, the West Siberian Basin became increasingly isolated from the Peri-Tethys Ocean. The final stage of this marine connection is marked by sediments of the Tavda Formation that were deposited during the Bartonian and Priabonian. We have analyzed the composition, structure and diversity of benthic foraminiferal assemblages in core material from the Kyshtyrla Quarry located in the southwest of Western Siberia to reconstruct the depositional environment during the terminal phase of marine sedimentation in the West Siberian Basin (Upper Tavda Subformation). The foraminiferal record was jointly used with lithological and geochemical multi-proxy data to infer the chronology of events that shaped the critical transition until the complete closure of the basin. Based on stratigraphic index markers, a Priabonian age is indicated for sediments of the Upper Tavda Subformation. From the bottom to the top of the core, the foraminiferal biotas progressively shift from shallow subtidal to low-diverse and stress-tolerant intertidal assemblages, indicative for an increasing isolation of the West Siberian Basin. The increasing shallowing of the marine basin is accompanied by a gradual shift in grain size, and the continuous presence of benthic foraminifera and ratios of geochemical proxies (Sr/Ba, Si/Al, Ti/Al, Zr/Al, K/Al, and U/Th) indicate that mainly marine to brackish water conditions prevailed.

**Keywords:** biostratigraphy, paleoecology, geochemistry indexes, sedimentation environments

## INTRODUCTION

The West Siberian Sea was among the largest shallow epicontinental basins of the Peri-Tethys and located in northern Eurasia (Akhmet'ev et al., 2010, 2012). Marine sediments show that a stable connection of the basin to the Peri-Tethys through the Turgay Strait was maintained until the Late Eocene. The final stage of this marine connection is marked by sediments of the Tavda Formation (Iakovleva and Heilmann-Clausen, 2010), and affected the entire oceanographic environment, including water exchange and circulation with the Peri-Tethys, ultimately leading to the isolation of the West Siberian Sea. The oceanographic restriction shifted most basins of Eurasia to long-term extreme anoxic bottom-water environments, characterized by stratified water masses, anomalous evaporitic or brackish conditions, or even endorheic lakes (Palcu and Krijgsman, 2022). The strangulation and subsequent disappearance of the great epicontinental West Siberian Sea resulted in a complete paleogeographic and paleoclimatic reorganization of the region and coincides with the period when the continents initiated the upheaval to the present-day constellation. In contrast to the extensive studies of the geologic evolution of the Peri-Tethys Ocean and adjacent marine areas, the terminal phase of marine sedimentation in the West Siberian Basin has been little studied.

Here we present new multiproxy data from core samples obtained from the Kyshtyrla Quarry located in the southwestern part of Western Siberia, to provide a better understanding of the depositional environment during the final phase of marine sedimentation in the Late Eocene. Our multiproxy approach includes the examination of geochemical and micropaleontological proxies from core material and shifts in foraminifera microfauna community structure to infer the chronology of events that marked the transition from a well connected to a severely restricted ocean basin. The study site is situated at the boundary between Western Siberia and the Turgay Strait and holds important clues to reconstruct the connection between the shallow epicontinental West Siberian Basin and the Peri-Tethys Ocean. Based on a modern taxonomic revision, we illustrate the entire benthic foraminiferal fauna and place the assemblages in a paleoenvironmental and paleoecological context.

## GEOLOGICAL SETTING

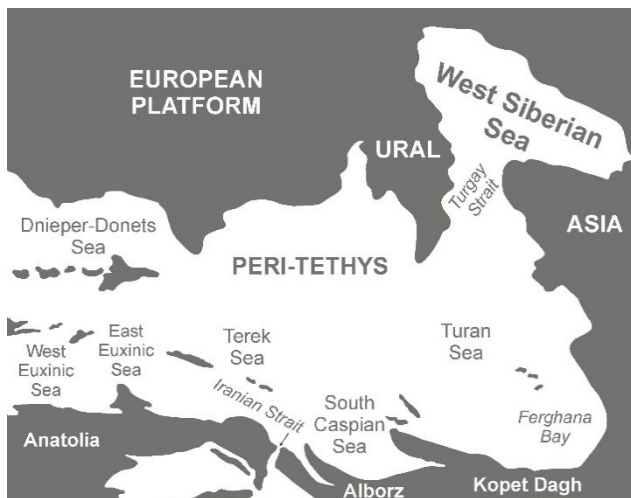
The West Siberian Basin has formed after the Late-Carboniferous and Permian collision of the Siberian and Kazakhstan continents with the Russian craton (Fedorov et al. 2004). It is flanked by the Eastern Slope of the Ural Mountains to the west, the Kazakh highlands to the south, the Siberian platform to the east, and extends north into the Kara Sea. The basins filling started in the Early Triassic when the newly formed collision structure underwent rifting, with the deposition of mainly basic and ultrabasic rocks. The rift structure, running north-south, shaped the basin's outline, a complicated elongated structure where oceanic water entered from both the north and south, and led to the deposition of marine sedimentary successions comprising Middle Triassic through Middle Paleogene clastic rocks.

The Tavda Formation widely covers Western Siberia and overlays the Lyulinovor Formation that is mainly represented by siliceous rocks such as diatomite, opoka, and tripolite (Smirnov and Konstantinov, 2017; Trubin and Yan, 2019; Nesterov et al. 2021; Smirnov et al. 2022). The formation is overlain by terrestrial sandstones of the Oligocene Kurtamysh Formation (Aleksandrova et al. 2012; Kuzmina et al. 2021).

The lithology of Tavda Formation mainly comprises marine polymineral illite-smectite and montmorillonite blue-green clays including pyrite, marcasite, siderite, and gypsum (Smirnov et al. 2019). In terms of stratigraphy, the Tavda Formation has been attributed to the Middle and Upper Eocene based on pollen, dinoflagellate cysts and magnetostratigraphy (Akhmet'ev et al. 2004a, b, 2010, 2012; Iakovleva, 2000, 2011; Iakovleva, and Heilmann-Clausen, 2010; Gnibidenko et al. 2020; Kuzmina et al. 2021). Additional stratigraphic and paleoenvironmental information was provided by findings of shark teeth (Malyshkina, 2006, 2012, 2021), teleost bone remains (Marrama et al. 2019), otoliths (Schwarzhan et al. 2021), molluscs (Trubin, 2018; Popov et al. 2019), and trace fossils (Nesterov et al. 2018). Studies on the diversity and biostratigraphy of foraminiferal assemblages were previously provided by Subbotina et al. (1964) and Podobina (1975, 1998, 2020).

During the Middle and Late Eocene, a barrier to the Arctic Ocean was established and the Siberian Basin transformed into a semi-enclosed basin (text-fig. 1), characterized by sand and clay sediments including

evidence of non-permanent Middle Eocene *Azolla* events (Akhmet'ev et al. 2010), as documented by organic-rich beds of the freshwater fern *Azolla*. The narrow Turgay Strait thus became the only significant connection to the southern equatorial Peri-Tethyan Ocean, much like the modern Black Sea that has a single connection to the Mediterranean through the Bosphorus and Dardanelles (Krijgsman et al. 2022). The growing strangulation of the West Siberian Basin resulted in reduced vertical mixing and stratified waters so that its bottom waters became slightly anoxic. With the gradual closure of the basin around the Eocene-Oligocene boundary, large rivers transformed the basin into a gigantic river-lake system, that was at times subject to marine water invasions (Akhmet'ev et al. 2004a, b; Oreshkina et al. 2020; Palcu and Krijgsman, 2022).



TEXT-FIGURE 1

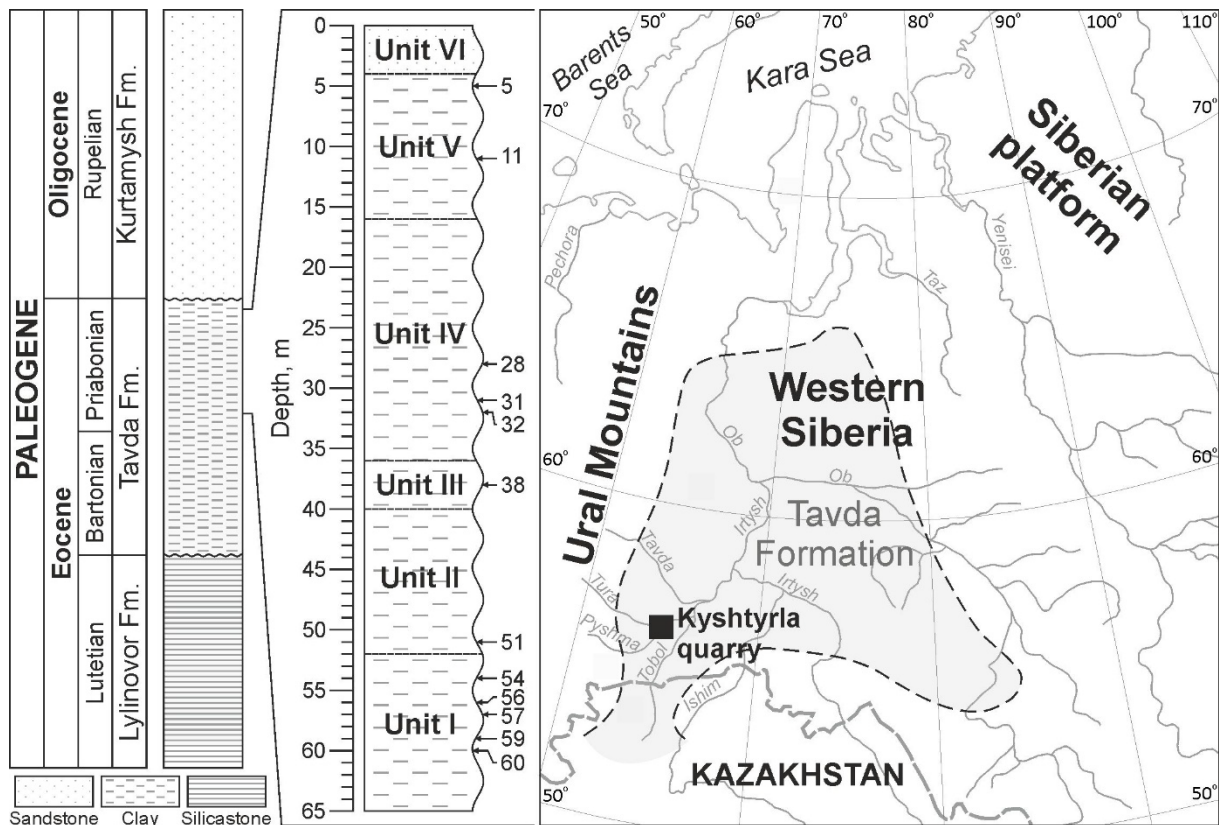
Paleogeography of the Eastern Peri-Tethys region during the Late Eocene (modified after Akhmet'ev et al. 2012 and Palcu and Krijgsman, 2022).

## MATERIAL AND METHODS

The material includes a total of 65 core drilling samples from the Kyshtyrla Quarry located on the southwestern periphery of Western Siberia (text-fig. 2; 55°55'15.50''N; 65°49'26.74''E). The drilling operation was performed in the northeastern part of the quarry, which has not been exploited yet.

Drilling was conducted down to a depth of 65 meters and core samples were taken every meter. Visual inspections and macroscopic analysis of the borehole samples revealed six different facies units. Unit I in the deepest part of the core (65–52 m) is represented by massive, gray siltstone. At a depth of 57 m, rare and small shark teeth and badly preserved mollusk test were present; Unit II (52–40 m) is also composed of massive gray siltstone but contains thin interbedded layers of blue clay; Unit III (40–36 m) consists of platy deposits of gray siltstone with intercalated layers of thin white sandstone; sedimentary Unit IV (36–16 m) is composed of blue clay and Unit V (16–4 m) is made up of brown and gray clay with large siderite concretions and small and rare crystals of gypsum. The uppermost Unit VI (0–4 m) consists essentially of very coarse sand with large, rounded rock fragments and are most probably quaternary deposits.

Chemical preparations for microbiota analyses included rock sample dissolution in hot water with  $\text{NaCO}_3$  and wet-sieving with freshwater over 63  $\mu\text{m}$  mesh sieves. The sieved residues were then oven-dried at 50°C. Dried sediments from all 60 samples were then examined for Foraminifera. Foraminifera were recovered from 12 samples (text-fig. 2). The tests were inspected by using a Zeiss Stemi 508 microscope and photographed via scanning electron microscopy (Hitachi TM3000). All specimens are archived in the micropaleontological collection of the Laboratory of Sedimentology and Paleobiosphere Evolution at the University of Tyumen, Russia.



TEXT-FIGURE 2

Location of the core drilling location at the Kyshtyrla Quarry, sedimentological units along the core, and stratigraphic subdivision of Tavda Formation after Gnibidenko et al. (2020) and Kuzmina et al. (2021). The depositional extension of Tavda Formation sediments is highlighted in light gray (modified after Akhmet'ev et al. 2012).

Picked foraminifera were then identified to species-level and numerical abundances of individual species were recorded. For the identification of benthic foraminifera and for reasons of consistency with previously published literature, we mainly follow the taxonomic concepts by Subbotina et al. (1964) and Podobina (1998) established for the Tavda Formation, literature records with first descriptions of new species (Voloshinova and Dain, 1952; Vassilenko, 1954; Ereemeeva and Belousova, 1961) and modern revisions (Brönnimann and Whittaker, 1988; Loeblich and Tappan, 1988; Parker, 2009).

Abundances wall structural types (agglutinated, porcelaneous, and hyaline-perforate) were recorded, and percent abundances of individual groups documented (Table 1). To analyze the structure and composition



of foraminiferal assemblages, relative abundances (RA) and the frequencies of occurrence (FO) of different genera and species were calculated. The RA was calculated by using the following equation:  $RA = n \cdot (100/T)$ , where n is the number of individuals of a taxon and T is the number of all benthic foraminiferal specimens in the sample. To determine the distribution of each taxon along the core interval, the FO was calculated as  $FO = p \cdot (100/P)$ , where p is the number of samples containing the taxon and P is the total number of samples. Special attention was paid to the stratigraphic distribution of species (Table. 1).

TABLE 1

Quantitative faunal data including number of individuals per species, percentages of wall structural types, and diversity and dominance index values.

Species \ Sample number	5	11	28	31	32	38	51	54	56	57	59	60
<i>Trochammina (?) gracills</i>	1	1	0	1	0	2	0	2	3	0	0	0
<i>Miliolinella</i> sp.	0	0	0	1	0	0	4	2	15	54	16	99
<i>Cibicides</i> sp.	0	0	0	18	0	1	0	0	4	6	0	6
<i>Criboelphidium parainvolutum</i>	0	0	0	1	0	0	1	3	27	22	12	13
<i>Criboelphidium</i> cf. <i>parainvolutum</i>	0	0	0	0	0	0	1	0	6	6	0	24
<i>Criboelphidium</i> sp.	0	0	0	0	0	0	0	0	0	0	0	5
<i>Ammonia</i> sp.	0	0	10	14	2	0	0	0	4	7	1	4
<i>Porosonion</i> sp.	0	0	0	1	0	1	0	1	2	0	1	7
Total number of individuals	1	1	10	36	2	4	6	8	61	95	30	158
Species richness	1	1	1	6	1	3	3	4	7	5	4	7
Dominance (SID)	1,0	1,0	1,0	0,4	1,0	0,4	0,5	0,3	0,3	0,4	0,4	0,4
Simpson 1-D	0,0	0,0	0,0	0,6	0,0	0,6	0,5	0,7	0,7	0,6	0,6	0,6
Shannon's H	0,0	0,0	0,0	1,1	0,0	1,0	0,9	1,3	1,6	1,2	0,9	1,2
Fisher $\alpha$ values	0,0	0,0	0,3	2,1	0,8	5,5	2,4	3,2	2,0	1,1	1,2	1,5
Perforate-hyaline (%)	0	0	100	94	100	50	33	50	70	43	47	37
Porcelaneous (%)	0	0	0	3	0	0	67	25	25	57	53	63
Agglutinated (%)	100	100	0	3	0	50	0	25	5	0	0	0

Geochemical sediment analysis was conducted via a S8 Tiger X-ray fluorescence (XRF) analyzer (Bruker, Germany) and include measurements of the relative abundance of 14 elements (Si, Al, Cu, Mo, Ti, K, Zn, V, Sr, Ba, Ca, Na, Th, and U). Individual measurements were conducted on powdered material for all 65 samples at micrometer size. For the analysis, the powder was stacked in capsules and covered

by plastic membrane. The concentrations of the biogenic-fractionated (Cu, Mo, and V) and terrigenous associated elements (Si, Ti, K, Zn; Chagué-Gof et al. 2002; Affouri et al. 2017; Judd et al. 2017) were normalized to Al (Martinez-Ruiz et al. 2015), in order to infer the source of terrigenous sediment (Engel et al. 2016). Since bulk element concentrations may be subject to large fluctuations due to variable proportions of biogenic and detrital minerals, we used the normalized concentrations of Al instead of major bulk concentrations as paleoenvironmental proxies. The terrigenous fraction characteristics are informative of the source and origin of the detrital input to the basin. The indices of Si/Al, Ti/Al, and Zr/Al were used to assess the aeolian detrital and the K/Al index for riverine detrital input (Tribovillard et al. 2006; Soua, 2011; Natalicchio et al. 2019). The V/Cr index was used as a proxy for paleoxygenation and redox conditions, U/Th for paleoproductivity, and Sr/Ba for salinity (Brumsack, 1986, 2006; Jones and Manning, 1994; Calvert and Pedersen, 2007; Martinez-Ruiz et al. 2015; Zhang et al. 2021). The Chemical Index of Alteration (CIA) was used to assess the extent of feldspar conversion to clay, which is influenced by different climatic conditions. It is computed using molar proportions as  $CIA = 100(Al_2O_3 / (Al_2O_3 + CaO^* + Na_2O + K_2O))$ . CaO\* is the amount of CaO incorporated in the silicate fraction of the rock.

To determine the Total Organic Carbon content (TOC), samples were heated to 450 °C for 16 h to decompose the organic substance. The Total Inorganic Carbon residues (TIC) were then analyzed via an EL vario cube element analyzer. TOC values were calculated from the difference between Total Carbon (TC) and TIC. The TC content was previously measured with the vario EL cube. The loss on ignition at 450 °C was determined in duplicate (duplicate determination). Variations of major geochemical element ratios and sedimentological (sediment texture and structure), paleontological as well as organic matter richness data were used to characterize facies types for all cores and to infer environmental changes.

Grain size analysis was performed at 1-meter intervals and measured with a laser diffraction particle size analyzer LS 13 320 «Beckman Coulter» (USA) using the Aqueous Liquid Module. The fraction < 2 mm was prepared by using sodium pyrophosphate and obtained by wet sieving using about 2 grams of sediment. The average grain size distribution of samples was recognized as fine clay (<0.0002 mm), coarse clay (0.0002–0.002 mm), fine silt (0.002–0.02 mm), coarse silt (0.02–0.05 mm), very fine sand

(0.05–0.1 mm, fine sand (0.1–0.25 mm), medium sand (0.25–0.5 mm), coarse sand (0.5–1.0 mm), and very coarse sand (1.0–2.0 mm).

## RESULTS

### *Composition and structure of the foraminiferal fauna*

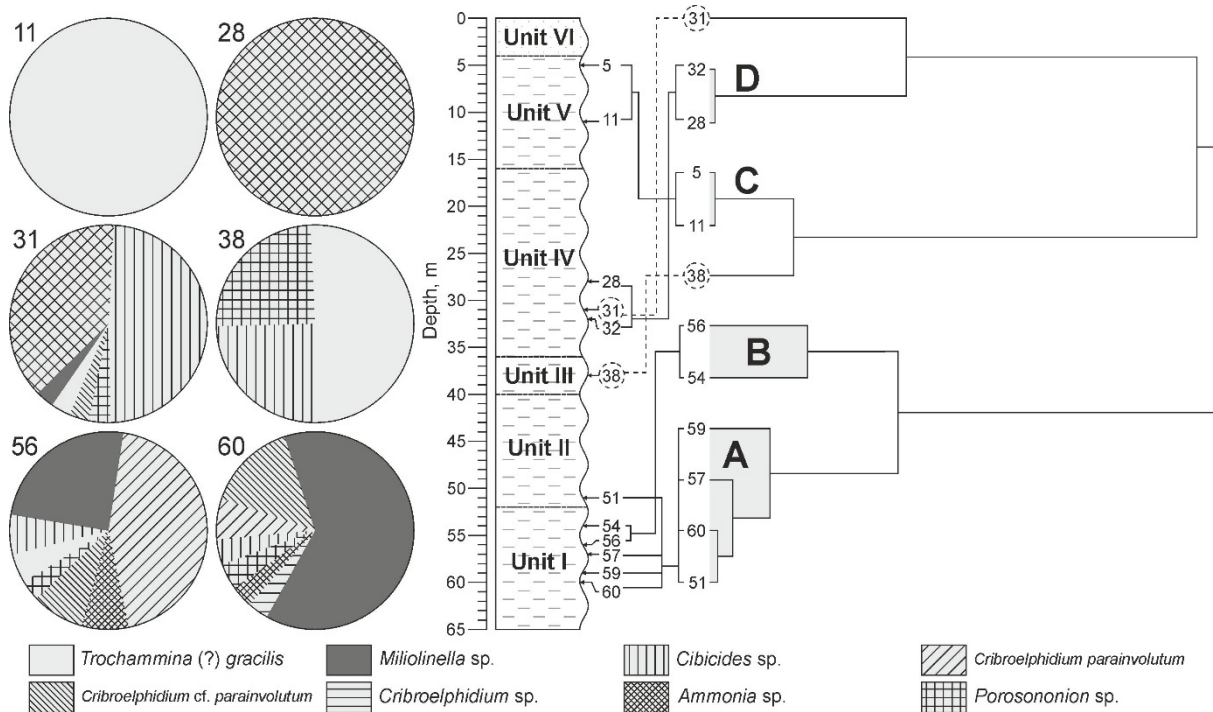
A low-diverse assemblage, comprising 8 species of benthic foraminifera, was identified from a total of 412 picked specimens. This includes 6 perforate-hyaline, 1 porcelaneous and 1 agglutinated species. Perforate-hyaline and porcelaneous species are dominant and constitute 51.2% and 46.4% of the total assemblages, respectively. Agglutinated tests are rare and contribute 2.4% to the foraminiferal biotas. The number of picked foraminifera from individual samples varied and ranged between 1 and 158. The largest numbers of individuals were found in samples in the deeper part of the core (samples 56, 57, 59, 60).

### *Cluster analysis and assemblages*

Cluster analysis resulted in four major clusters (A, B, C, and D, text-fig. 3) and two outliers (samples 38 and 31, text-fig. 3). Cluster A includes samples 51, 57, 59 and 60, and is dominated by porcelaneous individuals of *Miliolinella* sp. and variable amounts of *Cibicides* sp., *Ammonia* sp., *Porosononion* sp., and three species of genus *Criboelphidium* (*C. parainvolutum* Uschakova in Subbotina 1964, *C. cf. parainvolutum* Uschakova in Subbotina 1964, and *C. sp.*). Cluster B includes samples 56 and 54 and is composed of mostly *Criboelphidium parainvolutum* and *Miliolinella* sp., and low amounts of *Trochammina(?) gracilis* Lipman, 1960, *Cibicides* sp., *Porosononion* sp., *Criboelphidium cf. parainvolutum*, and *Ammonia* sp.. Cluster C and Cluster D are each represented by two samples (samples 5, 11 for C, and samples 28 and 32 for D) and comprise exclusively monospecific assemblages composed of *Trochammina (?) gracilis* (C) and *Ammonia* sp. (D).

The outlier sample 38 is dominated by the agglutinated species *Trochammina(?) gracilis* but also contains low amounts of *Cibicides* sp. and *Porosononion* sp. The second outlier sample 31 is dominated by

*Cibicides* sp. and *Ammonia* sp., with low amounts of *Trochammina*(?) *gracilis*, *Miliolinella* sp., *Porosonion* sp., and *Criboelphidium* cf. *parainvolutum*.



TEXT-FIGURE 3

Depth and position of samples across the core, sedimentological units (I–VI), cluster dendrogram, and percent abundance analyses of foraminiferal groups of cluster-typical samples.

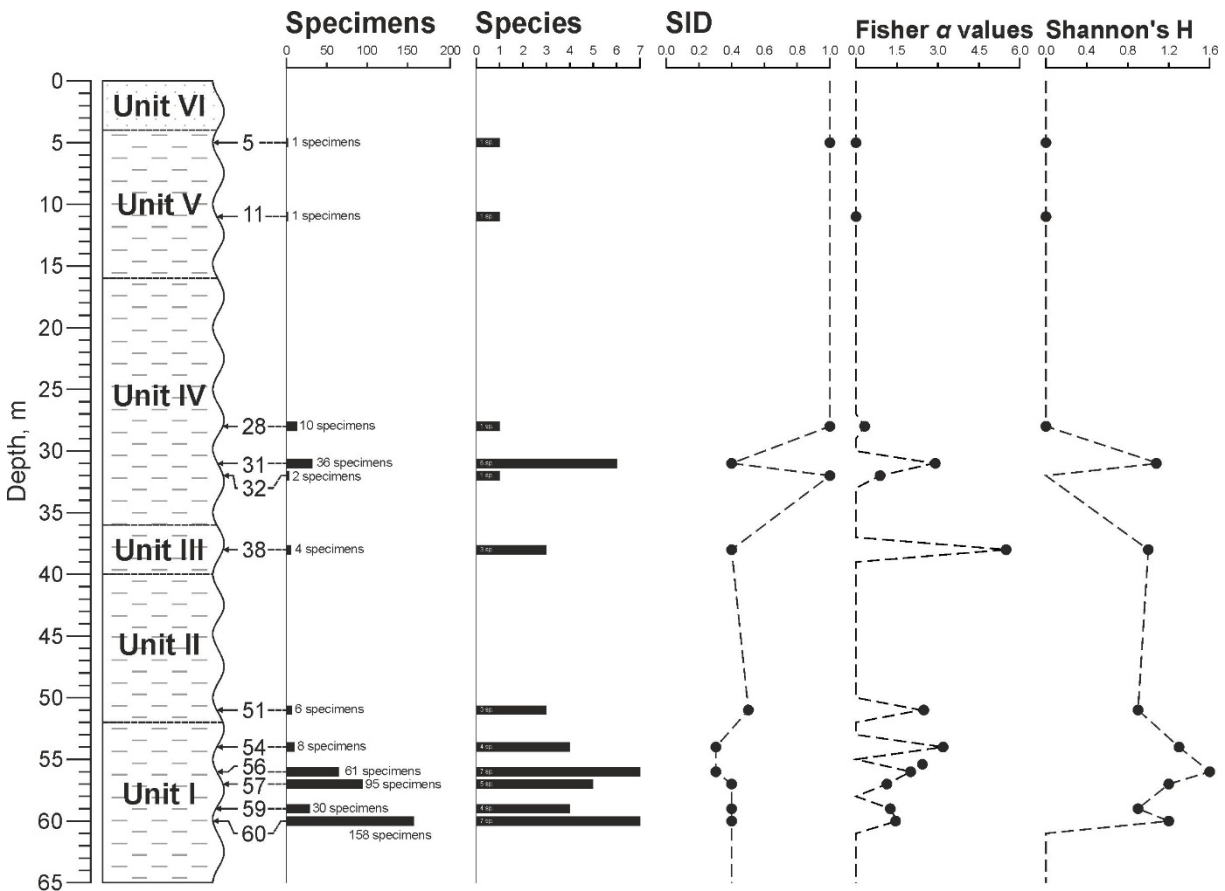
### ***Species richness, diversity, frequency and abundances***

The species richness in the samples varies, is generally low and ranges between 1 and 7 (Table 1). In general, higher species richness data were recorded in the deeper part of the core. Diversity index computations (Table 1) revealed Fisher  $\alpha$  values that range between 1.1 and 5.5, except for the monospecific clusters, where the value is less than 1. Shannon H values range between 0.9 and 1.6, with values of 0 for the monospecific samples of cluster C and D), and Simpson index values range between 0.5 and 0.7, except for the samples from the monospecific clusters C and D, where values are 0. The highest Fisher  $\alpha$  value was recorded in sample 54 of cluster B ( $\alpha = 3.2$ ) and the lowest values were

computed in samples 5 and 11 (Fisher  $\alpha$  index 0). This trend is generally followed by the Shannon H and Simpson1-D indices (Table 1).

Species with the highest relative abundances (RA) include the porcelaneous taxon *Miliolinella* sp. (46.4%) and the perforate-hyaline *Criboelphidium parainvolutum* (19.2%), *Ammonia* sp. (10.2%), *Criboelphidium* cf. *parainvolutum* (9.0%), and *Cibicides* sp. (8.5%). Other hyaline-perforate forms are less abundant with values of 3.2% for *Porosonion* sp. and 1.2% for *Criboelphidium* sp. The agglutinated taxon *Trochammina* (?) *gracilis* is rare and occurs only sporadically (2.4%).

Based on frequency of occurrence data (FO), *Miliolinella* sp., *Criboelphidium parainvolutum*, *Ammonia* sp., *Porosonion* sp., and *Trochammina* (?) *gracilis* were the most ubiquitous and occurred (FO > 50%) in the samples analyzed. Among the 8 species recovered, 2 species, *Cibicides* sp. and *Criboelphidium* cf. *parainvolutum*, are common (FO > 25%), and *Criboelphidium* sp. (8.3%) occurs only occasionally (FO > 10%) (text-fig. 4).



## TEXT-FIGURE 4

Total number of individuals and species, indices of species richness and diversity.

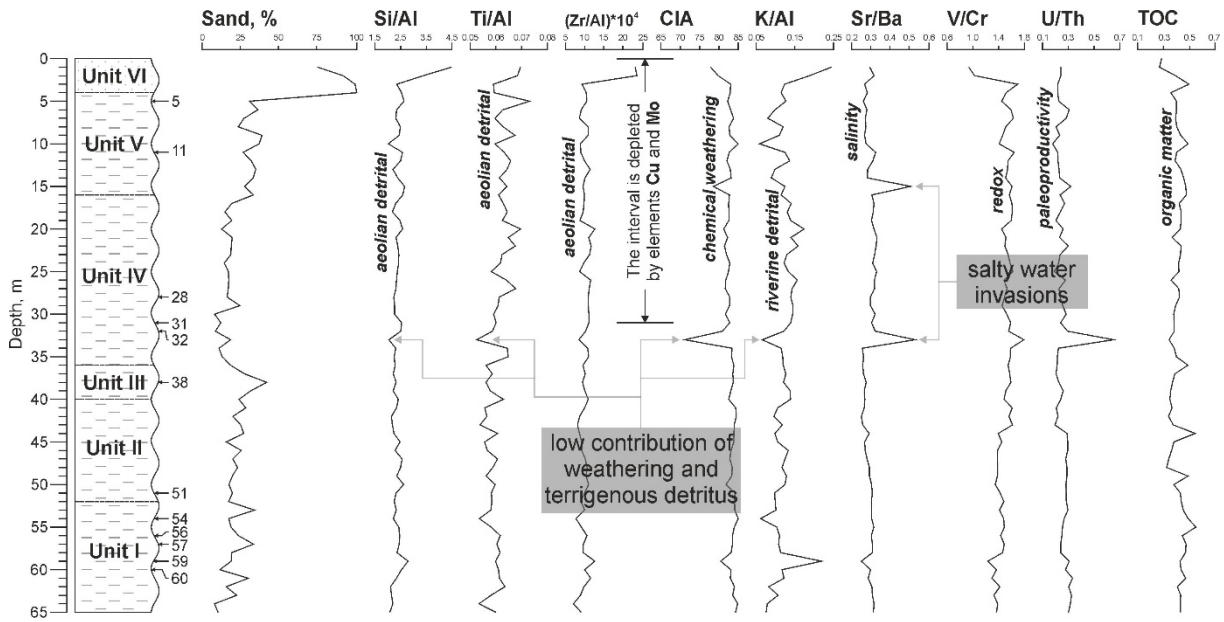
### *Lithological and geochemical proxies*

The aeolian detrital (Si/Al, Ti/Al, and Zr/Al) and riverine detrital input (K/Al) ratio indices revealed only little fluctuations throughout the core and remained nearly constant for the CIA index as well. However, higher negative excursions were recorded at 33 m for the detrital indices and the CIA-index.

Values of the V/Cr ratio, an indicator for paleoxygenation and the redox state, also remained quite constant throughout the core, never exceeded values of 2, thus indicating more oxidizing conditions (Jones and Manning, 1994). From the low and nearly constant values of the U/Th ratio throughout the section, oxic states can also be inferred, except for a high-amplitude deflection at 33 m, where the values approach 0.7. Down-core variations of the TOC ranged between ~0.25–0.55% with moderately higher amplitude fluctuations in the lower part of the core. Values of Sr/Ba ratios were generally low and range between 0.2–0.3, except for two prominent positive excursions at 15 and 33 m core depth, where values of 0.6 and 0.7 were recorded respectively.

Based on lithology and grain size distribution, 6 units can be distinguished in this section. The first two units (Unit I, 52–65 m and Unit II, 40–52 m) are represented by gray siltstone with intercalated layers of blue clay. These units have a sand content (SC) of about 21%, indicative for shallow-water, sublittoral conditions. Unit III (36–40 m) is represented by clay with intercalated layers of white sandstone (SC 27–42%) and considered to be deposited in a shallow, probably are littoral environment. Units IV (16–36 m) and V (4–16 m) consist essentially of clay. In both units, a continuous increase in sand content is observed (text-fig. 5), consistent with the scenario of increasing isolation of the basin and decreasing water depth.

Measurements on the content of Cu and Mo indicate a clear zonation within the studied core profile: while in the lower core section (65–31 m) average values of 39.2 ppm for Cu and 0.9 ppm for Mo were measured, the values for both elements in the upper core section (31–4 m) were below the detection limit.



TEXT-FIGURE 5

Indices and geochemical ratios along of the core from the Kyshtyrla Quarry in Western Siberia.

### Stratigraphy

The Tavda Formation deposits were deposited during the Bartonian and Priabonian (~40.5–33.5 Ma) and span the time interval from the top of Nannoplankton Zone NP 16 to the lower part of NP 21 (Akhmet'ev et al. 2010). The Formation is subdivided into the Lower and Upper Tavda Subformations, and begins with the *Rhombodinium draco* zone, a dinoflagellate marker zone indicative for the basal Bartonian (Vasil'eva, 1990; Akhmet'ev et al. 2010; Iakovleva and Kulkova, 2003). The Lower Tavda Subformation is characterized by abundant and diverse agglutinated foraminifera, including species of *Haplophragmoides* and *Gaudryina*. The Upper Tavda Subformation in turn, generally lacks agglutinated taxa, but is marked by frequently occurring individuals of the hyaline-perforate foraminifer *Criboelphidium*, an assemblage considered to be representative for the Priabonian (Akhmet'ev et al. 2004a). Additional detailed stratigraphic information for the Tavda Formation was also provided by studies on dinoflagellates (Iakovleva and Heilmann-Clausen, 2010), pollen (Kuzmina et al. 2021), and

magnetostratigraphy (Gnibidenko et al. 2020). Findings of various *Criboelphidium* species, including *C. parainvolutum*, *C. cf. parainvolutum*, and *C. sp.*, the presence of diverse, perforate-hyaline and porcelaneous foraminifera, and the almost complete absence of agglutinated taxa, strongly suggest that the core material analyzed corresponds to the Upper Tavda Subformation and is of Priabonian age.

## DISCUSSION

During the Late Eocene, the West Siberian Basin was a shallow epicontinental sea with connection to the Peri-Tethys through the narrow Turgay Strait (Akhmet'ev et al. 2010). As the West Siberian Basin became more and more isolated from the Tethys Ocean (Akhmet'ev et al., 2010, 2012; Palcu and Krijgsman, 2022), the inflow of marine waters was further reduced, changing conditions to a system where rivers became dominant. The chronology of the basins increasing isolation and limited exchange with waters of the Peri-Tethys Ocean is reflected in (1) the composition and diversity of the benthic foraminiferal fauna, (2) geochemical proxies, and (3) grain size distribution.

As pointed out above, the foraminiferal assemblages recorded in the core material comprise typical stratigraphic indicator taxa for the Priabonian Upper Tavda Subformation (Akhmet'ev et al. 2010). The benthic foraminiferal biotas recovered are characterized by low species richness and diversity indices and mainly composed of taxa that are indicative for shallow-water subtidal and, tidal conditions (Murray, 2006). However, from the bottom to the top of the section, abundance, species richness and diversity values markedly decrease, suggesting an increase in environmental stressors. While the lowermost units (Units 1–3 and the lower portion of Unit 4; 60–33 m core depth) comprise an amalgamation of moderately low diverse subtidal and intertidal taxa (*Miliolinella*, *Cibicides*, *Criboelphidium*, *Porosonion*, *Ammonia*, *Trochammina*) with Fisher  $\alpha$  values of up to 5.5, the upper core units are almost exclusively composed of monospecific, typical intertidal and stress-tolerant species (e.g. *Ammonia*, *Trochammina*; Murray, 2006; Debenay, 2000; Scott, 2001; Fajemila et al. 2015; Langer et al., 2016a,b; Hayward et al. 2021). The pronounced decrease in diversity and species richness towards the top of the section is accompanied by a marked decrease in the abundance of individual taxa and associated diversity



indices (Table 1). The deterioration of environmental conditions can also be seen in the composition of the wall structures, which indicate a three-stage change from a fauna dominated by mainly miliolids and hyaline-perforated taxa, to mainly hyaline-perforated, and finally a purely agglutinated foraminiferal fauna (Table 1). The faunal changes recorded from the bottom to the top of the core are considered to indicate a transition from a shallow subtidal to a tidal influenced habitat, a scenario that is in line with (1) the findings of Akhmet'ev et al. (2010), who noted a regression at the end of the Priabonian, and (2) increasing SC values from the bottom to top of the core (text-fig. 5). In the upper section, abundant gypsum crystals are present on pyrite-sand aggregates. Their occurrence is probably related to the oxidation of the sulfidic primary sediments (Pirlet et al. 2009).

The geochemical background throughout the core section with respect to Si/Al, Ti/Al, Zr/Al, K/Al, V/Cr, and U/Th ratios as well as the CIA index remains comparatively stable, except for a few low-amplitude fluctuations at around 15 and 33 m core depth. These proxies are commonly used to infer weathering rates, salinity changes, oxygenation conditions and redox states (Jones and Manning, 1994; Martinez-Ruiz et al. 2015; Zhang et al. 2021). Ratio values of the redox sensitive markers V/Cr remained low throughout the core ( $<2$ ), thus indicating oxic environmental conditions during the time of deposition (Jones and Manning, 1994; Ferriday and Montenari, 2016).

The CIA index has been widely used as a proxy for chemical weathering, where higher CIA values indicate an increased conversion of feldspars to clays and stronger chemical weathering rates (Nesbitt and Young, 1982, Li and Yang, 2010). The record of a strong negative amplitude at about 33 m possibly indicates a short-term pulse of higher physical than chemical weathering rates, consistent with a peak value for U/Th and lower Si/Al, Ti/Al, Zr/Al K/Al indices (text-fig. 5) in this core interval.

Throughout the core, low Sr/Ba values were recorded ( $<1.0$ ). In theory, values lower 1.0 are typical for terrestrial sediment, as Ba is typically enriched in terrestrial and freshwater sediment and Sr is poor when compared to marine deposits (Zwolsman and van Eck, 1999; Wang et al. 2021; Dashtgard et al. 2022). However, the continuous presence of shallow marine benthic foraminifera clearly indicates marine or brackish water conditions (Iglikowska and Pawłowska, 2015), consistent with very low Sr/Ba records ( $<1$ ) from marine sediments (Ross and Bustin, 2009; Wei and Algeo, 2020; Wang et al. 2021). Remnants,

traces or deposits of the freshwater fern *Azolla*, an indicator for freshwater pulses (Brinkhuis et al., 2006), were not found throughout the core. The prevalence of mainly marine conditions is underscored by the entire suite of geochemical proxies (Sr/Ba as a proxy for salinity accompanied by low detrital indices of Si/Al, Ti/Al, Zr/Al, K/Al, and U/Th as proxies for weathering and chemical alteration) and the continued presence of benthic foraminifera. Consistently higher levels of copper and molybdenum, elements that perform vital metabolic functions in biological systems, also suggest that marine conditions were more conducive to life in the lower core area, consistent with the scenario of an increasing isolation of the West Siberian Basin. The analysis of litho-geochemical and micropaleontological multiproxy data from the core material of the Kyshtyrka Quarry of Western Siberia thus provides a basis for reconstructing the environmental conditions documenting the transition from an open to an increasingly isolated basin.

## CONCLUSIONS

In the Upper Eocene, the West Siberian Basin became increasingly isolated from the Peri-Tethys Ocean. To reconstruct the environmental conditions associated with the increasing isolation of the basin, microfaunal and geochemical multiproxy analyses were performed on drill core sediments from the Tavda Formation in Western Siberia. Analyses of the benthic foraminiferal faunas show that the studied Tavda sediments can be assigned to the Priabonian and represent the transition from an open to an increasingly closed basin. The transition is reflected in the reduction of individual abundances, the decrease in species richness of the foraminiferal faunas, and geochemical proxy data. From the bottom to the top of the core, the foraminiferal biotas progressively shift from normal marine, shallow subtidal to extremely low-diverse, and possibly brackish water assemblages. The transition from shallow subtidal to intertidal conditions is also reflected in an overall increase in sand content, dominance of stress-tolerant taxa, and decreasing Cu and Mo proxy data, consistent with a scenario of increasing isolation of the West Siberian Basin.

## ACKNOWLEDGEMENTS

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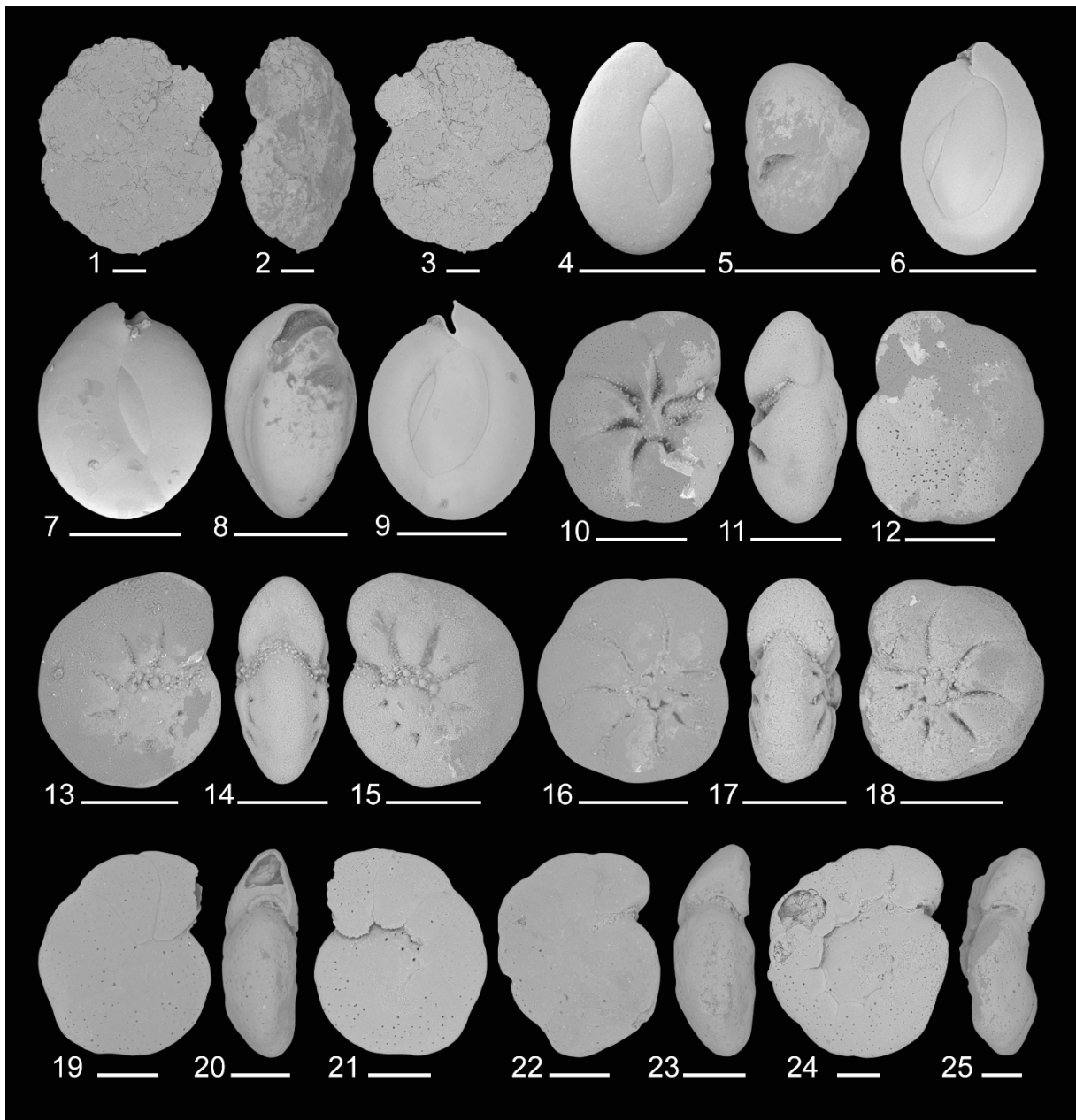


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**PLATE 1**

Scale bar = 100  $\mu$ m

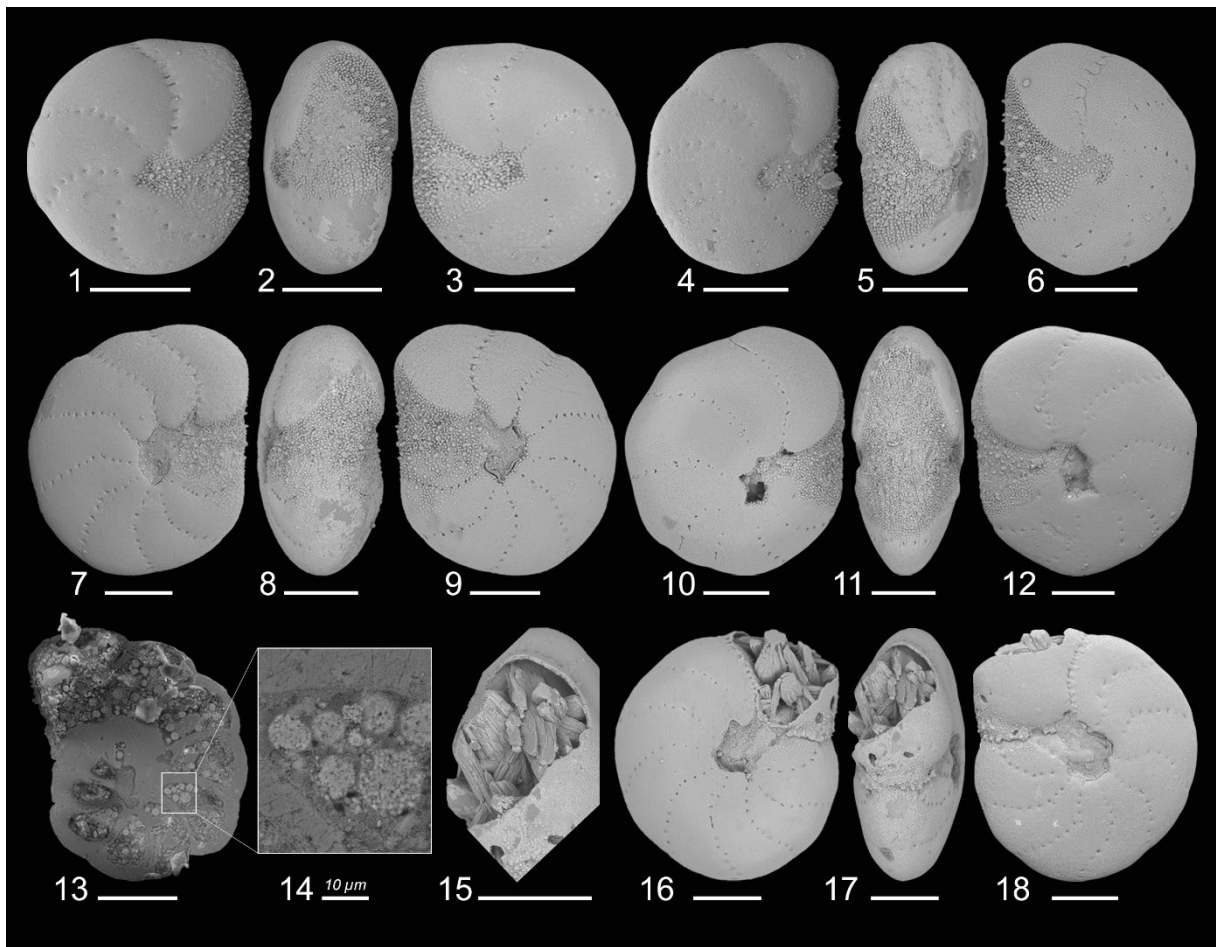
1–3 *Trochammina* (?) *gracills* Lipman, 1960 (sample 38).

4–9 *Miliolinella* sp. (sample 60).

10–12 *Ammonia* sp. (sample 31).

13–18 *Porosononion* sp. (sample 60).

19–25 *Cibicides* sp. (sample 60).



**PLATE 2**

Scale bar = 100 µm except for fig. 14 (10 µm)

1–6 *Cribroelphidium* cf. *parainvolutum* Uschakova in Subbotina 1964 (sample 60).

7–14 *Cribroelphidium parainvolutum* Uschakova in Subbotina 1964 (sample 60).

15–18 *Cribroelphidium* sp. (sample 60).

## Chapter 4: Publication

# Bioerosion Structures on Benthic Foraminiferal Tests from the Upper Cretaceous and Paleogene of Western Siberia

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**Abstract**—Bioerosion structures, including holes, pits, and grooves, on the surface of benthic foraminiferal tests from the Upper Cretaceous and Paleogene of Western Siberia are studied. Their morphology is examined, their possible origin and the paleogeographic and stratigraphic distribution in sections representing marine basins of Western Siberia are discussed. The ichnospecies assemblage studied includes *Oichnus simplex* Bromley, 1981, *O. paraboloides* Bromley, 1981, *O. gradatus* Nielsen et Nielsen, 2001, and *O. ovalis* Bromley, 1993.

**Keywords:** ichnofossils, behavioral strategies, bioerosion, *Oichnus*, Cretaceous, Paleogene, Western Siberia

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## INTRODUCTION

Ichnofossils (traces produced by organisms during their life) have been the focus of many paleontological studies of the Mesozoic and Cenozoic of Western Siberia. However, the most attention is given to macroscopic ichnofossils that can be studied without the use of instruments (Vakulenko et al., 2011; Nesterov et al., 2018; Trubin and Yan, 2020, etc.). Information on borings on foraminiferal tests has not previously been published in the scientific literature, despite numerous finds in the Mesozoic and Cenozoic of Western Siberia. In the Russian-language literature, rare references to such structures can be found, but without detailed descriptions, systematization, or photographs (Maslakova, 1974). However, traces of lifetime damage on foraminiferal tests have been widely published on, for both benthic (Reyment, 1966; Collen, 1973; Douglas, 1973; Sliter, 1975; Hickman and Lipps, 1983; Arnold et al., 1985; Nielsen, 2002; Malumian et al., 2007; Sengupta and Nielsen, 2009; Vohnik, 2021) and planktonic taxa (Sliter, 1971; Nielsen, 1999; Nielsen and Nielsen, 2001; Nielsen et al., 2003; Frozza et al., 2020). A classification of structures and their terminology has been developed, and possible means of formation of these structures have been proposed (Wisshak et al., 2019). Thanks to

improvements to electron microscopy methods, and the accumulation of a large micropaleontological collection, the present authors have collected new data on the ichnotaxonomic diversity of bioerosion structures on foraminiferal tests from the Cretaceous and Paleogene of Western Siberia, as well as on their stratigraphic and paleogeographic distribution.

## PREVIOUS STUDIES

The study of bioerosion structures on the surface of foraminiferal tests began at the beginning of the 20th century (Heron-Allen, 1915; Livan, 1937). Sliter (1971, 1975) was the first to attempt to classify holes in foraminiferal tests. The features underlying the classification were based on the shape and orientation of structures in space, which made it possible to distinguish two groups: the first includes rounded and oval holes located at an angle to the surface; the second includes only rounded holes oriented perpendicular to the surface. Further study made it possible to establish the ichnogenus *Oichnus* Bromley, 1981 with two ichnospecies: *Oichnus simplex* Bromley, 1981 and *O. paraboloides* Bromley, 1981, the first of which is considered a type. This ichnogenus united all subcircular and suboval small holes on the foraminiferal tests and mollusk shells (Bromley, 1981, p. 60; supple-

mented by Nielsen and Nielsen, 2001, pp. 102–103; Wisshak et al., 2015, pp. 448–449). The criteria for identifying ichnospecies were the shape of the longitudinal and transverse sections and the nature of the outer contour of the holes (Bromley, 1981, 1993, 2004; Kowalewski, 1993; Wisshak et al., 2015). The subsequent proposal of the new ichnogenus *Tremichnus* Brett, 1985 for similar but non-penetrating small pits on the shell surface has sparked a series of still-ongoing discussions (Brett, 1985; Nielsen and Nielsen, 2001; Zonneveld and Gingras, 2014; Wisshak et al., 2015, 2019). In the course of further research, five more ichnospecies were established, which are currently accepted (Wisshak et al., 2019): *Oichnus ovalis* Bromley, 1993, *O. cornatus* Nielsen et Nielsen, 2001, *O. asperus* Nielsen et Nielsen, 2001, *O. gradatus* Nielsen et Nielsen, 2001, *O. solus* (Nielsen et al., 2003) (Fig. 1). Following Wisshak et al. (2019), we assign the ichnogenus *Oichnus* to the ichnofamily Oichnidae and the ethological category of Praedichnia (predation traces) or Fixichnia (attachment traces).

## MATERIAL AND METHODS

The material used for the study was a collection of foraminifers from the Gankino Formation (Maastriichtian, Upper Cretaceous) and Tibeisale Formations (Dania, Paleocene, Paleogene) of the Kharasavey structural boreholes; Leplya Formation (Campanian, Upper Cretaceous–Danian, Paleocene, Paleogene) from a hydrogeological parametric boreholes near the town of Uray; the Sokolovo Formation (Thanetian, Paleocene, Paleogene), exposed in the section of the Sokolovo iron-ore quarry; the Tavda Formation (Bartonian and Priabonian, Eocene, Paleogene), studied in the Kyshtyrla quarry (Fig. 2).

A total of 3570 tests from 328 rock samples were studied in the collection. Bioerosion structures were found on the surface of about 80 foraminiferal tests. The samples were prepared for microfauna using the procedure adopted in the Laboratory of Sedimentology and Evolution of the Paleobiosphere of Tyumen State University. The tests were examined using a Hitachi TM3000 scanning electron microscope at 500–1200x magnification. Holes, grooves, or pits on the test surface of benthic foraminifers were analyzed, and structures formed as a result of bioerosion activity were selected for study. The terminology used and the methodology for studying traces followed Nielsen and Nielsen (2001) and Wisshak et al. (2015, 2019). This work uses the classification of ichnofossils proposed by Wisshak et al. (2019).

## SYSTEMATIC PALEONTOLOGY

### Ichnofamily Oichnidae Wisshak, 2019

#### Ichnogenus *Oichnus* Bromley, 1981

Type species. *O. simplex* Bromley, 1981.

Diagnosis. Round and subcircular holes of biogenic origin, formed on the surface of a solid substrate. The holes can perforate the test, or end in the substrate in the form of shallow cylindrical or subcylindrical pits.

Species composition. *Oichnus simplex*, *O. paraboloides* Bromley, 1981; *O. ovalis* Bromley, 1993; *O. cornatus* Nielsen et Nielsen, 2001; *O. asperus* Nielsen et Nielsen, 2001; *O. gradatus* Nielsen et Nielsen, 2001; *O. solus* (Nielsen et al., 2003).

Comparisons. In contrast to the morphologically similar ichnogenus *Tremichnus* Brett, 1985, it can be represented as perforating holes. In the case of non-perforating holes, it is distinguished by a clear and even edge without concentric undulating grooves and other structures.

Remarks. The diagnosis was modified in later studies (Nielsen and Nielsen, 2001; Wisshak et al., 2015), which considered not only round holes, but also subrounded, suboval and rounded-diamond-shaped forms. *Oichnus* unites all small holes and pits on the surface of the substrate, and formed as a result of boring from small predatory organisms or from the attachment of epibionts.

#### *Oichnus simplex* Bromley, 1981

Plate 19, figs. 1–26

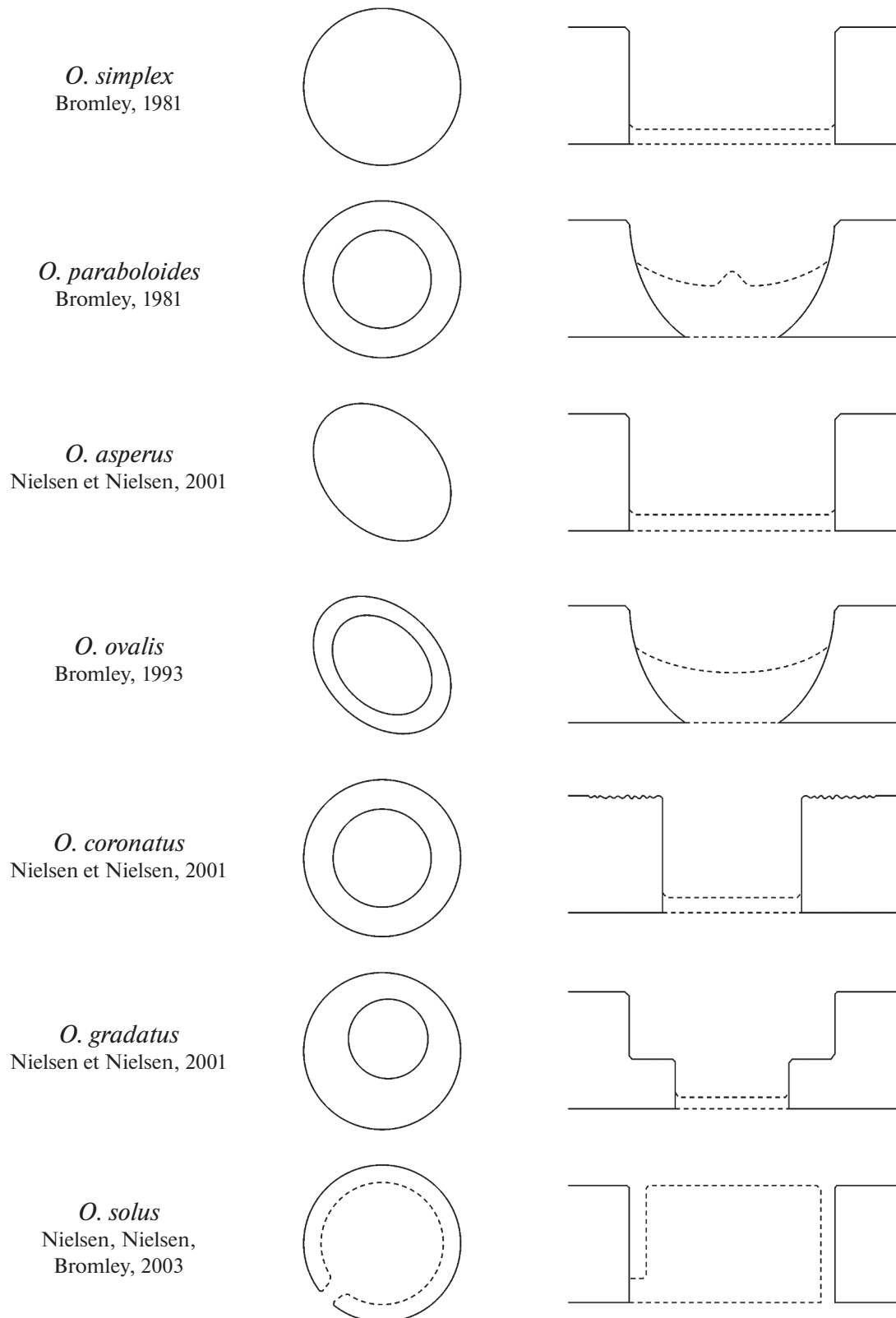
*Oichnus simplex*: Bromley, 1981, p. 60, pl. 3, fig. 3; Ruiz-Munoz and Gonzalez-Regalado, 1989, text-figs. 2, 3; Pickerill and Donovan, 1998, pp. 163–164, pl. 1, figs. 1–3, pl. 2, figs. 2–4; Ruggiero, 1999, text-figs. 1c, 1e, 1g, 1h; Nielsen and Nielsen, 2001, p. 103, text-figs. 1a, 1b, 5; Ruggiero and Annuziata, 2002, pl. 1, figs. 3; Donovan and Jagt, 2003, p. 72, text-fig. 4a; Nielsen et al., 2003, text-figs. 12c–12d; Santos et al., 2003, p. 134, text-figs. 3a, 3b, 7a, 7b; Blissett and Pickerill, 2004, text-fig. 7.6; Ruggiero, 2006, p. 181, text-fig. 12, 14–17; Daley, 2008, text-fig. 7/1; Donovan and Harper, 2007, text-fig. 2; Gibert et al., 2007, text-fig. 9d; Zamora et al., 2008, text-fig. 3/13; Buosi et al., 2014, text-fig. 4a–4e, 5a; Donovan et al., 2014, text-fig. 5d, 8c; Wisshak et al., 2015, text-figs. 1e, 1f; Breton et al., 2017, text-fig. 4a; Abdel-Fattah, 2018, text-figs. 3a, 3b, 4a; Gormus et al., 2019, text-fig. 8.1; El-Sorogy et al., 2020, pp. 7–8, text-figs. 5h–5j; Charo et al., 2021, text-fig. 9c; Ortiz-Jeronimo et al., 2021, text-figs. 5a–5e, 6a–5i.

*Sedilichnus simplex*: Zonneveld and Gingras, 2014, p. 899–900, figs. 1/2, 1/3; Pokorný and Stofik, 2016, pp. 5, 7, 8, text-figs. 3c–3e.

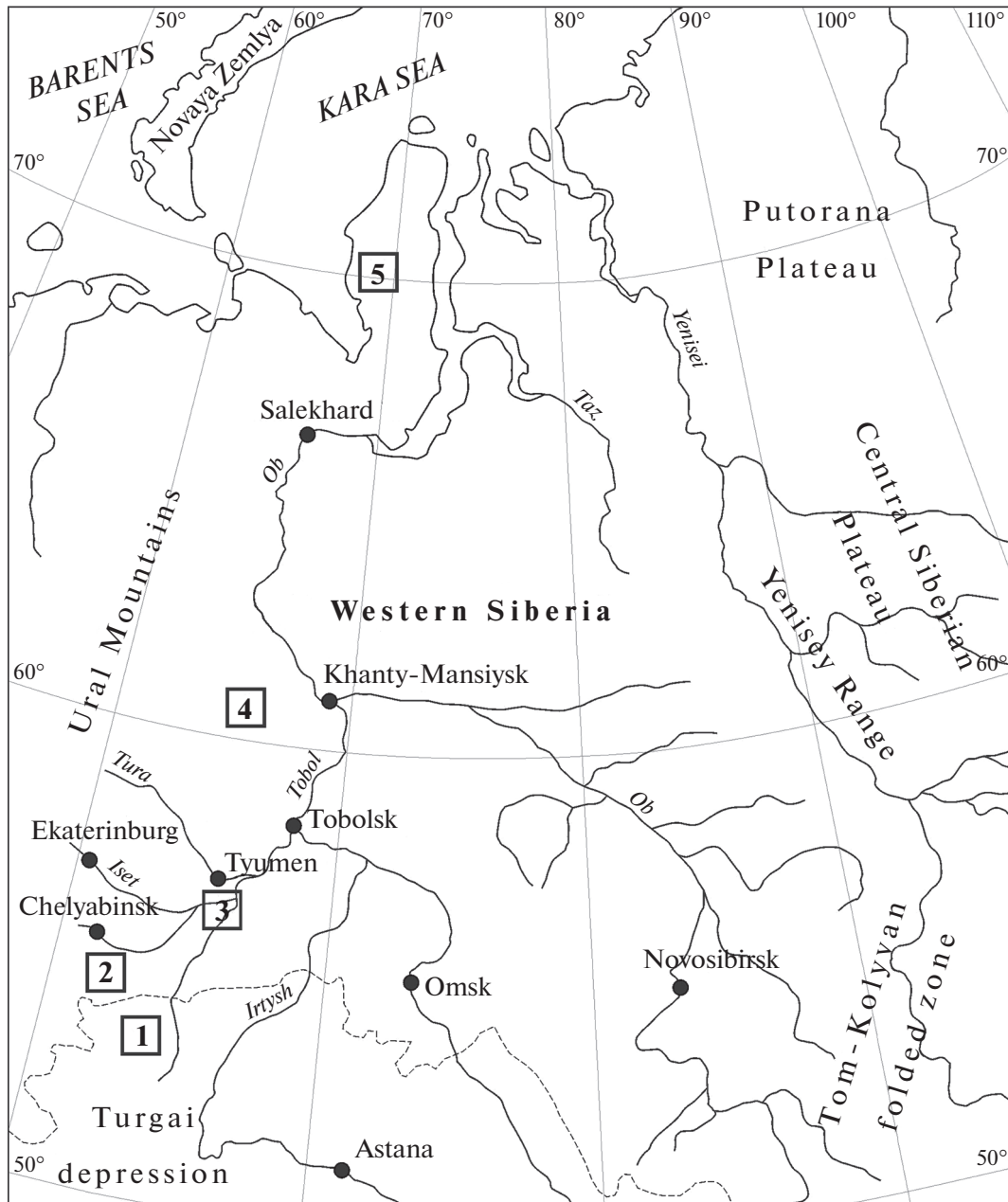
Holotype. Specimen MGUH 15351, Geological Museum of the University of Copenhagen (Denmark); opening in valve of *Arctostrea diluviana*; Skåne, Sweden; Campanian, Upper Cretaceous.

Description. Openings of a simple cylindrical or subcylindrical shape, located perpendicular or at a slight angle to the substrate. The edges are clear and even. The walls are smooth. Non-perforating struc-





**Fig. 1.** Ichnospecies diversity of *Oichnus* Bromley, 1981 according to the ichnotaxonomy provided by Wisshak et al. (2019) with additions.



**Fig. 2.** Location of the studied sections: (1) Sokolovo iron-ore quarry; (2) structural borehole no. 9 near Troitsk; (3) borehole drilled in the Kyshtyrla quarry; (4) hydrogeological parametric borehole near the town of Uray; (5) structural boreholes drilled on the territory of the Kharasaveyskoye Field.

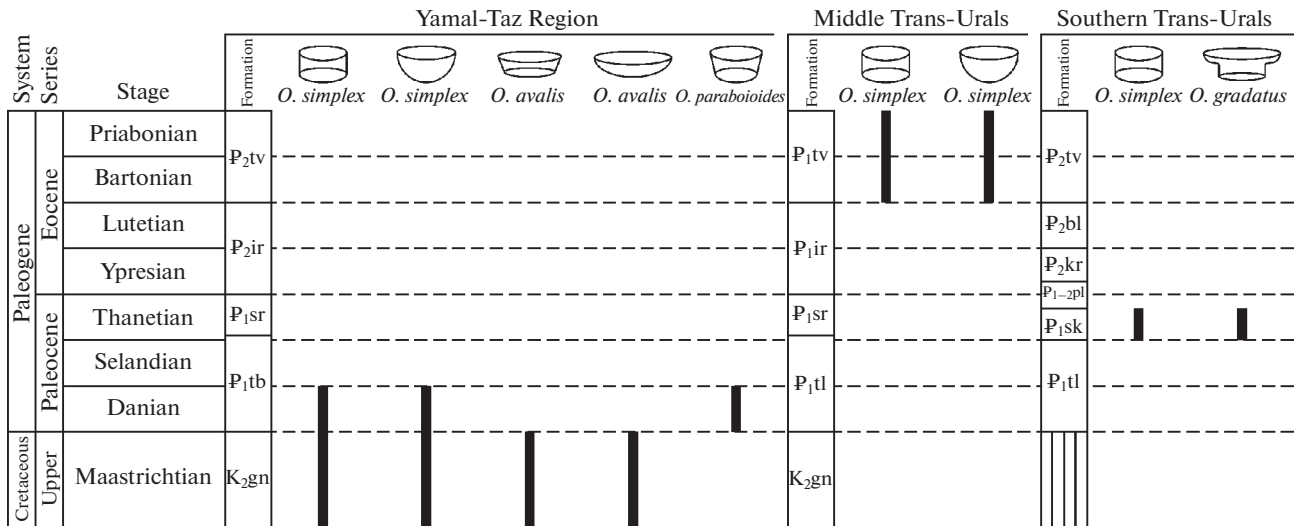
tures are represented by semirounded pits with a flattened base.

Dimensions in mm. Diameter from 0.002 to 0.02.

**Comparison.** It differs from co-occurring morphologically closely related ichnospecies primarily in its cylindrical shape versus the truncated-conical shape in *Oichnus paraboloides* and the oval shape in *O. ovalis*.

**Remarks.** *Oichnus simplex* is one of the most common forms attributed to the ichnogenus *Oichnus*. Size, as in all *Oichnus* ichnospecies, is not considered an essential classification feature (Bromley, 1981). Perforating holes are probably caused by predation by juvenile gastropods. Hemispherical pits may be the result of epibiont attachment (Wisshak et al., 2015, 2019).

**Material.** Holes and pits on the surface of 10 tests from the Gankino Formation (Maastrichtian, Upper Cretaceous) opened by the Kharasavey struc-



**Fig. 3.** Stratigraphic distribution of bioerosion microstructures on foraminifera shells in the studied sections of the Upper Cretaceous and Paleogene of Western Siberia. K<sub>2</sub>gn—Gankino Formation, P<sub>1</sub>tb—Tibeisale Formation, P<sub>1</sub>tl—Talitsa Formation, P<sub>1</sub>sk—Sokolovo Formation, P<sub>1</sub>sr—Serov Formation, P<sub>1-2</sub>pl—“Banded Serie”, P<sub>2</sub>kr—Kachar Series, P<sub>2</sub>bl—Belinskaya Series, P<sub>2</sub>ir—Irbit Formation, P<sub>2</sub>tv—Tavda Formation.



**Fig. 4.** Supposed ethological interpretations of the studied bioerosion structures on the surface of foraminifera tests from the Upper Cretaceous and Paleogene of Western Siberia: A—predation; B—postmortem colonization inside of chambers; C—attaching of epibionts on the test surface.

tural boreholes. Holes on the surface of 30 tests from the Sokolovo Formation (Thanetian, Paleocene, Paleogene), opened in the Sokolovo iron-ore quarry. Holes and pits on the surface of 10 tests from the Tavda Formation (Bartonian and Priabonian, Eocene, Paleogene system), uncovered in the Kyshtyrla quarry.

**Occurrence.** Ordovician, Silurian and Devonian of North America; upper Cretaceous system of Europe; Paleogene of Western Siberia and North Africa; Neogene of southern Europe and North Africa; Holocene, Quaternary, cosmopolitan.

***Oichnus paraboloides* Bromley, 1981**

Plate 19, fig. 27

*Oichnus paraboloides*: Bromley, 1981, p. 62, pl. 1, figs. 4, 5; Pickerill and Donovan, 1998, p. 163, pl. 1, figs. 4–6, pl. 2, figs. 1, pl. 3, figs. 1–7; Nielsen and Nielsen, 2001, p. 103, text-figs. 1c–1d, 5; Donovan and Jagt, 2003, pp. 70–72, text-figs. 2b, 3c, 3d, 4b; Lorenzo and Verde, 2004, p. 324, text-figs. 3i–3d; Blissett and

Pickerill, 2004, text-fig. 7.6; Ruggiero, 2006, pp. 179–181, text-figs. 13; Ruiz-Munoz and Gonzalez-Regalado, 1989, text-figs. 2, 3; Nielsen et al., 2003, figs. 12a–12c; Gibert et al., 2004, fig. 5d; Dietl and Kelley, 2006, p. 103, fig. 1; Donovan and Harper, 2007, fig. 1; Blissett and Pickerill, 2007, p. 89, pl. 3, fig. 2; Zamora et al., 2008, text-fig. 5/9; Donovan et al., 2014, text-figs. 10b, c, e; Wisshak et al., 2015, text-figs. 1g, 1h; Donovan, 2017, text-fig. 1; Abdel-Fattah, 2018, text-figs. 3c–3f, 4a, 4b; Donovan and Jagt, 2019, fig. 3; El-Sorogy et al., 2020, p. 7, text-figs. 4f, 4g, 5g, 5k; Ortiz-Jeronimo et al., 2021, text-figs. 5f–5l, 6j–5o.

*Sedilichnus paraboloides*: Zonneveld and Gingras, 2014, p. 900–901, figs. 1/4–1/10; Pokorny and Stofik, 2016, pp. 8, 9, text-figs. 3k–3l, 7a–7c.

*Tremichnus paraboloides*: Brett, 1985, pp. 627–628, text-figs. 1, 2.

*Tremichnus cysticus*: Brett, 1985, pp. 628–629, text-fig. 3.

*Tremichnus minutus*: Brett, 1985, p. 629, text-figs. 4, 5.

*Tremichnus* sp. aff. *T. puteolus*: Brett, 1985, pp. 630–631, text-fig. 6.

*Tremichnus cysticu*: Eckert, 1988, fig. 1.

**H o l o t y p e.** Specimen MGUH 15352, Geological Museum of the University of Copenhagen (Den-

mark); hole in the shell of *Natica millepunctata*; Rhodes, Greece; Pleistocene, Quaternary.

**Description.** The holes are truncated-conical in longitudinal section and rounded in transverse. The holes are located perpendicular or at a slight angle to the substrate. The contour is clear and even. The walls are smooth.

**Dimensions** in mm. Diameter from 0.002 to 0.005.

**Comparison.** It is most similar to *O. simplex*, from which it differs in a truncated-conical shape in longitudinal section. Differs from *O. ovalis* in its rounded shape in cross-section.

**Remarks.** They were probably produced by juveniles of predatory gastropods or other boring organisms (Nielsen and Nielsen, 2001).

**Material.** About 15 foraminifers from the Tibeisale Formation (Danian, Paleocene, Paleogene) were found on the surface.

**Occurrence.** Ordovician, Silurian and Devonian of North America; Upper Cretaceous of Europe; Paleogene of Western Siberia and North Africa; Holocene, cosmopolitan.

***Oichnus gradatus* Nielsen et Nielsen, 2001**

Plate 19, fig. 28

*Oichnus gradatus*: Nielsen and Nielsen, 2001, pp. 104, 108, text-figs. 2e–2f; Blissett and Pickerill, 2007, p. 89, pl. 3, fig. 4.

*Sedilichnus gradatus*: Zonneveld and Gingras, 2014, p. 901, fig. 2/1; Pokorný and Stofik, 2016, pp. 11–12, text-fig. 7g.

**Holotype.** Specimen. MGUH 24773, Geological Museum of the University of Copenhagen (Denmark); Great Australian Bight; Holocene, Quaternary.

**Description.** The hole consists of two interconnected concentric formations with a sharply changing diameter. The contour is clear and even. The walls and axis of the holes are perpendicular to the substrate.

**Dimensions** in mm. Diameter of the outer and inner circles is 0.02 and 0.005  $\mu\text{m}$ , respectively.

**Comparison.** The described ichnospecies differs, first of all, from co-occurring ichnotaxa in a well-recognized stepped shape, which consists of two concentric formations of different sizes.

**Remarks.** It is identified by the characteristic “scalate” form. Probably the result of predation (Nielsen and Nielsen, 2001).

**Occurrence.** Thanetian, Paleocene, Paleogene of Western Siberia; Eocene, Paleogene of Jamaica; Pliocene, Neogene of Rhodes; Holocene, Quaternary of the Australian Gulf, the Gulf of Aqaba, the Red Sea and the coast of West Greenland.

**Material.** It is observed on the surface of three foraminiferal tests from the Sokolovo Formation (Thanetian, Paleocene, Paleogene).

***Oichnus ovalis* Bromley, 1993**

Plate 19, figs. 29, 30

*Oichnus ovalis*: Bromley, 1993, pp. 170–171, figs. 5a; Ruggiero, 1999, p. 169, figs. 1f; Nielsen and Nielsen, 2001, p. 104; Harper, 2002, text-figs. 1, 2; Ruggiero, 2006, pp. 178–179, figs. 11, 12; Blissett and Pickerill, 2007, p. 89, pl. 3, figs. 2, 5.

*Sedilichnus ovalis*: Zonneveld and Gingras, 2014, p. 901, figs. 2/7, 2/8; Pokorný and Stofik, 2016, pp. 9, 11, text-figs. 7d–7e, 9.

**Holotype.** Specimen MGUH 22057, Geological Museum of the University of Copenhagen (Denmark); opening in the valve of *Pecten jacobaeus*; Rhodes, Greece; Pliocene, Neogene.

**Description.** The holes are oval or round-diamond-shaped with a noticeable narrowing towards the inner side of the substrate wall. The holes are located perpendicular or at a slight angle to the substrate. Non-perforating formations are represented by oval-elongated pits. The contour is clear and even. The walls are smooth.

**Dimensions** in mm. Diameter from 0.01 to 0.02.

**Comparison.** The described ichnospecies differs from the common ones by an oval contour and walls sloping towards the inner side of the test.

**Remarks.** The holes may be the result of predation by small cephalopods, worms, or other borers (Bromley, 1993).

**Material.** Holes and pits were found on the surface of nine foraminiferal tests from the Gankino Formation (Maastrichtian Stage of the Upper Cretaceous System).

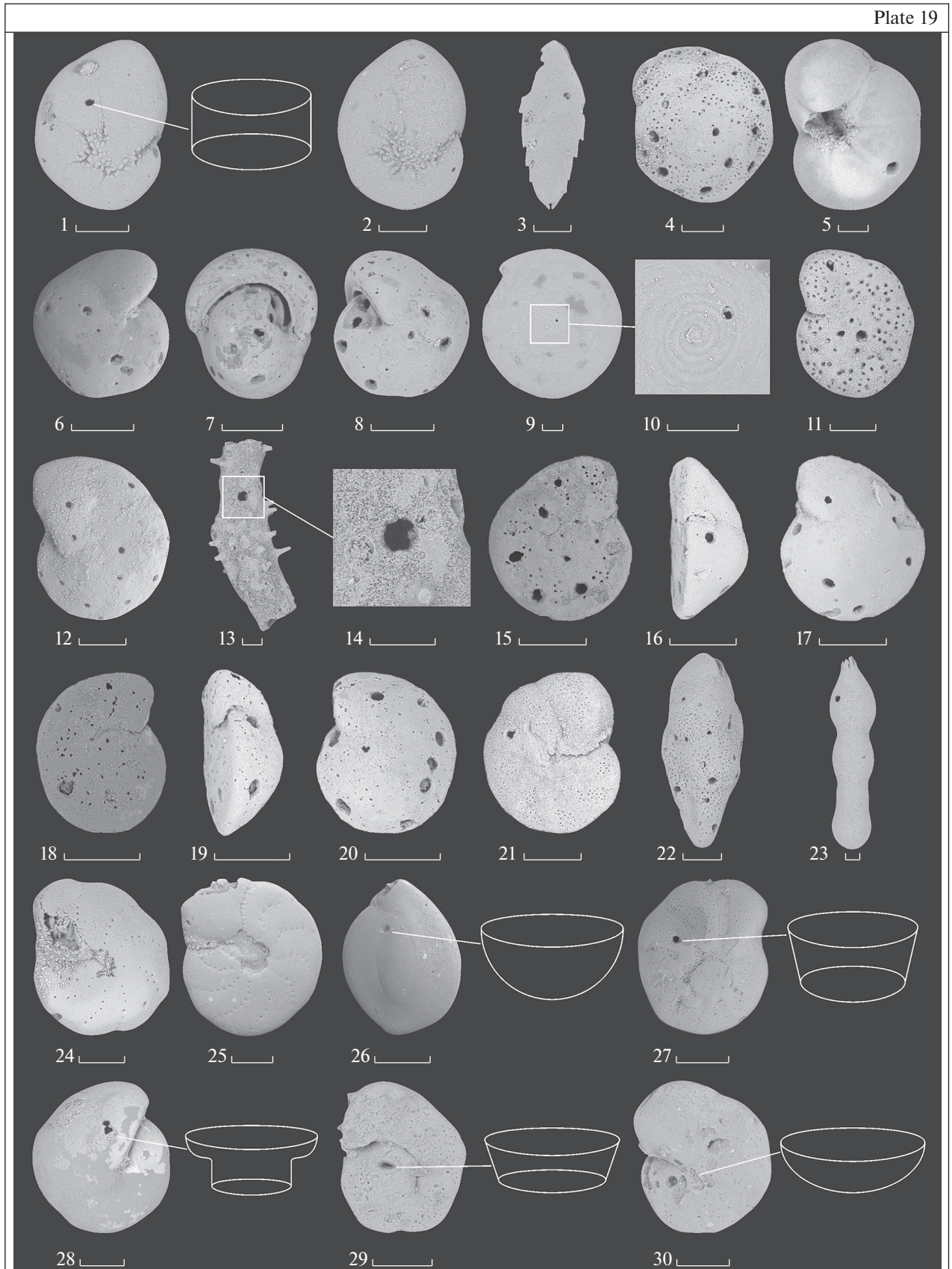
**Occurrence.** Maastrichtian, Upper Cretaceous, Western Siberia; Pliocene, Neogene of Apulia, Rhodes and Florida; Pleistocene, Quaternary of Florida; Holocene, Quaternary of the Gulf of Australia, Red Sea, Alboran Sea and the North Atlantic.

## STRATIGRAPHIC DISTRIBUTION OF BIOEROSION STRUCTURES

Bioerosion structures are confined to certain stratigraphic units in the Upper Cretaceous and Paleogene deposits, which reflects the evolution of the predation strategies of the microbenthos of the fossil biocenoses of Western Siberia. In total, four ichnological assemblages have been distinguished: (1) *Oichnus simplex* and *O. ovalis* (Gankino Formation, Maastrichtian, Upper Cretaceous), (2) *O. simplex* and *O. paraboloides* (Tibeisale Formation, Danian, Paleocene, Paleogene), (3) *O. simplex* and *O. gradatus* (Sokolovo Formation, Thanetian, Paleocene, Paleogene), (4) *O. simplex* (Tavda Formation, Bartonian and Priabonian, Eocene, Paleogene) (Fig. 3).

The *Oichnus simplex* and *O. ovalis* assemblage from the Upper Cretaceous of the Gankino Formation is characterized by the rare presence of these ichnospecies.





Bioerosion manifests itself either in the form of small single perforating holes *Oichnus simplex* on the surface of chambers of the last whorl of foraminifera *Nonionella kalinini* Voloshinova, 1952, or in the form of single perforating holes, unfinished borings *Oichnus ovalis* and multiple traces of incomplete boring *Oichnus simplex*, merging into a complete suboval groove with bridges, on tests of the foraminifers *Valvulinoides umovi* (Kyprianova, 1960).

In the north of the region, the Tibeisale Formation contains the *Oichnus simplex* and *O. paraboloides* assemblage. It is characterized by the presence of numerous *Oichnus simplex* in the form of single holes on the tests of the foraminifers *Cornuspira sibirica*, *Ceratolamarckina tuberculata*, and *Gavellinella* sp., traces of incomplete borings on the tests of *Criboelphidium* sp. and manifestations of multiple holes on the tests of *Pullenia kasakhstanica*, *Eponides lunatus*

and *Criboelphidium* sp. The *Oichnus simplex* and *O. gradatus* Assemblage was established in the Sokolovo Formation of the southern Trans-Urals. The assemblage contains only manifestations of completed holes of *Oichnus simplex* in the form of single holes on the tests of the foraminifera *Cibicoides favorabilis*, *Gavellinella* sp. and multiple borings *Oichnus simplex* on the surface of the tests of *Cibicoides succedens*. Single borings *Oichnus gradatus* are also observed on tests of *Pullenia cretacea*.

In the lower part of the Tibeisale Formation and in the Sokolovo Formation, a high diversity of bioerosion structures is observed in comparison with the rest of the section of the Upper Cretaceous and Paleogene of Western Siberia.

In the Tavda Formation, bioerosion structures are rare and are represented by perforating holes of *Oichnus simplex* on the tests of the foraminifer *Criboel-*

← Explanation of Plate 19

**Figs. 1, 2.** *Oichnus simplex* Bromley, 1981. A single perforating hole on a test of *Nonionella kalinini* Voloshinova, 1952. Hydrogeological parametric borehole near the town of Uray, Gankino Formation, Maastrichtian, Upper Cretaceous.

**Fig. 3.** *Oichnus simplex* Bromley, 1981. A single perforating hole on a test of *Bolivina incrassata* (Reuss, 1926). Hydrogeological parametric borehole near the town of Uray. Gankino Formation, Maastrichtian; Upper Cretaceous.

**Fig. 4.** *Oichnus simplex* Bromley, 1981. Multiple perforating holes on a test of *Eponides lunatus* Brotzen, 1948. Kharasaveyskoe Deposit. Tibeisale Formation, Danian, Paleocene, Paleogene.

**Fig. 5.** *Oichnus simplex* Bromley, 1981. A single perforating hole on a test of *Ceratolamarckina tuberculata* (Brotzen, 1948). Kharasaveyskoe Deposit. Tibeisale Formation, Danian, Paleocene, Paleogene Deposit.

**Figs. 6–8.** *Oichnus simplex* Bromley, 1981. Multiple perforating holes on a test of *Pullenia cretacea* Cushman, 1936 (Reuss, 1851). Kharasaveyskoe Deposit. Tibeisale Formation, Danian, Paleocene, Paleogene.

**Figs. 9, 10.** *Oichnus simplex* Bromley, 1981. Single perforating hole on a test of *Cornuspira sibirica* (Podobina, 1975). Kharasaveyskoe Deposit. Tibeisale Formation, Danian, Paleocene, Paleogene.

**Fig. 11.** *Oichnus simplex* Bromley, 1981. Single perforating hole on a test of *Gavellinella* sp. Kharasaveyskoe Deposit. Tibeisale Formation, Danian, Paleocene, Paleogene.

**Fig. 12.** *Oichnus simplex* Bromley, 1981. Multiple perforating holes on a test of *Cibicoides* sp. Kharasaveyskoe Deposit. Tibeisale Formation, Danian, Paleocene, Paleogene.

**Figs. 13, 14.** *Oichnus simplex* Bromley, 1981. Single perforating hole on a test of Polymorphonidae gen. et sp. ind. Sokolovo iron-ore quarry. Sokolovo Formation, Thanetian, Paleocene, Paleogene.

**Figs. 15–20.** *Oichnus simplex* Bromley, 1981. Multiple perforating holes on a test of *Cibicoides succedens* Brotzen, 1948. Sokolovo iron-ore quarry. Sokolovo Formation, Thanetian, Paleocene, Paleogene.

**Fig. 21.** *Oichnus simplex* Bromley, 1981. Single perforating hole on a test of *Cibicoides* sp. Kharasaveyskoe Deposit. Tibeisale Formation, Danian, Paleocene, Paleogene.

**Fig. 22.** *Oichnus simplex* Bromley, 1981. Multiple perforating holes on a test of *Reusella paleocenica* Brotzen, 1966. Sokolovo iron-ore quarry. Sokolovo Formation, Thanetian, Paleocene, Paleogene.

**Fig. 23.** *Oichnus simplex* Bromley, 1981. Single perforating hole on a test of *Nodosaria* sp. Sokolovo iron-ore quarry. Sokolovo Formation, Thanetian, Paleocene, Paleogene.

**Fig. 24.** *Oichnus simplex* Bromley, 1981. Single non-perforating hole on a test of *Criboelphidium rischtanicum* (N. Bykova, 1939). Kyshtyrla quarry. Tavda Formation, Bartonian and Priabonian Stages, Eocene, Paleogene.

**Fig. 25.** *Oichnus simplex* Bromley, 1981. Single non-perforating hole on a test of *Criboelphidium differensapertio* Uschakova, 1964. Kyshtyrla quarry. Tavda Formation, Bartonian and Priabonian Stages, Eocene, Paleogene.

**Fig. 26.** *Oichnus simplex* Bromley, 1981. Single non-perforating hole on a test of *Quinqueloculina* sp. Kyshtyrla quarry. Tavda Formation, Bartonian and Priabonian Stages, Eocene, Paleogene.

**Fig. 27.** *Oichnus paraboloides* Bromley, 1981. Single perforating hole on a test of *Criboelphidium* sp. Kharasaveyskoe Deposit. Tibeisale Formation, Danian, Paleocene, Paleogene.

**Fig. 28.** *Oichnus gradatus* Bromley, 1981. Single perforating hole on a test of *Pullenia quinqueloba* (Reuss, 1851). Sokolovo iron-ore quarry. Sokolovo Formation, Thanetian, Paleocene, Paleogene.

**Fig. 29.** *Oichnus ovalis* Bromley, 1981. Single perforating hole on a test of *Gyrodinia soldanii* d'Orbigny, 1826. Hydrogeological parametric borehole near the town of Uray. Gankino Formation, Maastrichtian, Upper Cretaceous.

**Fig. 30.** *Oichnus ovalis* Bromley, 1981. Single non-perforating hole on a test of *Gyrodinia soldanii* d'Orbigny, 1826. Hydrogeological parametric borehole near the town of Uray. Gankino Formation, Maastrichtian, Upper Cretaceous.

Scale bar is 100 µm.

*phidium rischtanicum*, single non-penetrating *Oichnus simplex* in the area of the chambers of the last whorl of tests of *Criboelphidium rischtanicum* and *C. differens-apertio* and sutures in the foraminifer of *Quinqueloculina* sp.

#### PALEOECOLOGICAL INTERPRETATION OF BIOEROSION STRUCTURES

Holes of *Oichnus* studied are mainly interpreted as evidence of predation to obtain nutrients from the cell's protoplasm (Douglas, 1973; Arnold et al., 1985) (Fig. 4A). There is an opinion that foraminiferal tests could have been populated posthumously and their chambers were developed as habitats or shelters (Sliter, 1971, 1975; Culver and Lipps, 2003) (Fig. 4B). Evidence for this may be the frequent occurrence of nematodes in partially vacated chambers of live or completely empty chambers of dead benthic foraminifera in laboratory cultures (Sliter, 1965), although this behavior is rare in the natural population (Sliter, 1971). Also, the formation of such holes as a result of the settlement of the test surface and the fixation of epibionts on it is not excluded. (Lipps, 1988; Todd, 1965; Banner, 1971; Alexander and DeLaca, 1987; Cherchi and Schroeder, 1991; Wisshak et al., 2019) (Fig. 4C). Perforating holes in *Oichnus*, by analogy with similar large structures, might have been made by predatory gastropods, especially, their juvenile forms (Shonman and Nybakken, 1978; Arnold et al., 1985). However, this assumption is questionable (Sliter, 1971), since gastropods, even juvenile ones, form larger holes than those observed on foraminifera shells (Arnold et al., 1985). These holes were more likely produced by smaller, soft-bodied organisms, most likely nematodes or polychaetes (Sliter, 1971, 1975; Douglas, 1973). Also, scaphopods (Bilyard, 1974; Langer et al., 1995), some sipunculids (Heeger, 1990), or isopods (Svavarsson et al., 1991) (Fig. 4) are sometimes considered as borers producing holes in *Oichnus*.

#### CONCLUSIONS

(1) In deposits of the Upper Cretaceous and Paleogene systems of Western Siberia, four ichnospecies of bioerosion structures were found on the surface of benthic foraminiferal tests: *Oichnus simplex*, *O. paraboloides*, *O. gradatus*, and *O. ovalis*.

(2) The stratigraphic distribution of the bioerosion structures studied has been established. The Gankino Formation (Maastrichtian, Upper Cretaceous System) contains *Oichnus simplex* and *O. ovalis*. The Tibeisale Formation (Danian, Paleocene, Paleogene) contains *Oichnus simplex* and *O. paraboloides*. The Sokolovo Formation (Thanetian, Paleocene, Paleogene) contains *Oichnus simplex* and *O. gradatus*. The Tavda Formation (Bartonian and Priabonian, Eocene, Paleogene) contains *Oichnus simplex*.

(3) The most likely producers of holes could be small predatory borers. Pits and grooves on the surface were formed by organisms attached to tests.

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#### CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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## Chapter 5: Publication

## ENVIRONMENTAL SIGNATURES PRESERVED IN EXTREMELY SHALLOW-WATER BENTHIC FORAMINIFERAL ASSEMBLAGES FROM OMAN, ARABIAN SEA

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### ABSTRACT

**The composition and preservation state of testate foraminiferal assemblages is of highest importance for paleo-environmental and paleoclimatic reconstructions. Nearshore coastal areas, however, are often subject to harsh conditions, being shaped by continuous wave action and exposed to turbulence, erosion, and dynamic processes of sediment reworking. Situated at the interface between land and water, the environmental signatures preserved in assemblages of benthic foraminifera from coastal environments are therefore prone to taphonomic alterations, which potentially bias the fossil record and compromise accurate reconstructions. In this study, we have analysed the composition and preservation of benthic foraminifera from a suite of extremely shallow-water habitats along the Dhofar coastline (Oman) to document the structure of assemblages and illustrate their species richness. Our analyses show that extremely shallow foraminiferal assemblages from the southern coast of Oman retain the environmental signatures of their habitats despite intense environmental processes, making them useful for paleoenvironmental studies. Features of these signatures are recorded in the structural composition, species richness, dominance, and diversity indices of foraminiferal communities, in addition to numerical abundances of shell preservation groups.**

### INTRODUCTION

The Dhofar region on the southern coast of Oman is situated at the heart of one of the largest upwelling areas of the world and fuels high primary productivity conditions both coastally and up to 300 km offshore (Currie et al., 1973; Locarnini et al., 2019). The shallow water areas support a wide variety of habitats, including seagrass meadows, mangrove ecosystems, brackish water embayments, harbour inlets, and extensive sand bays, in addition to the unique co-existence of coral reef and macroalgal communities. Upwelling zones have a deep impact on coastal areas. They displace oligotrophic water masses and influence the settlement and dispersal of highly diverse tropical coral reefs and larger symbiont-bearing foraminifera (LBF). The unusual mix of tropical oligotrophic and temperate eutrophic conditions forms species assemblages that are globally unique (Wilson, 2000; Schils & Copejahn, 2003; Förderer et al., 2018; Langer et al., 2022).

The environmental conditions provide a setting for presumably unique foraminiferal faunal assemblages, but despite intensive research on tropical foraminifera, detailed studies on modern coastal foraminifera from Oman have not been

conducted. Previous studies have identified a distinct biogeographic break between the East African Red Sea and eastern Indian Ocean faunal provinces (Reiss & Hottinger, 1984; Langer & Hottinger, 2000; Förderer et al., 2018). Situated at a key position between the high-diversity Coral Triangle and the tropical Red Sea/eastern African coast, the coastal waters of Oman act both as a biogeographic steppingstone and as a nutrient-rich and cold-water barrier for reef-forming symbiont-bearing taxa (Hood et al., 2017; Spreter et al., 2022).

The coast of Oman is among the few tropical areas that has not received detailed attention and where only a few studies on modern benthic foraminifera have been published. These were mainly oriented toward the identification of selective assemblages that are indicative of overwash/tsunami deposits (Pilarczyk et al., 2011; Pilarczyk & Reinhardt, 2012) or contain fragmentary lists of a few shallow-water species (Oman: Pilarczyk et al., 2011; Pilarczyk & Reinhardt, 2012; Al-Sayigh et al., 2015; Yemen: Al-Wosabi et al., 2017). Pilarczyk et al. (2011, 2012) reported on foraminiferal assemblages from a 1945 tsunami event from the northern coast of Oman (Sur Lagoon) and found a total of 22 species. Al-Sayigh et al. (2015) reported 27 taxa of benthic foraminifera from the southern and northern coast of Oman. The low species richness of the shallow-water areas contrasts with the much higher species numbers from the inner Arabian Gulf and adjacent areas ( $N = 87-753$ ), but these data include biotas from greater depth ranges and areas of the deep sea (Amao et al., 2022; see also Chapman, 1895; Stubbings, 1939; Cherif et al., 1997). Studies on modern benthic foraminifera from deeper parts of the Oman margin (~400–4000 m) include those of Hermelin & Shimmield (1990) and Gooday et al. (2000) and comprise data (~100 species) from the deep oxygen minimum zone (OMZ) and below.

Foraminiferal assemblages from extremely shallow-water habitats face hostile conditions to their existence and preservation, where the formation of dead assemblages is the result of post-mortem processes, among which out-of-habitat transport and the destruction and disintegration of tests are most significant. Assemblages subjected to transport and destruction generally record low species richness and are prone to severe information loss through taphonomic processes (Kidwell & Flessa, 1996; Goldstein & Watkins, 1999; Murray & Alve, 1999a, b; Martin et al., 2003). We examined habitat-specific samples from extreme shallow-water areas to: (1) illustrate and document the species richness and preservation status of foraminiferal assemblages, (2) assess whether the foraminiferal biotas preserve sufficient environmental information to be useful for paleoenvironmental inferences, and (3) provide novel insight into the diversity and composition of benthic foraminifera along the varied habitats of the southern Oman coast.

### MATERIAL AND METHODS

The southern part of the Sultanate of Oman is situated on the southern corner of the Arabian Peninsula and lies in the

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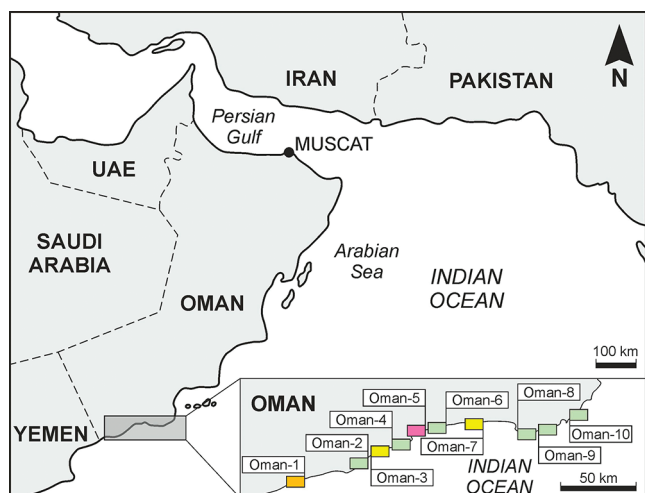


FIGURE 1. Sampling area along the southern coast of Oman with sampling sites enclosed in a rectangle. The colour coding corresponds to the four habitat types outlined in the text (ocher = harbour, yellow = sand bay, green = phytal-associated habitat, and purple = mangrove-lined bay inlet).

monsoon belt. During the wet monsoon period (mid-June to mid-September) the area is under the influence of cold upwelling waters that rapidly cool the moist winds against the steep seaward-facing escarpment. The intense upwelling fertilizes coastal waters, drives strong primary productivity processes, and triggers extensive phytoplankton blooms (Morrison et al., 1998). Most wadi systems in this area are deeply incised canyons that carry seasonal loads of freshwater, and some of them house permanent water systems. Coastal environments in this region are strikingly varied and include a mosaic of extensive sand bays, shallow-water embayments with patchy seagrass meadows, harbour inlets, muddy brackish-water inlets and estuaries, and scattered mangrove forests with pure stands of *Avicennia marina*. Tides along the Oman coastlines are semi-diurnal with a daily range averaging 1.5–2 m, and a maximum range of ~3 m (Al-Hatrush et al., 2014; Hereher et al., 2020).

Ten sites were sampled and examined for benthic taxa (Fig. 1, Table 1). The sample sites are situated 20–80 m off shore and represent four different types of shallow-water habitats (Fig. 2): (a) a muddy tidal influenced harbour inlet (Dalkut Port = site 1); (b) extensive sand bays lacking phytal coverage (Mugh-sail Beach, Samharam Beach = sites 3, 7); (c) sand bays associated with patches or extensive seagrass meadows

(Fazayat-, Oasis-, Alhafa-, Eagles Bay Beach, Sadah Port = sites 2, 4, 6, 8–10); (d) muddy inlets lined by stands of *Avicennia marina* mangrove trees (Khwar Al Qurm Al Kabir, site 5). Seagrasses along the southern coast of Oman occur patchily or as dense meadows and mainly consist of *Halodule wrightii* and *Thalassodendron ciliatum* (Jupp et al., 1996).

Samples of foraminifera from southern Oman were collected by MRL in March 2019, while snorkeling, by filling small plastic containers (300 ml) with sediment from the top 2 cm. The protocol was to sample benthic foraminiferal assemblages from different habitats with the aim to provide general environmental data useful in paleoecology. Our samples are thus time-averaged (total assemblages) and as such, provide an effective means of defining habitats (Glenn-Sullivan & Evans, 2001; Langer & Lipps, 2003).

All samples were washed over 63- $\mu$ m mesh sieves and dried, and the foraminifera were then picked from each. A total of 3896 foraminifera were recovered from the samples, identified to species level and individuals of each species were counted. In order to compare disparate samples, we used rarefaction (Ludwig & Reynolds, 1988), where foraminifera were picked from each sample until no new species were discovered. This involved picking and examining hundreds of specimens, except for a few samples that contained fewer than 200 specimens. All species were identified and photographed using Scanning Electron Microscopy (SEM; Figs. 3–7).

To determine the structure in the foraminiferal data set, a Q-mode cluster analysis was performed using the weighted average clustering technique with correlation coefficients as a similarity index (Fig. 8). This technique groups together samples with similar faunal assemblages. Foraminiferal assemblage diversity and dominance indices were computed for each site (Fisher  $\alpha$ , Shannon's H', Simpson's Index of Diversity (SID); Fisher et al., 1943; Murray, 1973). Fisher  $\alpha$  indices were plotted in a bar chart to compare resulting index values of habitat-specific assemblages (Fig. 9). Their relation can be directly determined by comparing Fisher  $\alpha$  diversity indices from habitat-specific assemblages. In addition, the Frequency of Occurrence (FO) was counted for each species (Table 2). To document compositional differences among habitat-specific foraminiferal assemblages, percent abundances were then calculated for agglutinated, miliolid, calcarinid, opportunistic taxa (Debenay, 2000; Murray, 2006), and for the genera *Cibicides*, *Amphistegina*, *Elphidium*, *Ammonia* (Table 1). Average percentages for each group are shown in pie charts (Fig. 10).

TABLE 1. Sample site information with location details and habitat types.

Sample number	Locality	Longitude	Latitude	Depth	Habitat
1	Dalkut Port	53°15'11.09"E	16°42'11.84"N	2 m	Harbour environment
2	Fazayat Beach	53°41'15.04"E	16°49'00.15"N	2 m	Sand bay with seagrass patches
3	Mugh-sail Beach	53°46'38.69"E	16°52'43.36"N	3 m	Sand bay with seasonal freshwater influence
4	Oasis Beach, Salalah Port	53°59'42.03"E	16°55'46.56"N	2 m	Sand bay with seagrass patches
5	Khwar Al Qurm Al Kabir	54°01'08.87"E	16°59'00.89"N	1 m	Mangrove inlet
6	Alhafa Beach, Salalah	54°6'36.31"E	16°59'59.15"N	3 m	Sand bay with seagrass patches
7	Samharam Beach	54°26'12.66"E	17°01'46.88"N	3 m	Sand Bay
8	Eagles Bay Mirbat	54°47'40.77"E	16°56'42.70"N	3 m	Sand bay with seagrass patches
9	Eagles Bay Mirbat	54°47'50.00"E	16°56'23.01"N	3 m	Sand bay with seagrass patches
10	Sadah Port	55°04'23.20"E	17°02'50.49"N	3 m	Sand bay with seagrass patches





FIGURE 2. Photographs of coastal sampling sites showing habitats. A) Fazayat Beach, site 2; B) Eagles Bay, site 8 and 9; C) Alhafa Beach with patches of seagrass, site 6; D) Muddy bay inlet lined by stands of *Avicennia marina* mangrove trees Khwar Al Qurm Al Kabir, site 5; E) Monotone sand bay at Samharam Beach lacking phytal substrates, site 7; F) Dalkut Port bay inlet with seagrass patches, site 10.

To assess the effects of wave action on the preservation of foraminiferal tests in extremely shallow coastal environments, we examined the foraminiferal tests systematically and applied a preservation grade scheme. This approach has proven useful to document environmental changes (Weinmann & Langer, 2017; Pavlopoulos et al., 2018;). Previous studies have documented that optimally preserved tests can be used as a good approximation of the living or in situ fauna, whereas poorly preserved tests show allochthonous origins or reworking (Yordanova & Hohenegger, 2002). For the grades, we follow Yordanova & Hohenegger (2002) and Weinmann & Langer (2017) and categorized the foraminiferal tests into four groups (Fig. 11): (1) “well preserved” specimens do not exhibit any or only minor signs of microscopically visible damage; (2) “moderately preserved” tests show minor abrasion and/or slight breakage; (3) “abraded and broken” specimens, the overall shape and outline of the test shows distinct features of abrasion, depressions, pits or scratches, and often breakage of the last chambers and breakage of chambers/spines (Cottey & Hallock, 1988; Peebles & Lewis, 1991); and (4) “fully damaged, broken and abraded” tests reveal strong features of transport or reworking altering the overall form and outline of the test (test damage, breakage, strong abrasion, polished surfaces where most test ornaments are fully abraded; Peebles & Lewis, 1991; Yordanova & Hohenegger, 2002; Weinmann & Langer, 2017). Identification of species at this preservation state is based on the few remaining morphological details, requires substantial experience, and can drive every morphologist to despair (Kidwell & Flessa, 1996). Percent abundances for each category were then calculated according to site and habitat and plotted in diagrams (Fig. 12). The

material is stored in the micropaleontological collections at the Institute of Geosciences at the University of Bonn (collection numbers OM-ML-2019, 1-10).

## RESULTS

### STRUCTURE AND COMPOSITION OF FORAMINIFERAL ASSEMBLAGES

A total of 45 species of benthic foraminifera were identified from 3896 picked specimens (Table 2). This consists of 24 perforate-hyaline, 16 porcelaneous, and 5 agglutinated taxa. Individuals of perforate-hyaline species are dominant and constitute 82.6%, porcelaneous taxa make up 16.2%, and foraminifera with agglutinated tests are rare and contribute only 1.2% to the total assemblages. Because individual samples contained different amounts of foraminifera, the number of picked specimens varied and ranged between 122 and 999. In general, larger numbers of individuals were obtained from habitats characterized by phytal coverage ( $N = 261\text{--}999$  individuals), whereas only smaller amounts were available from sandy bays ( $N = 205\text{--}347$ ), mangrove ( $N = 122$ ), or seasonally influenced fresh-water sites ( $N = 292$ ).

Foraminifera with a hyaline-perforate wall structure constitute the most abundant group among all foraminifera along the southern coast of Oman and contribute between 49.2 and 92.5% to the total assemblage at individual sampling sites (Table 2). Values at all sites ranged between 75.1 and 92.4%, except for site 5 (Khwar Al Qurm Al Kabir), the only sampling site lined by *Avicennia marina* mangrove trees and where perforate species make up only 49.1%. At this site, porcelaneous foraminifera (mainly smaller miliolids) contribute almost equal amounts to the total assemblage (47.5%). At all other sites, numerical abundances of porcelaneous foraminifera range between 7.1 and 24.9%. Within

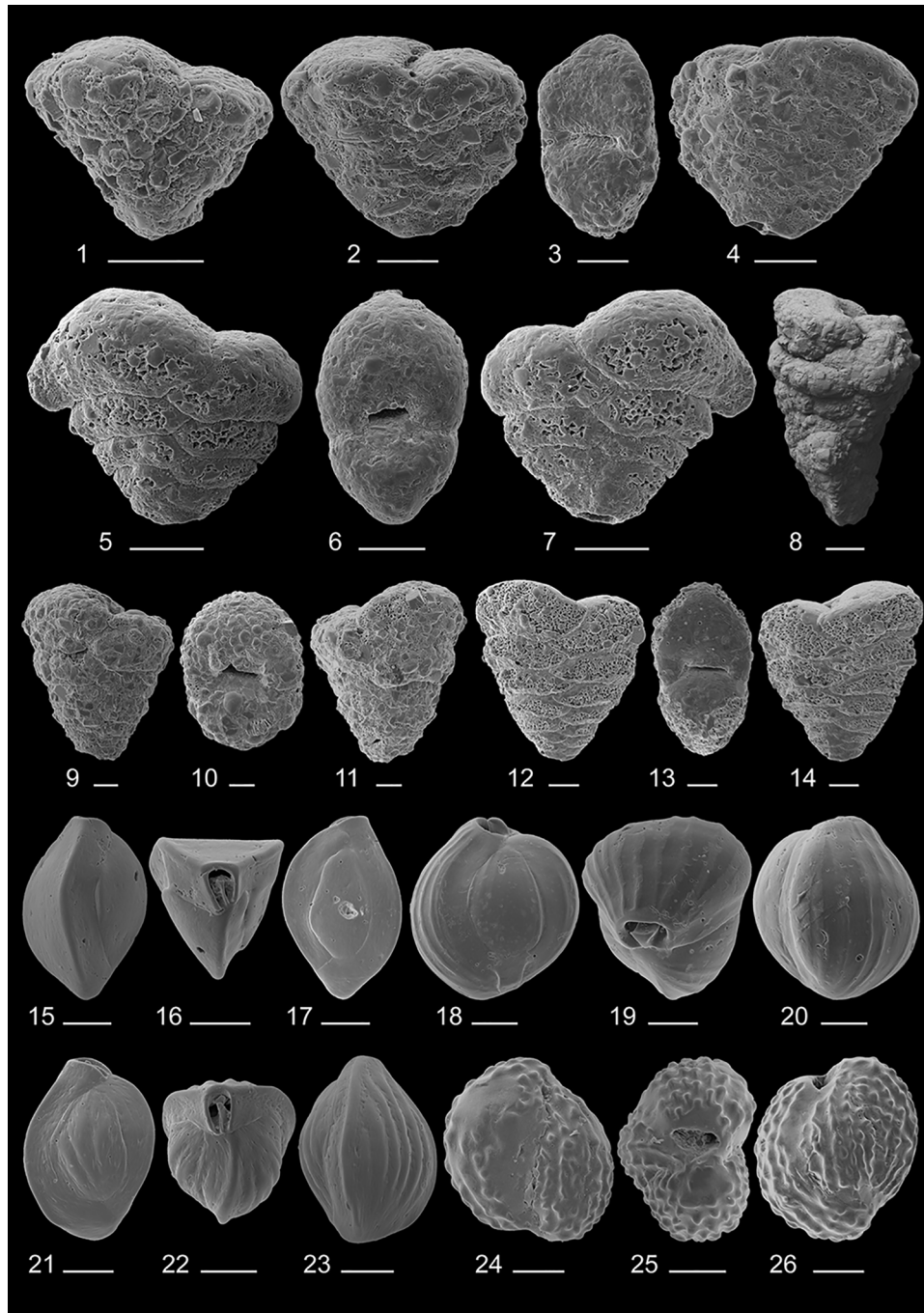


FIGURE 3. Benthic foraminifera from the southern coast of Oman. 1–4 *Textularia pseudosolita* Zheng, 1988. 5–7 *Textularia* sp. 2. 8 *Pseudogaudryina* sp. 9–11 *Textularia agglutinans* Seguenza, 1862. 12–14 *Textularia* sp. 1. 15–17 *Triloculina affinis* d'Orbigny, 1852. 18–20 *Triloculina fichteliana* d'Orbigny, 1839. 21–23 *Triloculina* sp. 1. 24–26 *Pseudotriloculina echinate* d'Orbigny, 1826. Scale bar = 100  $\mu$ m.

the shallow water environments of Oman, agglutinated foraminifera were found to be particularly rare and contributed only between 0.4 and 3.3% to the total assemblages. The highest recording was noted within the mangroves at site 5, and no agglutinated foraminifera were found at the easternmost site 10.

#### SPECIES RICHNESS AND DIVERSITY

Species richness among the habitats varies accordingly and ranges between 16 and 34 (Table 2). Habitats with

phytal coverage yielded between 19 and 34 species, while sand bays, mangrove, and seasonally influenced fresh-water sites only housed 16 and 22 taxa. The highest species richness was found at Eagles Bay (34 species), the only collection site located directly within a dense seagrass meadow.

Diversity computations revealed Shannon's  $H'$  values between 1.6 and 2.7 and Fisher  $\alpha$  index values between 3.5 and 6.8 (Fig. 9). Fisher  $\alpha$  index values for sites with phytal coverage were between 4.5 and 6.8, including the highest value recorded from within the seagrass meadow at Eagles



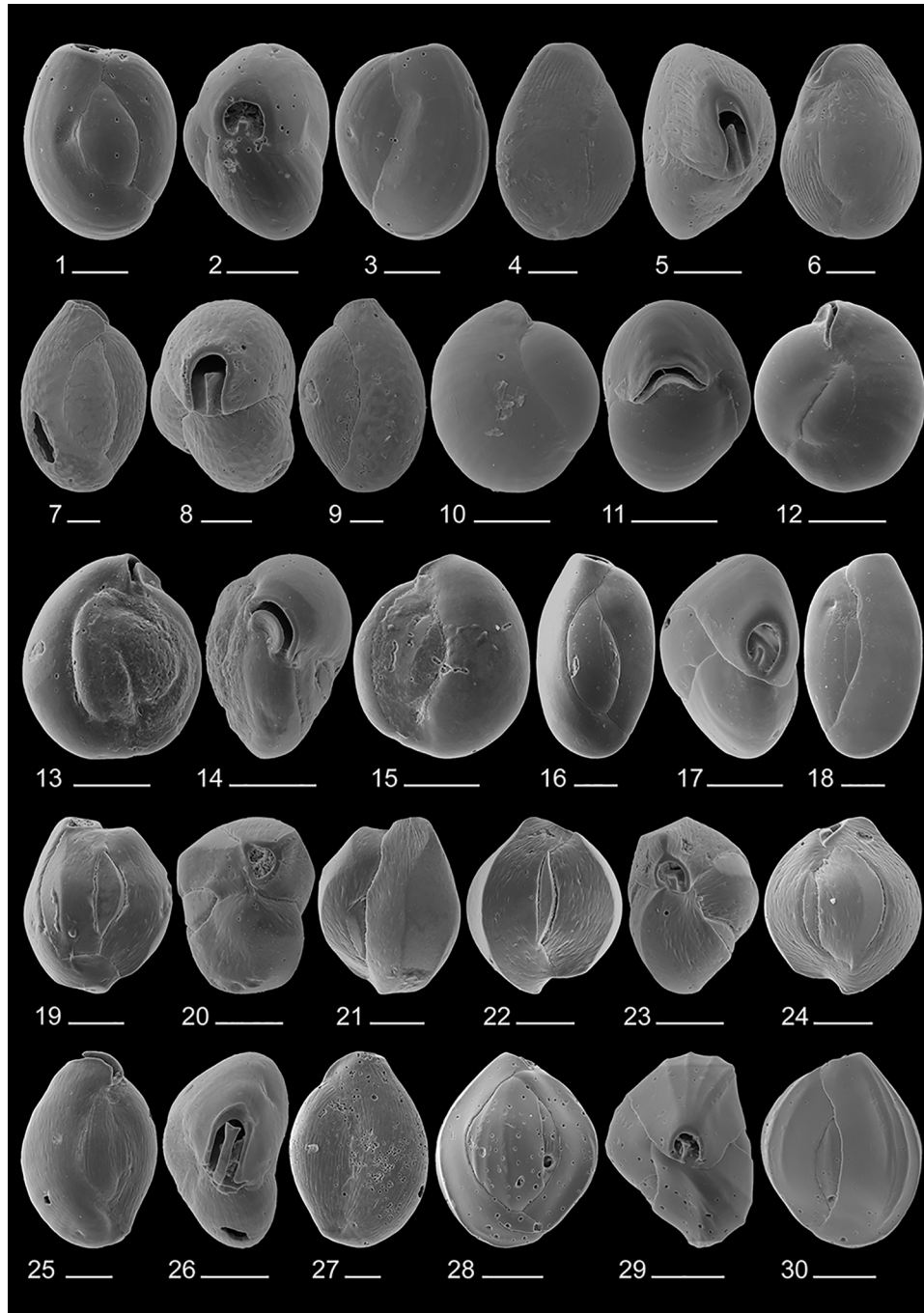


FIGURE 4. Benthic foraminifera from the southern coast of Oman. 1–3 *Pseudotriloculina* sp. 1. 4–6 *Pseudotriloculina* sp. 2. 7–9 *Pseudotriloculina* sp. 3. 10–12 *Milionella circularis* (Bornemann, 1855). 13–15 *Sigmamiliolinella australis* (Parr, 1932). 16–18 *Quinqueloculina seminula* (Linnaeus, 1758). 19–21 *Quinqueloculina* aff. *multimarginata* 1. 22–24 *Quinqueloculina* aff. *multimarginata* 2. 25–27 *Quinqueloculina* sp. 1. 28–30 *Quinqueloculina* sp. 2. Scale bar = 100  $\mu$ m.

Bay (site 9). The lowest value (3.5) was found at sample site 7, an extensive and monotone sand bay lacking phytal coverage (Samharam Beach). The trend towards higher species richness values at sites with higher phytal coverage, moderate values at mangrove and harbour sites, and low values at sand bay sites (sites 3 and 7), is reflected also in Fisher  $\alpha$  index values (Fig. 9). Shannon  $H'$  and SID data show similar structure with subtle but clear demarcations of values between phytal-associated and sand bay

habitats, and intermediate values at harbour and bay inlet sites.

#### CLUSTER ANALYSIS AND HABITAT-SPECIFIC COMPOSITION OF FORAMINIFERAL ASSEMBLAGES

Cluster analysis resulted in two major clusters (A and B; Fig. 8) and two outliers (sites 5 and 7; Fig. 8). Cluster A comprises all habitats with phytal coverage (sites 2, 4, 6, 8–10).



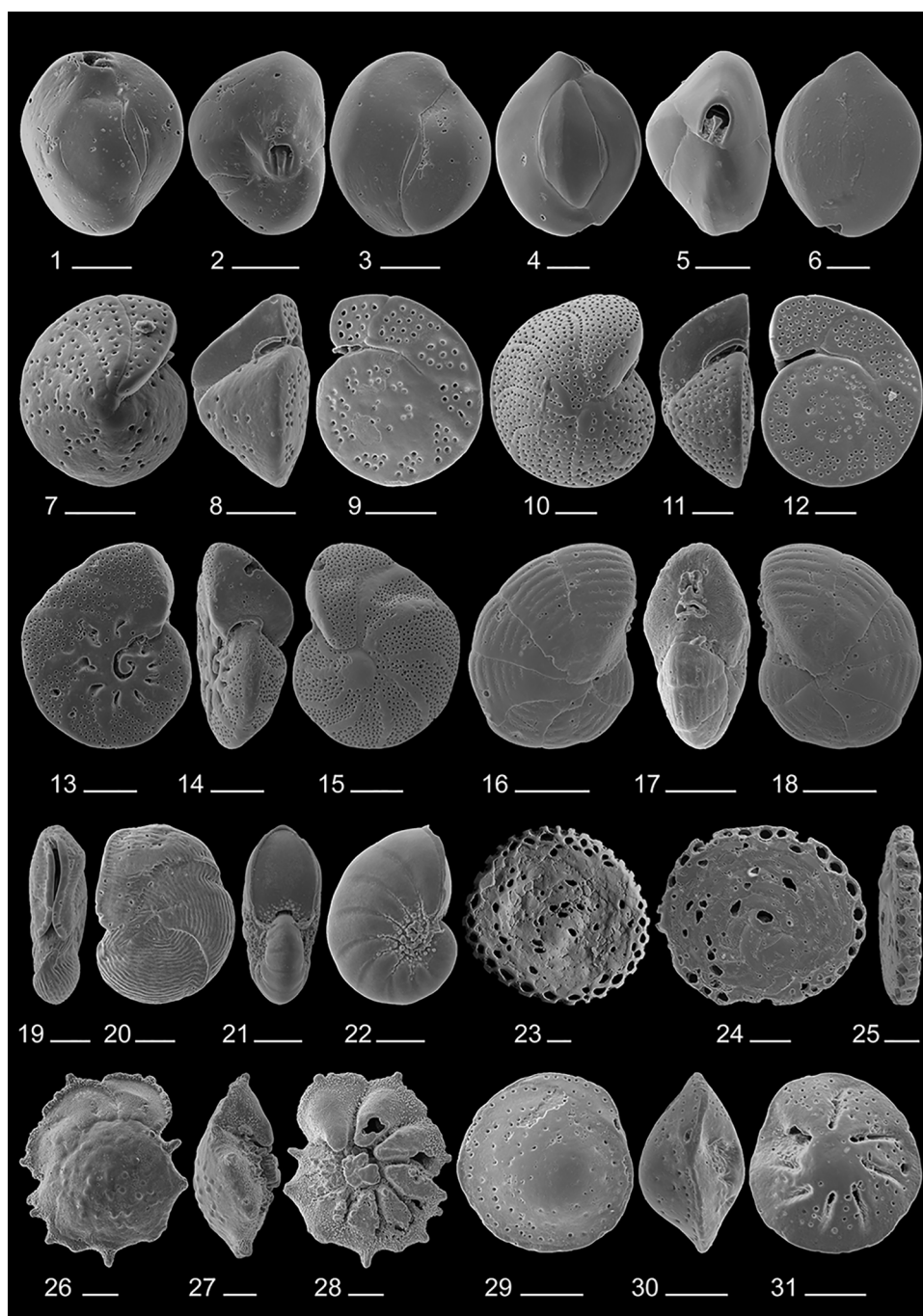


FIGURE 5. Benthic foraminifera from the southern coast of Oman. 1–3 *Quinqueloculina* sp. 3. 4–6 *Quinqueloculina* sp. 4. 7–9 *Cibicides refulgens* Montfort, 1808. 10–12 *Cibicides* sp. 13–15 *Hanzawaia* cf. *H. nipponica* Asano, 1944. 16–18 *Peneroplis pertusus* (Forsskål in Niebuhr, 1775). 19, 20 *Vertebratulina striata* d'Orbigny, 1826. 21, 22 *Nonion* sp. 23–25 *Sorites orbiculus* (Forsskål in Niebuhr, 1775). 26–28 *Pararotalia calcariformata* McCulloch, 1977. 29–31 *Lamellogiscorbis* sp. 1. Scale bar = 100  $\mu$ m.

Cluster B includes sites 1 and 3, representing the shallow tidal-influenced harbour habitat (site 1) and a sandy beach habitat that is influenced by seasonal fresh-water runoff (site 3). In addition, cluster analysis suggested two outliers—sites that stand alone and for which localized features may play an important role. The two outliers (sites 5 and 7) flank clusters A and B and comprise two different habitats: the bay inlet lined by mangrove trees (site 5) and an extensive sand bay habitat (site 7).

Phytal-associated cluster A includes almost three quarters of all species recorded (36 species) and revealed the highest diversity index values (Table 2). Dominance in this species-rich cluster remains low (SID = 0.1–0.2). The assemblages are characterized by abundant occurrences of amphisteginids (27.5–47.3%), miliolids (7.1–24.9%), elphidiids (4.4–17.0%), cibicidiids (1.9–9.7%), and ammoniids (1.5–9.2%). The most abundant species in this cluster are *Sigmamiliolinella australis*, *Quinqueloculina seminula*, *Q.* aff. *Q. multimarginata*

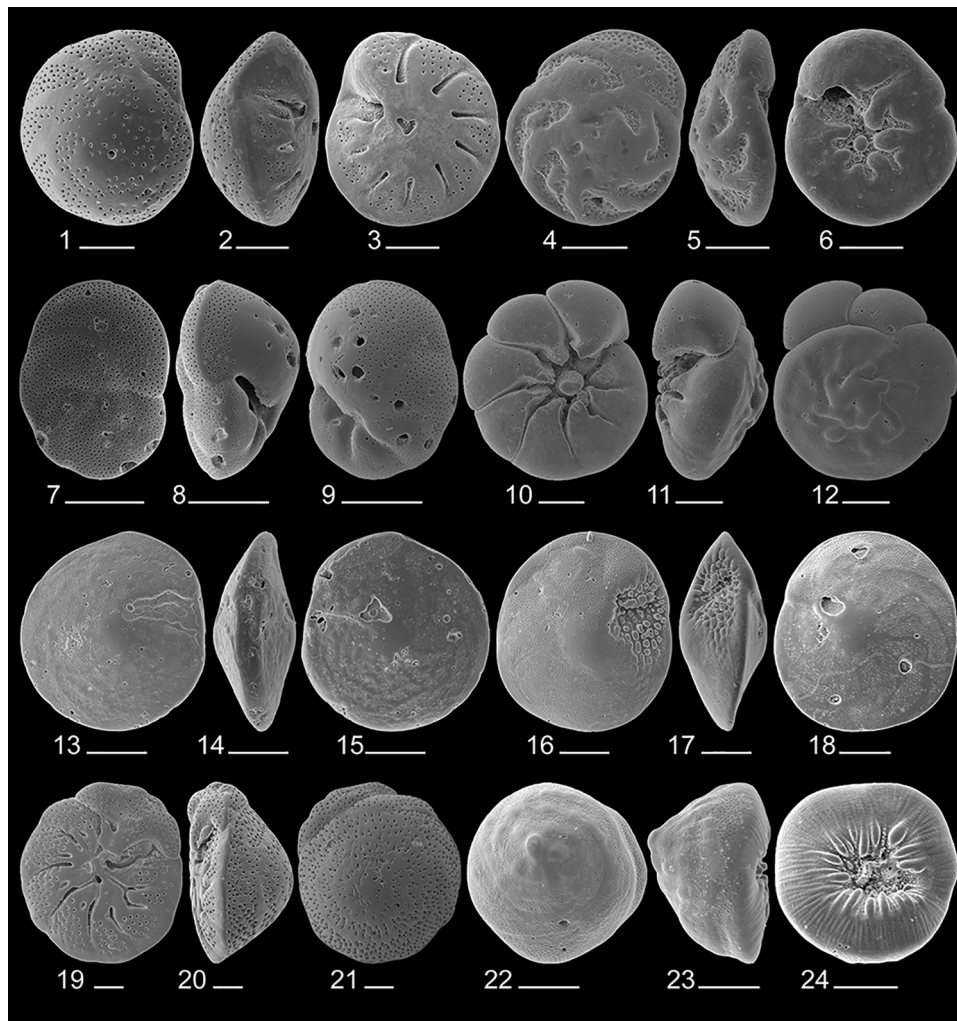


FIGURE 6. Benthic foraminifera from the southern coast of Oman. 1–3 *Pararotalia calcariformata* McCulloch, 1977. 4–6 *Rosalina* aff. *R. orientalis* (Cushman, 1925). 7–8 *Baggina* sp. 10–12 *Ammonia amurensis* Shchedrina, Mayer, 1975. 13–15 *Amphistegina radiata* (Fichtel, Moll, 1798). 16–18 *Amphistegina lessonii* d'Orbigny in Guérin-Méneville, 1832. 19–21 *Rotorbis* sp. 22–24 *Glabratellina* sp. Scale bar = 100  $\mu$ m.

type 2, *Pararotalia calcariformata*, *Amphistegina radiata*, *A. lessonii*, *Elphidium* cf. *E. limbatum*, *Cibicides* sp. 1, and *Ammonia amurensis*. Temporarily attached indicator taxa of phytal substrates (cibicidiids) constitute on average 6.5% of the total assemblage in phytal-associated habitats.

Cluster B comprises a total of 23 species, and the assemblages are characterized by a dominance of elphidiidae (28.4–47.7%), amphisteginidae (17.3–30.1%), and miliolidae (15.3–16.4%). The most abundant species are *Quinqueloculina* aff. *Q. multimarginata* 2, *Amphistegina radiata*, *A. lessonii*, and *Elphidium* cf. *E. limbatum*. Fisher  $\alpha$  and Shannon H' diversity index values in this cluster are low (Table 2).

The mangrove site outlier (site 5) is characterized by a dominance of smaller miliolids (47.5%), a comparatively large amount of cibicidiid (13.1%) and elphidiid (6.6%) foraminifera and contains a total of 18 species. Larger symbiont-bearing taxa are rare and comprise very few and mostly abraded amphisteginids, *Pararotalia calcariformata*, and *Sorites orbiculus*. Compared to all other sites, agglutinated foraminifera are more abundant in the mangrove environment (3.3%). The most abundant species at this site include *Sigmamiliolinella*

*australis*, *Quinqueloculina* aff. *Q. multimarginata*, and *Cibicides* sp. 1.

The second outlier is site 7, representing an extensive and monotone sand bay habitat at Samharam Beach. The foraminiferal assemblage at this site is characterized by the dominance of *Pararotalia calcariformata* (60.2%) and low amounts of amphisteginids (4.0%). Other abundant species at this site include *Quinqueloculina seminula* and *Q.* aff. *Q. multimarginata* 2. Epiphytic cibicidiid foraminifera are present in low abundance and constitute only 3.2% at this site. Among all the samples analyzed, the dominance index value (SID) for this site is the highest value recorded (0.4).

The taxa with the highest relative abundances (RA) over all the samples include the symbiont-bearing *Amphistegina radiata* (21.9%), *Pararotalia calcariformata* (13.0%), *A. lessonii* (9.1%), and a smaller non-symbiont-bearing elphidiid (*Elphidium* cf. *E. limbatum*, 14.1%). All of them are members of the hyaline-perforate Rotaliida. Among the porcelaneous miliolids, *Quinqueloculina* aff. *Q. multimarginata* type 2 (RA = 7.5%) and *Sigmamiliolinella australis* (3.0%) were found to be the most abundant, followed by *Quinqueloculina seminula* (2.4%). *Textularia agglutinans* is the



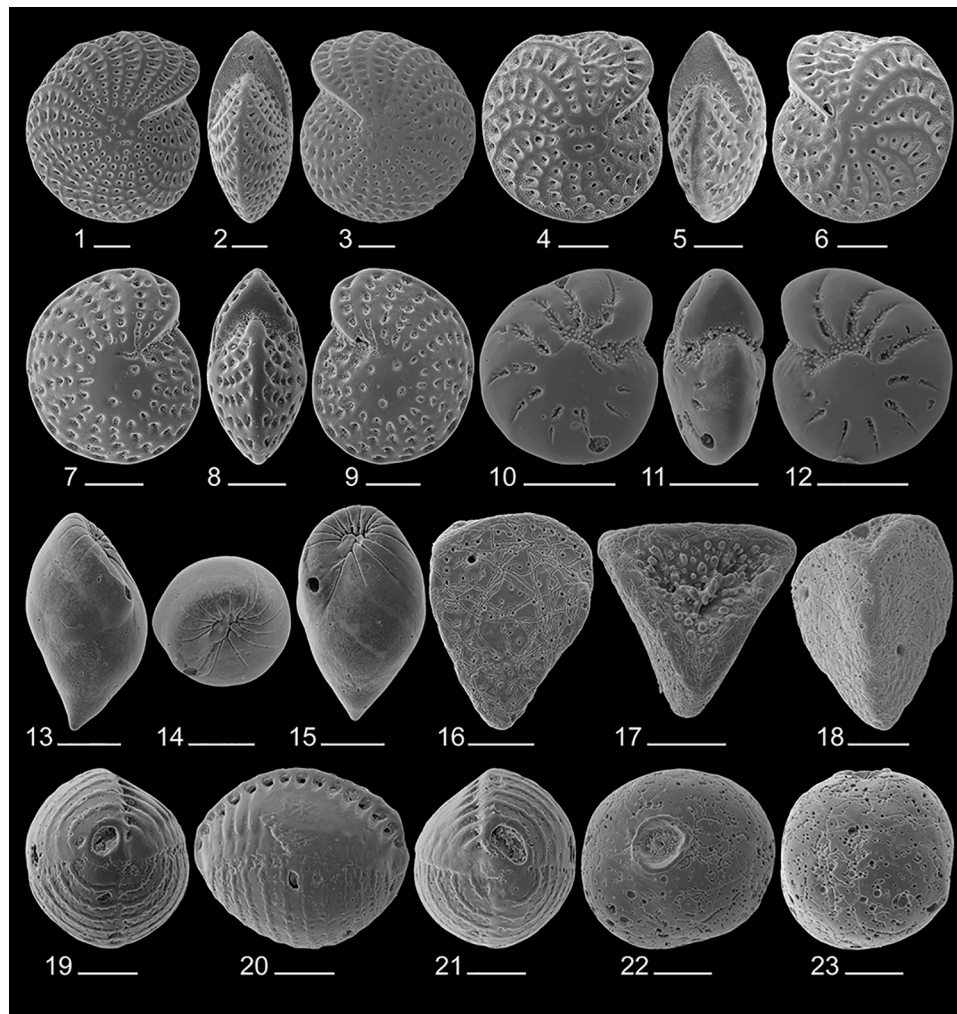


FIGURE 7. Benthic foraminifera from the southern coast of Oman. 1–3 *Elphidium* cf. *craticulatum* (Fichtel & Moll, 1798). 4–6 *Elphidium* cf. *limbatum* (Chapman, 1907). 7–9 *Elphidium* sp. 1. 10–12 *Elphidium* sp. 2. 13–15 *Elongobula milletti* (Cushman, 1933). 16–18 *Fijiella simplex* (Cushman, 1929). 19–21 *Borelis schlumbergeri* (Reichel, 1937). 22, 23 *Siphoninoides laevigatus* (Howchin, 1889). Scale bar = 100  $\mu$ m.

most abundant agglutinated species (RA = 0.5%). At the generic level, *Amphistegina* shows the highest relative abundance (RA = 30.9%), followed by *Elphidium* (16.3%), *Quinqueloculina* (12.7%), *Cibicides* (6.6%), and *Ammonia* (5.8%).

Among all taxa recorded, seven species occur at all sites (FO = 100%): *Quinqueloculina seminula*, *Quinqueloculina* aff. *Q. multimarginata* type 2, *Pararotalia calcariformata*, *Amphistegina lessonii*, *Elphidium* cf. *E. limbatum*, *Cibicides* sp. 1, and *Nonion* sp. 1. Four species were recorded at 90% of all sites: *Sigmamiliolinella australis*, *Amphistegina radiata*, *Sorites orbiculus*, and *Lamellodiscorbis* sp. 1 (FO = 90%). Among the 45 species identified, 22 are common (FO >50%), 6 species occur at every fourth site (FO >25%), and 17 taxa occur occasionally (FO >10%). A total of 11 species are represented by a single individual only.

#### LARGER SYMBIONT-BEARING FORAMINIFERA

Six different species of larger symbiont-bearing foraminifera (LBF) were recorded within the shallow water habitats: They are the hyaline-perforate taxa *Amphistegina radiata*, *A. lessonii*, and *Pararotalia calcariformata*, and three porcelaneous species:

*Borelis schlumbergeri*, *Sorites orbiculus*, *Peneroplis pertusus*. Percent abundances of the amphisteginids range between 4.1 and 47.3%, with lowest values at the coastal mangrove site (site 5) and highest values at Fazayat Beach (site 2). Coastal habitats characterized by phytal substrates show amphisteginid abundances ranging from 27.5 to 47.3%. Percent abundances of *Pararotalia calcariformata* vary substantially from site to site (1.2–60.2%) with highest recordings from the monotone sandy bay at Samharm Beach (site 7) and lowest values from the mangrove inlet at site 5. Unlike perforate symbiont-bearing species, LBF with a porcelaneous wall structure (*Borelis schlumbergeri*, *Sorites orbiculus*, and *Peneroplis pertusus*) are mostly rare and never constitute more than 6.9% of the total assemblage at each site.

#### ELPHIDIIDS

Elphidiid foraminifera are represented by four species (*Elphidium* cf. *E. craticulatum*, *Elphidium* cf. *E. limbatum*, *Elphidium* sp. 1, and *Elphidium* sp. 2) and show a wide range of abundance values when grouped (4.3–28.4%). Highest abundance values were recorded in the muddy tidal flats of the

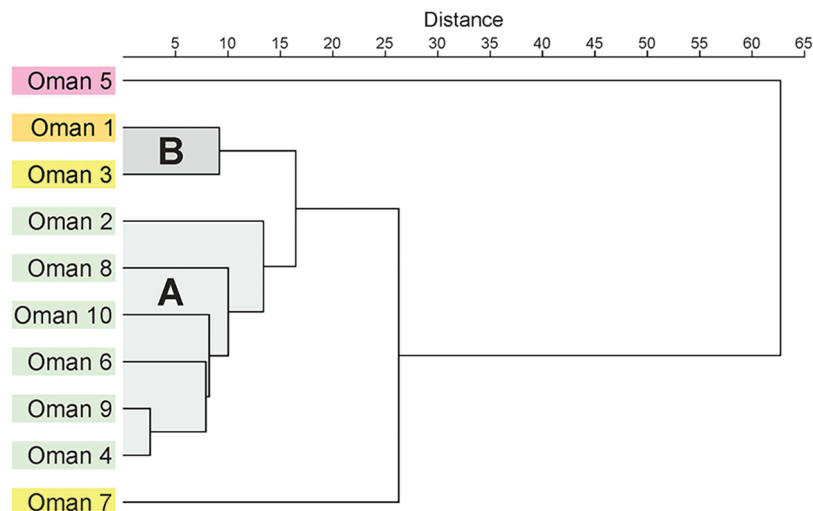


FIGURE 8. Cluster dendrogram showing Cluster A and B flanked by two outliers. The colour coding corresponds to the four habitat types outlined in the text and caption of Figure 1.

harbour (site 1; 47.7%) and at the sandy bay and fresh-water-influenced coastal site 3 (28.4%). In habitats with phytal coverage, elphidiid foraminifera contribute between 4.4 and 17.0% to the total assemblage, but in mangrove and sand bay environments percent abundances were much lower (6.6%).

#### HETEROTROPHIC FORAMINIFERA

The heterotrophic foraminifera are represented by 32 species from 12 families and four orders. The most abundant representatives of the heterotrophic foraminifera are the Miliolidae (Hauerinidae) and the Rotaliida (Cibicididae and Discorbidae). Among the heterotrophic Miliolidae, *Sigmamiliolinella australis*, *Quinqueloculina seminula*, and *Q. aff. multimarginata* type 2 are the most abundant species. The heterotrophic Miliolidae dominated only in the mangrove environment (47.5%; site 5). The Cibicididae consist of two species: *Cibicides refulgens* and *Cibicides* sp. 1. The two species contribute 13.1% to the total fauna recovered from the mangrove environment (site 5). The contribution of the Cibicididae to all other assemblages ranges between 1.9% (site 10) and 9.7% (site 9).

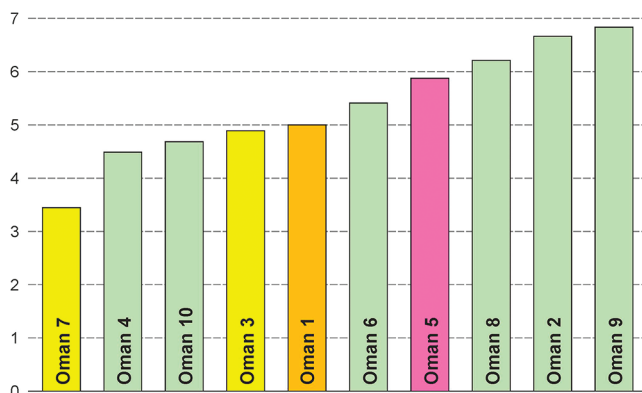


FIGURE 9. Fisher  $\alpha$  values in shallow-water habitats along the coast of Oman. The colour coding corresponds to the four habitat types outlined in the text and caption of Figure 1.

#### OPPORTUNISTIC FORAMINIFERA

Opportunistic taxa, species that respond rapidly to changing environmental conditions (Murray, 2006), are represented by *Ammonia amurensis*, *Nonion* sp. 1, and *Elongobula milletti*, with *A. amurensis* being the most abundant and widespread. At sites with phytal coverage, *A. amurensis* contributes between 1.5 and 9.2% to the total assemblage, but the species is absent from the bay inlet lined by *Avicenna* mangrove trees.

#### PRESERVATION STATUS

Our preservation status survey on the benthic foraminifera showed that the sample sites contain representatives of all four preservation grades (Figs. 11, 12; Table 3). The highest percentages of well-preserved and moderately well-preserved tests were recorded in habitats with phytal coverage, with the highest value recorded at site 9 where the sample was taken within the seagrass meadow. On the contrary, abraded, broken, and fully damaged specimens were most frequent in sandy coastal bay habitats (Table 3). Habitat-specific preservation differences are even more pronounced when percent abundances of category 1 and 2, and category 3 and 4 tests are pooled and computed as only two groups (Fig. 10). In habitats with phytal coverage and in the mangrove and the protected harbour environments, percent abundances of well- and moderately well-preserved tests range between 22 and 40%, while in more turbulent sandy beach habitats the values are lower and remain between 13 and 15%. Percent abundances of category 3 and 4 tests are highest in sandy bay habitats (87%) but remain consistently lower at all other sites (60–76%).

#### DISCUSSION

This survey provides the first faunal inventory and environmental analysis of recent benthic foraminifera from extremely shallow water habitats along the upwelling-influenced coast of southern Oman. As expected for extremely shallow-water benthic foraminifera assemblages, species richness and Fisher  $\alpha$  diversity values of individual samples were generally low

TABLE 2. Quantitative faunal data including the number of individuals per species, percentages of wall structural types, dominant groups and genera, and diversity and dominance (SID) index values. Species marked with a (\*) are considered opportunistic. The colour coding corresponds to the four habitat types outlined in the text and caption of Figure 1.

Species and indices	Sample sites									
	1	2	3	4	5	6	7	8	9	10
<i>Ammonia amurensis</i> *	0	3	17	44	0	31	23	27	75	4
<i>Amphistegina lessonii</i>	15	50	37	55	5	35	10	42	78	26
<i>Amphistegina radiata</i>	53	47	51	161	0	91	4	55	311	79
<i>Baggina</i> sp.	0	0	0	0	1	0	0	0	0	0
<i>Borelis schlumbergeri</i>	19	4	10	8	0	9	0	4	3	5
<i>Cibicides refulgens</i>	3	3	0	7	4	7	1	5	36	0
<i>Cibicides</i> sp.	17	14	7	33	12	17	10	14	61	5
<i>Elongobula milletti</i> *	2	1	0	2	0	2	0	0	3	0
<i>Elphidium</i> cf. <i>craticulatum</i>	1	0	0	0	0	0	0	0	0	0
<i>Elphidium</i> cf. <i>limbatum</i>	185	8	83	40	8	51	10	37	116	13
<i>Elphidium</i> sp. 1	1	1	0	8	0	27	3	10	18	5
<i>Elphidium</i> sp. 2	0	0	0	0	0	0	8	0	0	0
<i>Fijiella simplex</i>	0	1	0	0	0	0	0	0	0	0
<i>Glabratellina kermadecensis</i>	0	6	3	10	8	2	0	2	16	4
<i>Hanzawaia</i> cf. <i>H. nipponica</i>	0	0	0	0	4	0	0	3	0	0
<i>Lamellogobiosella</i> sp. 1	7	7	1	19	4	13	0	9	12	10
<i>Lamellogobiosella</i> sp. 2	10	0	0	0	0	0	0	2	8	0
<i>Milionella circularis</i>	0	0	0	0	1	0	0	0	0	0
<i>Nonion</i> sp.*	4	3	4	1	4	6	10	3	6	9
<i>Pararotalia calcariformata</i>	5	18	20	45	2	49	209	72	53	34
<i>Peneroplis pertusus</i>	4	8	0	5	0	18	4	5	14	0
<i>Pseudogaudryina</i> sp. 1	0	0	0	0	3	0	0	0	1	0
<i>Pseudotriloculina echinata</i>	0	0	1	0	0	1	0	3	4	0
<i>Pseudotriloculina</i> sp. 1	0	0	0	0	0	0	0	1	1	1
<i>Pseudotriloculina</i> sp. 2	0	0	1	0	0	0	0	0	0	0
<i>Pseudotriloculina</i> sp. 3	0	0	1	0	0	0	0	0	0	0
<i>Quinqueloculina</i> aff. <i>multimarginata</i> type 1	4	4	0	0	0	1	0	0	34	0
<i>Quinqueloculina</i> aff. <i>multimarginata</i> type 2	50	6	30	20	21	30	28	29	45	34
<i>Quinqueloculina seminula</i>	4	8	5	8	4	14	20	6	17	8
<i>Quinqueloculina</i> sp. 1	0	0	0	0	0	0	0	0	0	1
<i>Quinqueloculina</i> sp. 2	2	1	1	0	0	7	0	0	6	2
<i>Quinqueloculina</i> sp. 3	0	0	3	0	0	8	1	0	17	2
<i>Quinqueloculina</i> sp. 4	0	0	0	0	0	0	0	0	14	0
<i>Rosalina</i> aff. <i>R. orientalis</i>	0	2	0	1	5	2	0	1	4	0
<i>Sigmamiliolinella australis</i>	0	7	6	5	32	24	1	2	23	17
<i>Siphoninoides laevigatus</i>	1	0	0	0	0	0	0	0	0	0
<i>Sorites orbiculus</i>	2	1	8	2	3	9	0	3	7	2
<i>Textularia agglutinans</i>	0	0	3	2	1	0	5	5	2	0
<i>Textularia pseudosolita</i>	0	0	0	0	0	0	0	0	6	0
<i>Textularia</i> sp. 1	2	2	0	0	0	4	0	0	4	0
<i>Textularia</i> sp. 2	0	0	0	0	0	0	0	0	1	0
<i>Triloculina affinis</i>	0	0	0	1	0	0	0	2	1	0
<i>Triloculina fichteliana</i>	0	0	0	0	0	0	0	0	1	0
<i>Triloculina</i> sp. 1	0	0	0	0	0	0	0	1	1	0
<i>Vertebratolina striata</i>	1	0	0	0	0	0	0	0	0	0
Number of specimens	392	205	292	477	122	458	347	343	999	261
Number of species	22	23	20	21	18	24	16	25	34	19
Number of specimens per gram	98	121	62	149	59	151	347	142	242	139
Agglutinated, %	0,5	1,0	1,0	0,4	3,3	0,9	1,4	1,5	1,4	0,0
Miliolid, %	15,3	12,7	16,4	7,1	47,5	18,6	14,4	12,8	16,4	24,9
<i>Amphistegina</i> , %	17,3	47,3	30,1	45,3	4,1	27,5	4,0	28,3	38,9	40,2
<i>Pararotalia</i> , %	1,3	8,8	6,8	9,4	1,6	10,7	60,2	21,0	5,3	13,0
<i>Cibicides</i> , %	5,1	8,3	2,4	8,4	13,1	5,2	3,2	5,5	9,7	1,9
<i>Elphidium</i> , %	47,7	4,4	28,4	10,1	6,6	17,0	6,1	13,7	13,4	6,9
<i>Ammonia</i> , %	0,0	1,5	5,8	9,2	0,0	6,8	6,6	7,9	7,5	1,5
Accessory, %	12,8	16,1	8,9	10,1	23,8	13,3	4,0	9,3	7,3	11,5
Perforated, %	84,2	86,3	82,5	92,5	49,2	80,6	84,1	85,7	82,2	75,1
Symbiont-bearing, %	25,0	62,4	43,2	57,9	8,2	46,1	65,4	52,8	46,6	55,9
Heterotrophic, %	25,8	29,8	21,2	22,2	82,0	28,4	19,0	24,8	31,5	32,2

TABLE 2. Continued.

Species and indices	Sample sites									
	1	2	3	4	5	6	7	8	9	10
Opportunistic, %	1,5	3,4	7,2	9,9	3,3	8,5	9,5	8,7	8,4	5,0
Fisher $\alpha$ values	5,0	6,6	4,9	4,5	5,8	5,4	3,5	6,2	6,8	4,7
Shannon's H'	1,9	2,5	2,3	2,3	2,4	2,7	1,6	2,5	2,6	2,3
SID	0,3	0,1	0,1	0,2	0,1	0,1	0,4	0,1	0,1	0,1

(16–34 species, Fisher  $\alpha$  = 4.5–6.8) but revealed a distinct trend towards higher values in habitats with patches of phytal coverage and reached highest values at the sampling site within a dense seagrass meadow (site 9, Eagles Bay; Table 2). On the contrary, monotone sand bays (sites 3 and 7) revealed distinctly lower values (16–20 species, Fisher  $\alpha$  = 3.5–4.9). Moderate species richness and Fisher  $\alpha$  values were recorded from the semi-enclosed harbour and muddy mangrove bay habitats (18–22 species, Fisher  $\alpha$  = 5.0–5.8; Table 2). Species richness and Fisher  $\alpha$  trends are mirrored in both Shannon H' and SID values and support the conclusion that habitats with phytal coverage contain more diverse and heterogenous foraminiferal biotas than sand bays.

The low-diversity biotas are in coherence with previous shallow-water studies from Oman (Pilarczyk et al., 2011; Pilarczyk & Reinhardt, 2012; Al-Sayigh et al., 2015), with

shallow-water faunal data from the coast of Africa (Langer et al., 2013, 2016a, b; Thissen & Langer, 2017; Weinmann & Langer, 2017), and the Oman assemblages can be classified as low-diversity faunas following the diversity categories established by Langer & Lipps (2003) and Förderer & Langer (2018; with Fisher  $\alpha$  indices <10). The low species richness is due to shallow depths at our site locations, where rough, turbulent, and dynamic processes of sediment transport and reworking occur, and where the record is further filtered through intense taphonomic processes that particularly affect thin-shelled and fragile taxa and favor the preservation of robust, large and thick-shelled tests (Goldstein & Watkins, 1999; Murray & Alve, 1999a, b; Martin et al., 2003).

As outlined above and summarized in Table 4, a multitude of features characterizes the foraminiferal assemblages from different shallow-water habitats along the southern coast of

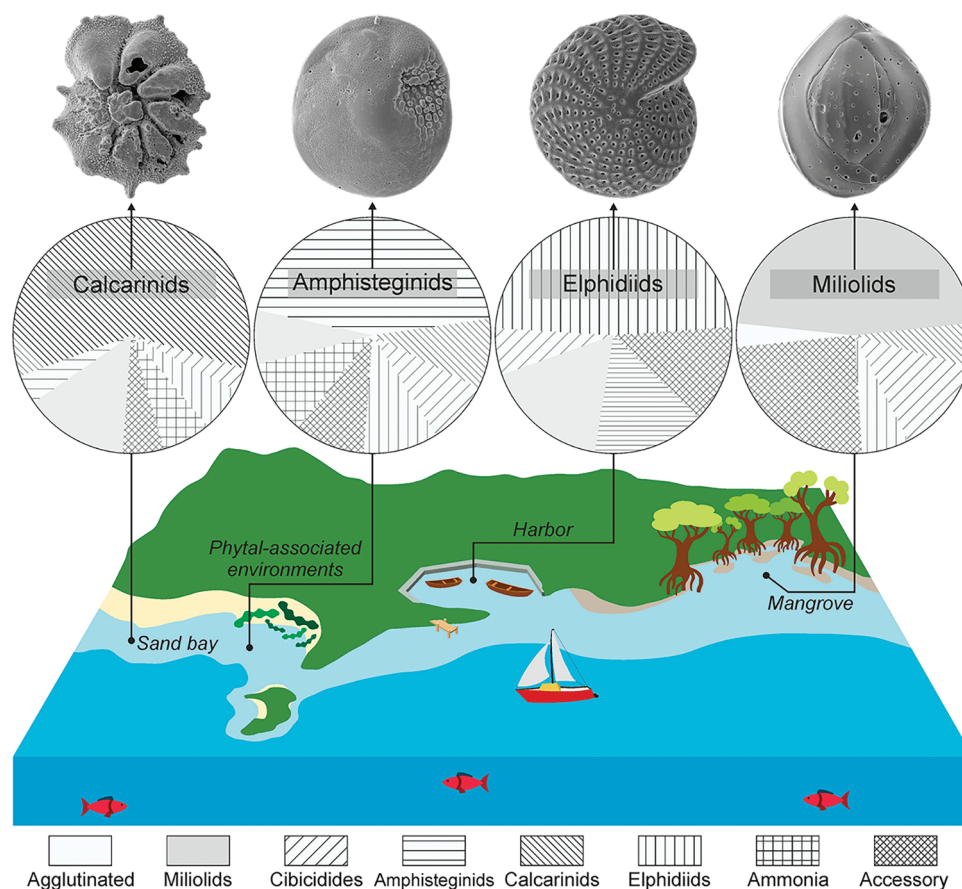


FIGURE 10. Schematic illustration of shallow-water habitats off the coast of Oman with circle diagrams showing average percentage values of individual groups of shallow-water benthic foraminifera.



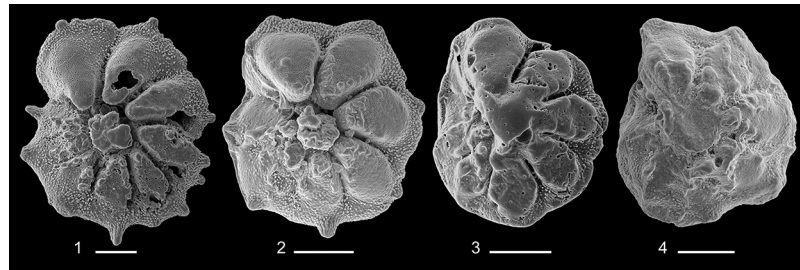


FIGURE 11. Preservation stages and categorization of foraminiferal tests: 1) well preserved, 2) moderately-well preserved, 3) abraded and broken, 4) fully damaged, broken and abraded.

Oman. This includes the composition, species richness, diversity, dominance, and preservation of benthic foraminiferal biotas. Assemblages from phytal-associated habitats contained mainly amphisteginids, various amounts of smaller miliolids, elphidiids, and *Pararotalia calcariformata*, and in addition to numerous species of heterotrophic foraminifera. Typical indicator taxa for phytal hard substrates (cibicides; Langer, 1988, 1993), are on average twice as abundant in phytal-associated habitats than in sand bays lacking phytal coverage (5.5% versus 2.7%). Sand bay habitats, in turn, are dominated by *P. calcariformata* (site 7), elphidiids, and *Amphistegina* (site 3) and reveal a distinctly lower species richness and diversity but higher dominance (Table 2). Samples from the mangrove bay inlet and the harbour, on the other hand, were dominated by smaller miliolids, and elphidiids, respectively.

Computational analysis of wall structural groups revealed that hyaline-perforate rotaliids dominate the foraminiferal biotas along the southern Oman coast. The dominance of perforate-hyaline taxa is mainly driven by the abundance of larger rotaliids, in particular amphisteginids and *P. calcariformata*. In terms of absolute abundance, robust, thick-

shelled amphisteginids are among the most abundant taxa, although their frequent occurrence and shell accumulation may well be the result of selective preservation processes. Amphisteginid foraminifera display the widest environmental tolerance among all LBF, are prolific carbonate producers in tropical reef settings (Langer et al., 1997; Langer, 2008), often act as ecosystem engineers, and contribute to the formation and stabilization of coastal environments (Langer & Hottinger, 2000; Langer et al., 2012, 2013; Weinmann et al., 2013; Langer & Mouanga, 2016). Hyaline calcareous rotaliids were also found to dominate the stained fauna within the OMZ at 412 m (Gooday et al., 2000), but the OMZ foraminiferal biotas differ substantially from our shallow-water assemblages and from mainly soft-shelled and agglutinated deep-water assemblages below the OMZ at 3350 m (allogro-miids, saccaminids, hormosinaceans, bathysiphonids, hippo-crepinaceans; Gooday et al., 2000).

Symbiont-bearing taxa are represented by six species, play a prominent role in the formation of Oman's foraminiferal assemblages, and in eight out of 10 samples they constitute more than 40% of all foraminifera. In the protected harbour

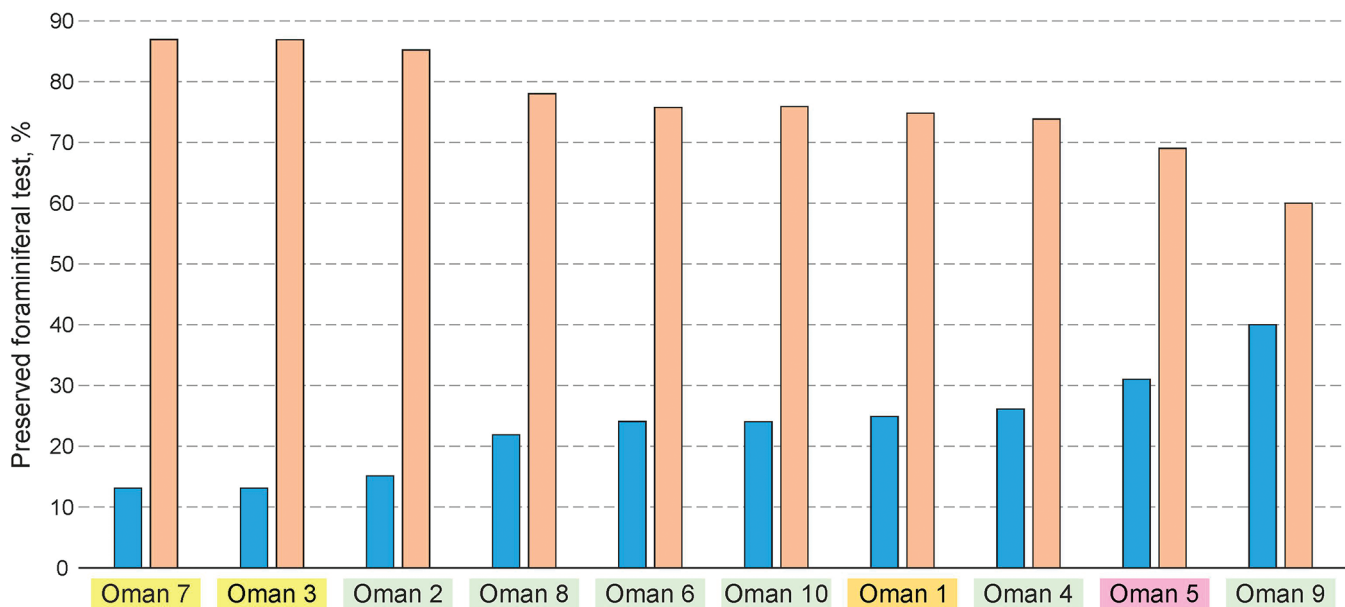


FIGURE 12. Percent abundance bar diagram showing the relation of well and moderately-well (blue) preserved versus abraded/broken and fully damaged (brown) foraminiferal tests in shallow-water habitats along the southern coast of Oman. Coloured sample site numbers refer to sand (yellow), harbour (brown), mangrove (purple), and phytal-associated habitats (green). Note low preservation values in sand bay habitats (sites 3 and 7), and higher values in mangrove, harbour and phytal-associated habitats. The highest value of combined high and medium preserved tests was found at site 9, a collection site located directly within a seagrass meadow (see also Table 3).

TABLE 3. Computation of individual preservation categories and pooled abundances of well and moderately-well preserved tests versus abraded/broken and fully damaged foraminiferal tests (in %).

Preservation status category	Sample sites									
	Oman 1	Oman 2	Oman 3	Oman 4	Oman 5	Oman 6	Oman 7	Oman 8	Oman 9	Oman 10
Well preserved	8	6	6	10	10	8	4	9	8	9
Moderately well preserved	17	9	7	16	21	16	9	13	32	15
Abraded and broken	33	31	32	32	29	36	41	35	32	29
Fully damaged	42	54	55	42	40	40	46	43	28	47
Pooled abundances										
Category 1 & 2										
Well and moderately well preserved	25	15	13	26	31	24	13	22	40	24
Category 3 & 4										
Abraded/broken and fully damaged	75	85	87	74	69	76	87	78	60	76

setting they make up only 25%, and in mangrove settings they merely contribute 8% to the total assemblage. The low number of only six LBF species is far below the estimated 20 species as prognosticated by species distribution modeling of Förderer et al. (2018), but is certainly an artifact of the extremely shallow water depth range analyzed (1–3 m).

The LBF recorded in our material comprise two orders (Rotaliida and Miliolida), five different families, five genera, and six species (Table 2). Among the LBF identified are two species of *Amphistegina*: *A. radiata* and *A. lessonii*. Amphisteginids are indicative of shallow, well-illuminated habitats and mostly associated with phytal substrates (Langer, 1993; Murray, 2006; Mateu-Vicens et al., 2014). Among the LBF,

*Pararotalia calcariformata* was found to be the dominant taxon in the monotone sand bay lacking phytal coverage (Samaharam Beach). The high percentage of damaged and abraded calcarinids in this assemblage indicates current-exposed environments and suggests common reworking of the sediments. According to Hohenegger (1994), calcarinids preferentially live in highly turbulent waters, an observation in accordance with the function of tubular spines as anchor in agitated waters (Röttger & Krüger, 1990) and in line with the current-exposed setting of the sand bay at Samharam Beach. All other symbiont-bearing LBF (*Peneroplis pertusus*, *Sorites orbiculus*, *Borelis schlumbergeri*) are rare and rather randomly distributed among habitats.

TABLE 4. Characteristics of faunal assemblages from shallow-water habitats of Oman.

Habitat	Habitat-specific assemblage characteristics	Preservation
Sand bays lacking phytal coverage	Low species richness (< 20) and diversity (Fisher $\alpha \leq 4.9$ ), high dominance ( <i>Pararotalia calcariformata</i> – 60.2%), abundant calcarinids, moderate to low amounts of thick-shelled miliolid foraminifera, agglutinated foraminifera rare. Typical epiphytic species (e.g. cibicidiids) with low abundances. Sand bays located in front of seasonally influenced estuary enriched in thick-shelled miliolid, elphidiid and amphisteginid foraminifera. Calcarinid foraminifera with low abundances.	Low percentages of moderately well (<9%) and well-preserved tests (4–6%). Disproportional accumulation of robust, thick-shelled tests.
Port inlet protected by harbour wall	Low species richness (<22) and diversity (Fisher $\alpha \leq 5.0$ ), but higher than in sand bays, abundant elphidiids (>47.7%), moderate amounts of diverse and more thin-shelled miliolid and hyaline perforate taxa. Agglutinated foraminifera rare or absent. Calcarinid foraminifera rare.	Percent abundances of well-preserved and moderately well-preserved tests constitute about 25% of the total assemblage, higher than in monotone sand bays, but lower than in phytal associated coastal habitats.
Sand bay habitats associated with seagrass meadows.	Low species richness (<34) and diversity (Fisher $\alpha \leq 6.8$ ), but generally higher than in sand bays. Diverse and heterogeneous composition of assemblages, with biotas dominated by amphisteginids, miliolids and elphidiids. LBF commonly present, constitute half of assemblages and include amphisteginids, followed by calcarinids and large miliolids.	Percent abundances of well-preserved and moderately well-preserved tests constitute about between 15 and 40% of the total assemblage, higher than in monotone sand bays. Abundant epiphytic species (e.g. cibicidiids).
Muddy bay inlets lined by stands of mangrove trees	Low species richness (<18) and diversity (Fisher $\alpha \leq 5.8$ ), but higher than in sand bays. Abundant smaller miliolids (~47%), moderate amounts of amoniid, cibicidiid (13.1%), and elphidiid (6.5%) taxa. Agglutinated foraminifera contribute ~3% to the total assemblage, calcarinid and other LBF with low amounts ( $\leq 8.20$ ).	Percent abundances of well-preserved tests (10%) and moderately well-preserved test (21%) reach >30 %, higher than in sand bays and in most phytal-associated habitats. LBF present mostly abraded or broken (amphisteginids).



Our recordings of substantial compositional differences are strongly supported by cluster analysis, where seagrass-associated habitats are clearly discernible from sandy bay, harbour, and mangrove assemblages (Fig. 8; summarized in Table 4). Moreover, seagrass-associated, harbour and mangrove faunas revealed lower test damage rates than sand bay biotas and show that destructive and taphonomic forces acting on the preservation of foraminiferal shells have a greater impact in sandy bays than in any other habitat. The dynamic processes under the extreme shallow-water conditions, including constant wave action, turbulence, and sediment movement, are reflected in the large number of poorly preserved foraminifera shells, indicating that the faunas were not deposited in situ. However, our detailed analyses of the structural composition, diversity, and preservation of foraminifera show that faunas were not deposited out-of-habitat but retain the characteristics of their habitat, record much ecological detail, and provide useful information for paleoecological and environmental studies.

#### UPWELLING OFF OMAN: A BIOGEOGRAPHIC BARRIER?

We found 45 species from shallow waters of Oman in contrast to 111 species from Bir Ali beach (Yemen: Al-Wosabi et al., 2017), 87 taxa reported from the Arabian Gulf (Cherif et al., 1997), and 86 taxa of benthic foraminifera from Socotra Island, Yemen (Al-Wosabi et al., 2011). Our records indicate, however, that only 11 species are shared among the localities and only seven species from Oman occur also in the Gulf of Aqaba (Hottinger et al., 1993). The same holds for the low number of LBF species recorded here (6), a number that is far below the anticipated number of symbiont-bearing taxa prognosticated by species distribution modeling (Förderer et al., 2018), and much lower than along the tropical eastern African continent (Thissen & Langer, 2017; Förderer et al., 2018). The Dhofar region is situated in the center of maximum upwelling (Currie et al., 1973; Spreter et al., 2022) and its coastal waters experience persistent upwelling conditions during the SW summer monsoon winds. It is certainly tempting to simply relate these differences to the upwelling conditions off Oman, but because our sample material covers only extremely shallow-water areas, the data collected to date provide only a limited snapshot. A larger sample set from deeper settings of the photic zone is needed to draw meaningful biogeographic conclusions.

However, significant differences were noted between the deep-sea dysoxic fauna of Oman and other upwelling areas (Gooday et al., 2000), possibly indicating that the shallow-water foraminiferal assemblages of southern Oman may also have a unique character that differs from other sites in the Arabian Gulf. The upwelling area affected off the coast of Oman extends 300 km offshore and is characterized by colder sea surface temperatures (SST) and higher nutrient concentrations (silicate, phosphate, nitrate; Barrat et al., 1986). With SST dropping to as low as 15.9°C (Savidge et al., 1990) and being situated on the crossroads between the high diversity Coral Triangle and the eastern African coast (Förderer et al., 2018), the Oman cold-water upwelling may constitute a potent biogeographic barrier for the dispersal of thermophile and temperature-dependent LBF (Langer & Hottinger, 2000), as has been suggested for peculiar assemblages of corals, fish, echinoderms, invertebrates, and marine floristics (Sheppard &

Salm, 1988; Wilson, 2000; Belanger et al., 2012; Claereboudt, 2019; Coleman, 2022; DiBattista et al., 2022).

#### CONCLUSIONS

Extremely shallow-water foraminifera are subject to intense environmental processes where the formation of dead assemblages is the result of postmortem processes, among which out-of-habitat transport and the destruction and disintegration of tests are most significant. Despite intense environmental processes, extremely shallow-water foraminiferal assemblages from the southern coast of Oman retain the environmental signatures of their habitats. Features of these signatures are preserved in the structural composition, species richness, and numerical abundances of epiphytic foraminifera and shell preservation groups, in addition to diversity and dominance index values.

With a total of 45 fully illustrated species, the foraminiferal assemblages can be classified as low-diversity biotas, but the number of taxa recorded exceeds previous shallow-water species counts from Oman. The foraminiferal fauna is mainly composed of hyaline-perforate taxa and differs substantially from neighboring regions, possibly due to the intense and nutrient-rich upwelling conditions located in front of the coast. Individuals of robust larger symbiont-bearing foraminifera constitute dominant components of the foraminiferal fauna with their disproportionate enrichment, possibly controlled by the selective destruction of small and fragile shells and taphonomic processes. Consistent with previous modeling studies, the number of LBF species is low, possibly indicating that the cold, nutrient-rich, and intense upwelling currents off Oman provide a biogeographic barrier to the dispersal of foraminifera.

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## Chapter 6: Publication



## Distribution patterns of living benthic foraminifera in Mahrés Bay (Gulf of Gabes, Tunisia): Linking habitats and faunal components

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With 4 figures and 2 tables

**Abstract:** Living benthic foraminifera were analyzed from Mahrés Bay (Gulf of Gabes, Tunisia) to document the spatial distribution of species and to relate the composition of the assemblages to habitat characteristics and environmental conditions. Mahrés Bay is a shallow, semi-enclosed coastal lagoon characterized by various habitats such as tidal channels, mudflats, sandflats, algal and seagrass patches, and *Salicornia* and *Suaeva* salt marsh meadows, and has gradually formed by the formation of a sandspit south of the Le Chaffar headland. Analysis of the foraminiferal fauna shows that the bay is characterized by an overall low-diversity fauna, but individual habitats are characterized by distinct faunal communities and by the dominance of a few indicator species. On the high intertidal inner margins, the dense *Salicornia* salt marshes are dominated by the agglutinated foraminifer *Trochammina inflata*. The less dense *Salicornia* meadows, the central inner part of the lagoon, and the areas along the tidal channels are predominantly colonized by species of *Ammonia*. Miliolids and other accessory species are found mainly in the southern part of the lagoon facing the sea and in the deeper tidal channels near the entrance channel, but may also be distributed in patches. The areas colonized by *Trochammina* and *Ammonia* show a clear spatial separation. The spatial partitioning is evident in both the cluster and ternary diagram analysis, indicating minimal lateral exchange of faunas or transportation outside their habitat. The highest abundances of living benthic foraminifera were found in the innermost northern areas covered by *Salicornia* meadows. Diversity and species richness of benthic species is generally low, increases slightly toward the open entrance area of the lagoon, and peaks in the algae-covered southern portion near the deepest tidal channel. Across the lagoon, dominance indices are generally high, showing maximum values at highest tidal elevations along the inner sandspit and in the innermost northernmost part. The individual composition of habitat-specific faunas observed diversity and abundance patterns, and the presence of indicator species are of interest for reconstructing the evolution of coastal bays and for interpreting past coastal habitats.

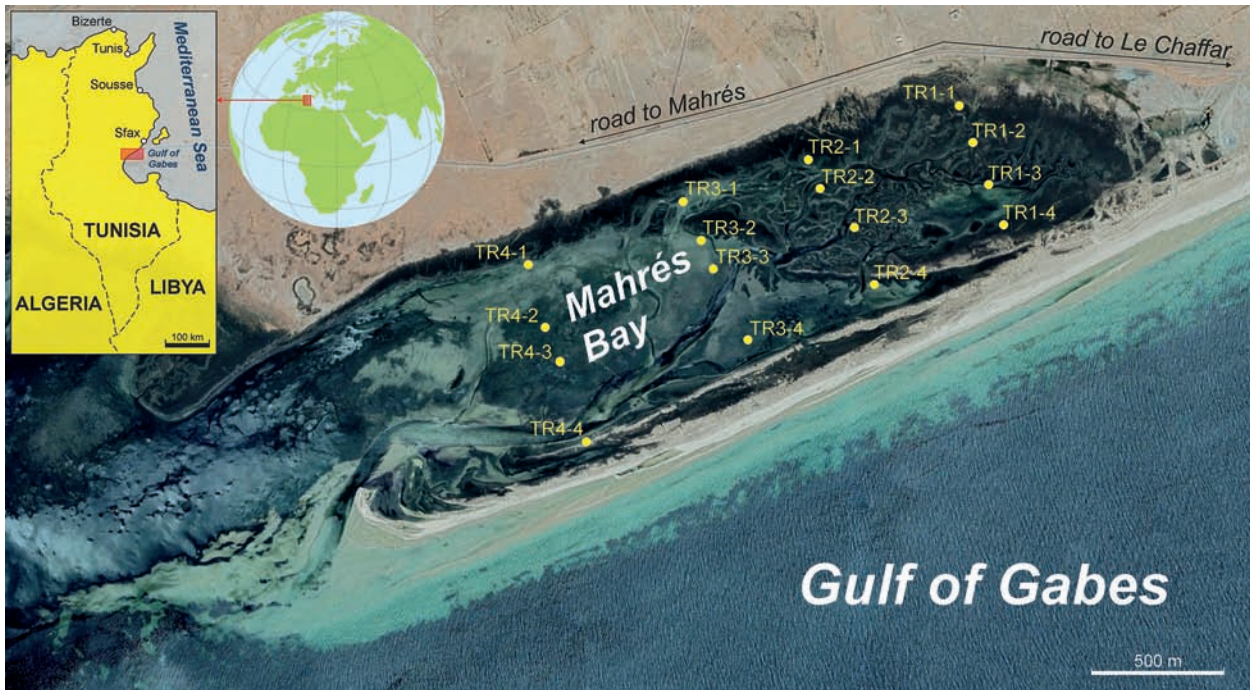
**Key words:** Living foraminifera, lagoon, tidal channels, mudflats, sandflats, *Salicornia*, salt marshes.

### 1. Introduction

Wetlands are prominent features along coastal environments in the Gulf of Gabes, Tunisia (OUESLATI 2022). Located at the interface between land and sea, they provide important ecosystem services, including serving as a buffer against waves, floods and storms, im-

proving water quality, and providing habitat and nurseries for a diverse array of plant and animal species. Mahrés Bay, situated 30 km south of the city of Sfax, is a small, semi-enclosed lagoon and partially covered by intertidal saltmarsh vegetation. It is protected from the ocean by a sandspit barrier and connected to the ocean via shallow tidal channel. Behind the sandspit barrier,





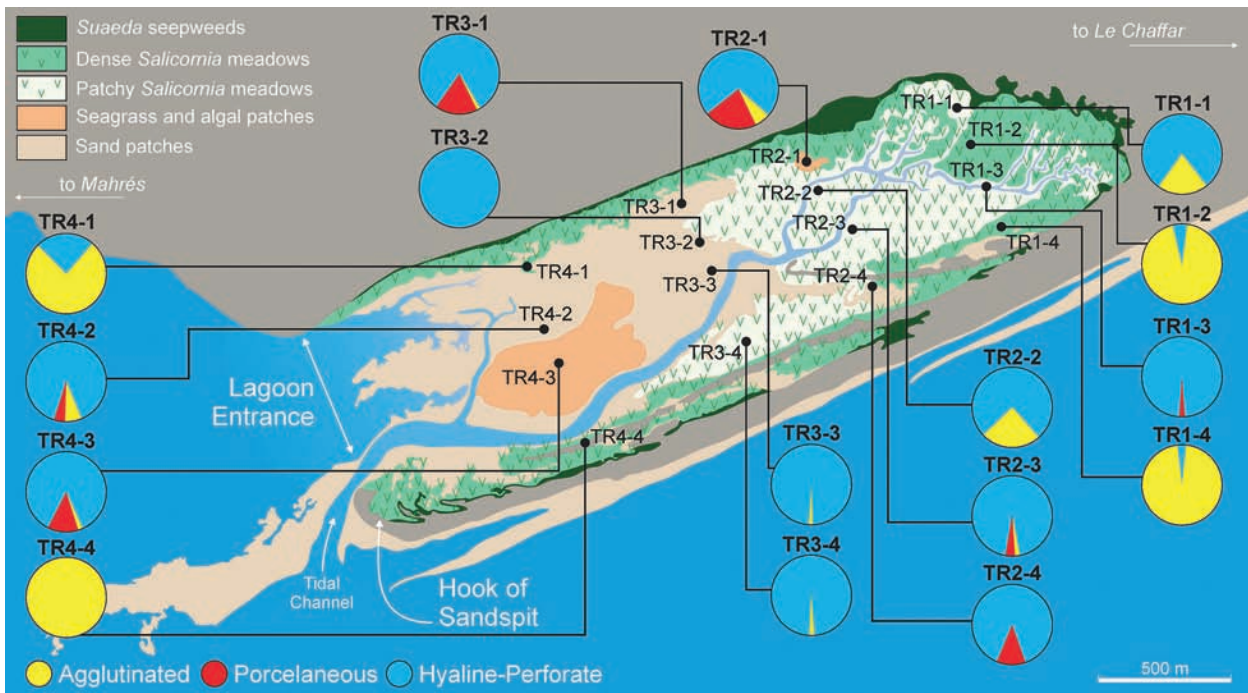
**Fig. 1.** Satellite image of Mahrés Lagoon in the Gulf of Gabes (Mediterranean Sea) and location of sampling sites along transects (the area shown corresponds to the red rectangle in the map above left; source Google Earth, mission 08-2019).

a mosaic of vegetated wetland saltmarshes and sandy and muddy tidal flats has developed, crisscrossed by an extensive network of tidal channels. The lagoon comprises as suite of habitats, including extensive meadows of the halophytic flowering plant *Salicornia* (*Sarcocornia fruticosa*), tidal channels, and sand and mud flats that are partially covered by microbial cyanobacteria mats. At its fringes and along some parts of the sandspit, the lagoon is populated by species of halophile seepweeds (*Suaeda vermiculata* and *Suaeda maritima*). These areas are located at the highest position where seawater covers the roots only during extreme tides. Habitats in intertidal zones are vertically stratified by tidal action. The zones span from peripheral areas, which are overgrown with *Suaeda* seepweeds, to somewhat deeper and in places densely populated *Salicornia* marsh meadows, to the mud and sand flats to the south, to deeper intertidal channels. To determine if there is a correlation between the distribution, diversity, and abundance of benthic foraminifera and their habitat and/or tidal elevation, we conducted a quantitative analysis of living species across four transects in the lagoon.

## 2. Material and methods

Mahrés Lagoon is located in the northern part of the Gulf of Gabes (Tunisia), and situated between the towns of Le Chaffar and Mahrés (Fig. 1). The lagoon is 1.75 km<sup>2</sup> in size, extends over a length of about 2.8 km and narrows inward. The width of the lagoon varies between 190 and 770 m. Within the tidal channels, the average water depth is about 0.5 m at low tide, with a maximum of 1.8 m at high tide. The semi-closed lagoon is separated from the Mediterranean Sea by a long and highly dynamic sandspit. Exchange between the ocean and lagoon occurs in the southern section via an approximately 450 meter-wide entrance and a smaller tidal channel (Fig. 2). Sediments consist mainly of sand, silty sand, and silt, with the sands found primarily in the southern part of the lagoon and the finer sediment components found in the northern interior of the lagoon and in the tidal channels (Figs. 1, 2).

A total of 16 surface sediment samples were collected over 4 transects within the lagoon (Figs. 1, 2; Table 1). Transects run across the long axis of the lagoon and cover all habitats, including the peripheral



**Fig. 2.** Distribution of habitats and percent abundances of agglutinated, hyaline-perforate and miliolid foraminifera across the Mahrés Lagoon. Circle diagrams represent 100 percent of the total living assemblage at individual sites (for details see Table 2).

high tide areas, the inner lagoon, tidal channels, and sample stations along the opposite sandspit. Sampling was performed by boat and snorkeling at high tide in August 2019 by filling ca. 50 mL of sediment from the topmost surface layer into 100 mL plastic containers. Excess water was decanted after settling and the sample containers were then filled with a solution of 90 % ethanol and 2 g Rose Bengal per liter to stain the cytoplasm of living foraminifera (MURRAY & BOWSER 2000). Sampling site locations were accurately georeferenced using GPS; site-specific details are provided in Table 1.

After 2 weeks, the material was washed with tap water over a 63 µm sieve and oven-dried at 50 °C. Rose Bengal stained, living foraminifera were picked and identified to species level. Individual species were counted and percent abundances were calculated for each taxon and for wall structural types (agglutinated, porcelaneous, hyaline-perforate; Table 2). For identification of taxa we used the catalogue of Mediterranean foraminifera (CIMERMAN & LANGER 1991), the work of LANGER & SCHMIDT-SINNS (2006), and the World Foraminifera Database (<http://www.marinespecies.org/foraminifera>, last access: 21 August 2023; HAY-

**Table 1.** Sample site information, including longitude and latitude coordinates. All samples were collected in August 2019.

Sample Site	Longitude	Latitude
TR1-1	10° 33' 25.08" E	34° 31' 45.82" N
TR1-2	10° 33' 26.90" E	34° 31' 41.89" N
TR1-3	10° 33' 29.30" E	34° 31' 38.23" N
TR1-4	10° 33' 31.80" E	34° 31' 33.77" N
TR2-1	10° 33' 3.27" E	34° 31' 42.44" N
TR2-2	10° 33' 5.71" E	34° 31' 37.52" N
TR2-3	10° 33' 8.68" E	34° 31' 31.97" N
TR2-4	10° 33' 10.57" E	34° 31' 27.73" N
TR3-1	10° 32' 52.83" E	34° 31' 37.64" N
TR3-2	10° 32' 54.33" E	34° 31' 33.44" N
TR3-3	10° 32' 53.76" E	34° 31' 30.73" N
TR3-4	10° 32' 57.16" E	34° 31' 21.73" N
TR4-1	10° 32' 32.28" E	34° 31' 31.36" N
TR4-2	10° 32' 33.20" E	34° 31' 25.48" N
TR4-3	10° 32' 34.76" E	34° 31' 20.65" N
TR4-4	10° 32' 36.59" E	34° 31' 12.03" N

**Table 2.** Numerical abundance data of individual species, including diversity and dominance indices of individual samples, percent abundances of hyaline-perforate, porcelaneous, and agglutinated foraminifera, and foraminiferal numbers (FN) per gram sediment.

Species / Sample Number	TR1-1	TR1-2	TR1-3	TR1-4	TR2-1	TR2-2	TR2-3	TR2-4	TR3-1	TR3-2	TR3-3	TR3-4	TR4-1	TR4-2	TR4-3	TR4-4	Total
<i>Ammonia aberdoveyensis</i> HAYNES 1973	44	8	3	0	5	11	0	0	0	0	70	0	66	7	30	0	244
<i>Ammonia falsobeccarii</i> (ROUVILLOIS 1974)	0	0	0	0	0	0	3	0	0	12	0	0	0	5	24	0	44
<i>Ammonia parkinsoniana</i> (D'ORBIGNY 1839)	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0	0	5
<i>Ammonia veneta</i> (SCHULTZE 1854)	25	3	297	1	147	257	281	280	233	244	170	301	0	26	68	0	2333
<i>Bolivina variabilis</i> (WILLIAMSON 1858)	0	0	0	0	0	0	0	0	0	0	7	0	0	0	15	0	22
<i>Buccella</i> sp.1	0	0	1	0	0	0	0	1	0	0	3	2	0	0	1	0	8
<i>Bulimina</i> sp.1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	13	0	15
<i>Cymbaloporetta</i> sp.1	0	0	0	0	0	0	0	0	2	0	0	1	0	0	2	0	5
<i>Discorbinaella bertheloti</i> (D'ORBIGNY 1839)	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	3
<i>Elphidium</i> sp.1	1	1	0	0	2	0	2	0	0	1	3	4	0	0	19	0	33
<i>Eponides</i> sp.1	0	6	1	0	9	8	0	0	0	0	19	0	14	0	0	0	57
<i>Haynesina depressula</i> (WALKER & JACOB 1798)	0	0	0	0	0	0	1	0	0	0	0	1	0	0	29	0	31
<i>Haynesina germanica</i> (EHHENBERG 1840)	0	0	3	0	0	0	18	10	1	35	0	6	0	0	8	0	81
<i>Haynesina</i> sp.1	0	0	0	0	44	0	0	0	0	0	12	0	0	0	0	0	56
<i>Lobatula lobatula</i> (WALKER & JACOB 1798)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	3
<i>Nonion</i> sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	6
<i>Peneroplis pertusus</i> (FORSSKÅL 1775)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Porosion</i> sp.1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Quinqueloculina seminulum</i> (LINNAEUS 1758)	0	0	0	0	10	0	0	7	8	0	0	0	0	0	0	0	25
<i>Quinqueloculina striata</i> D'ORBIGNY 1832	0	0	2	0	0	0	3	2	14	0	0	0	0	0	0	0	21
<i>Quinqueloculina vulgaris</i> D'ORBIGNY 1826	0	0	3	0	0	0	0	3	3	0	0	0	0	0	0	0	9
<i>Quinqueloculina</i> sp.1	0	0	0	0	55	0	10	27	26	0	2	5	0	2	34	0	161



Species / Sample Number	TR1-1	TR1-2	TR1-3	TR1-4	TR2-1	TR2-2	TR2-3	TR2-4	TR3-1	TR3-2	TR3-3	TR3-4	TR4-1	TR4-2	TR4-3	TR4-4	Total
<i>Rosalina bradyi</i> (CUSHMAN 1915)	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	5	10
<i>Rosalina globularis</i> D'ORBIGNY 1826	0	0	0	2	12	0	0	0	0	0	0	0	0	0	0	5	19
<i>Rosalina macropora</i> (HOFKER 1951)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
<i>Trochammina inflata</i> (MONTAGU 1808)	19	340	0	304	19	90	2	0	2	0	0	0	256	3	4	309	1348
Total number of specimens	91	359	310	307	306	369	317	333	289	280	292	280	333	44	269	309	4544
Total number of species	6	6	7	3	11	5	7	8	8	3	9	3	11	6	18	1	26
Agglutinated %	20.9	94.7	0.0	99.0	6.2	24.4	0.6	0.0	0.7	0.0	0.0	0.0	76.2	6.8	1.5	100.0	29.7
Porcelaneous %	0.0	0.0	1.6	0.0	21.6	0.0	4.1	11.7	17.6	0.0	0.7	1.5	0.0	4.5	12.6	0.0	4.8
Hyaline-Perforate %	79.1	5.3	98.4	1.0	72.2	75.6	95.3	88.3	81.7	100.0	99.3	98.5	23.8	88.6	85.9	0.0	65.6
Ammoniaids %	75.8	3.1	96.8	0.3	50.3	73.4	88.6	85.0	80.6	87.1	86.3	90.4	19.6	86.4	45.4	0.0	57.8
Shannon H	1.2	0.3	0.2	0.1	1.6	0.8	0.5	0.7	0.8	0.4	1.2	0.5	0.7	1.3	2.4	0.0	0.0
Fisher α	1.4	1.0	1.3	0.5	2.2	0.8	1.3	1.5	1.5	0.5	1.8	2.2	0.5	1.9	4.3	0.1	0.1
Berger-Parker max pi	0.5	0.9	1.0	1.0	0.5	0.7	0.9	0.8	0.8	0.9	0.6	0.9	0.8	0.6	0.3	1.0	1.0
Dominance D	0.4	0.9	0.9	1.0	0.3	0.5	0.8	0.7	0.7	0.8	0.4	0.8	0.6	0.4	0.1	1.0	1.0
Number of Individuals / 1 gr	79.0	690.5	469.5	667.5	113.5	1419.3	125.8	52.9	21.5	24.7	26.5	35.9	819.5	7.8	4.5	62.0	62.0

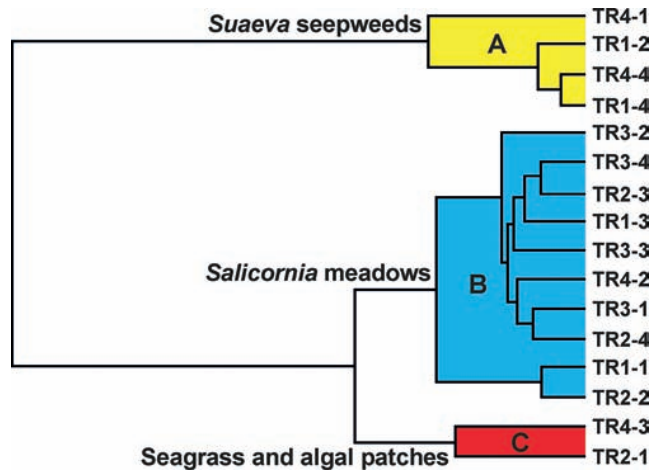
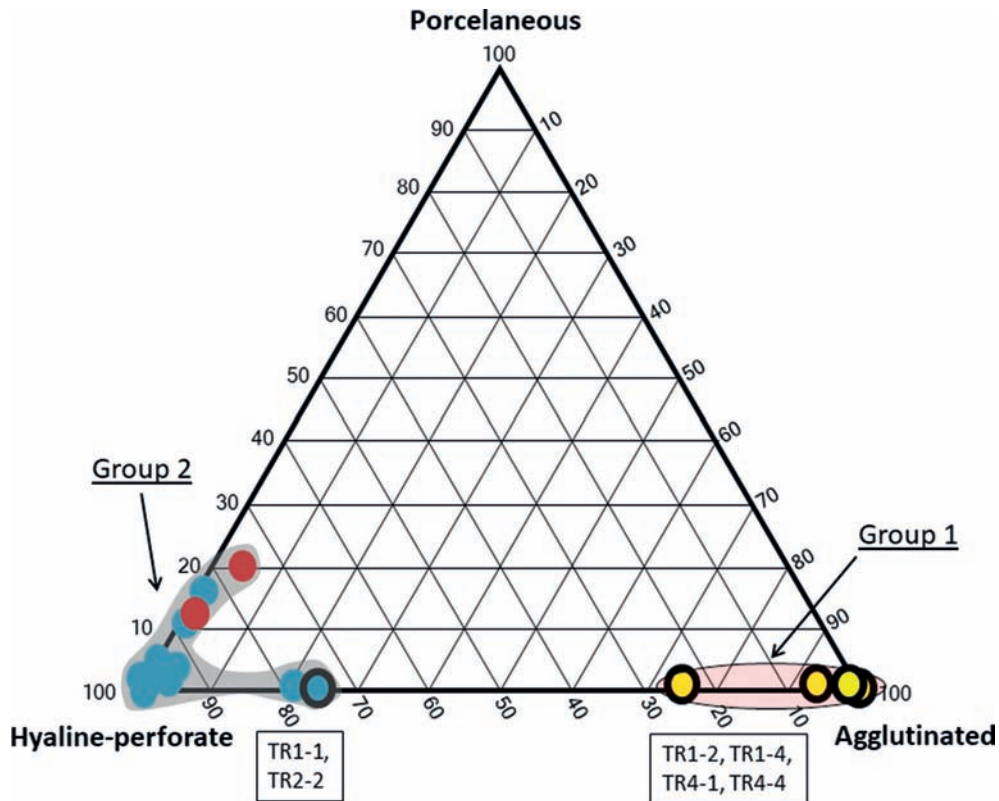


Fig. 3. Q-mode cluster analysis and distribution of cluster groups across Mahrés Lagoon.

WARD et al. 2022). To compute community parameters of species and assemblages (species richness (S)), Fisher α (FISHER et al. 1943), Shannon (H; SHANNON 1984), and Berger-Parker dominance indices (max pi, BERGER & PARKER 1970; see also HAYEK & BUZAS 2013), the software package PAST V2.04 was used (HAMMER et al. 2001; Table 2).

Cluster analysis was performed to obtain additional paleoenvironmental information and included all taxa (Fig. 3). A Q-mode cluster analysis was performed with the Ward's method using the Euclidian similarity index. This technique groups species with similar occurrence records in cluster assemblages and reveals a typology of environmental signatures embedded in a hierarchical dendrogram (THISSEN & LANGER 2017). Ternary diagram analysis was performed to accentuate assemblage differences from different bay habitats, by plotting percent abundances of wall structural types (agglutinated, porcelaneous, hyaline-perforate) present in each sample (Fig. 4; MURRAY 1973, MURRAY 1991). In addition, the foraminiferal number (FN) per gram of treated sediment sample was counted for all the sites (Table 2). Repository: The sample material and picked foraminifera are stored in the GEOGLOB laboratory of the University of Sfax, Tunisia.



**Fig. 4.** Ternary plot of the wall types of polythalamous foraminifera from Mahrés Lagoon. The individual sample stations are colour-coded to show matches with the cluster groups from Fig. 3 (yellow = sites of cluster A, blue = cluster B, red = cluster C). Bold circled sample stations are characterized by high FNs. Note consistently high FN values in the innermost, *Salicornia*-covered, northern parts of the lagoon and low values in the central portion and at the two southernmost middle sites facing the lagoon opening to the Mediterranean Sea (see Table 2).

### 3. Results

#### 3.1. Quantitative analysis

A total of 4544 living benthic foraminifera specimens were picked and identified to species level whenever possible. This resulted in the identification of 26 species belonging to 16 genera. The foraminiferal assemblage comprises 20 hyaline-perforate, 5 porcelaneous, and one agglutinated species (Table 2). Among all living foraminifera counted, hyaline-perforate foraminifera constitute 65.6% of all species, agglutinated species account for 29.7%, and porcelaneous taxa make up 4.8%. The agglutinated foraminifer *Trochammina inflata* dominates at two of the innermost samples sites of transect 1 (TR1-2, TR1-4; Fig. 2) and at the lagoonal periphery towards the entrance channel (TR4-1, TR4-4). These sites are situated at highest tidal elevations and are densely covered by *Sarcocornia*

*fruticosa* meadows. Abundance values at these sites range between 76.2 and 100%. Abundance values of hyaline-perforate species, mainly represented by species of *Ammonia*, were particularly high over most lagoonal sites (72.5–100%), but conspicuously low at highest tidal elevation levels along the periphery of the lagoon near the entrance channel (TR4-1, TR4-4; 0.0–23.8%) and at two sample stations located in the innermost part of the lagoon, respectively (TR1-2, TR1-4; 1.0–5.1%).

Among all foraminifera, porcelaneous miliolid foraminifera are the least abundant within the entire lagoon. At 11 out of 16 sample stations, their percentage is below 1.7 percent, and only at five stations do they reach values between 4.5 and 21.6%. The abundance of porcelaneous species corresponds to only 4.8% of the total population of benthic foraminifera of Mahrés Lagoon. Highest occurrences of miliolids were recorded within the dense *Salicornia* meadows (11.7–21.6%,

TR2-1, TR2-4, TR3-1), and within algal patches near the tidal channel in transect 4 (12.6%; TR4-3). Miliolids are absent or occur only with particularly low numbers in the innermost portion of the lagoon and at the periphery of the lagoon near the entrance channel.

### 3.2. Abundance of living foraminifera

The number of living foraminifera per gram sediment (FN) varies substantially among individual samples and ranges from 4 to 1419 per gram sieved sediment (Table 2). High ( $\geq 470$ ) and moderately high ( $\geq 53$ ) FN's were recorded in the innermost northern parts (TR1-1 – TR2-4), and at the southernmost peripheral sample sites near the southern entrance of Mahrés Lagoon (TR4-1, TR4-4). All these sample sites are densely covered by, or in close proximity to *Salicornia* meadows. Low FN values ( $> 4\text{--}36\text{ g}^{-1}$ ) were found on sand- and mudflats in the sparsely vegetated central portion of lagoon (transect 3, TR3-1 – TR3-4) and around the tidal channels facing the mouth of the lagoon (TR4-2, TR4-3).

### 3.3. Diversity and species richness

The number of benthic foraminifera present in Mahrés Lagoon was counted at all sites and the results are provided in Table 2. Species richness is generally low but varies across the lagoon and ranges between 1 and 18. Low ( $\leq 3$ ) and moderately low species richness values ( $\leq 9$ ) were generally recorded at the peripheral sites (TR1-1, TR4-1, TR4-4, TR3-2) and in the innermost northern part of the lagoon. A monospecific assemblage, consisting of abundant individuals of *Trochammina inflata*, was found at site TR4-4, a site located at the southern peripheral margin near the sandspit. Most sampling sites in the northern part of the lagoon covered by dense *Salicornia* meadows have moderate numbers of species ( $\leq 9$ ). Highest values (11–18) were recorded at sites TR4-3, TR3-4, and TR2-1.

Fisher  $\alpha$  diversity values are generally very low and range between 0.1 and 4.3 in the Mahrés samples (Table 2; Fig. 3). The highest Fisher  $\alpha$  value ( $\alpha = 4.3$ ) was recorded TR4-3, a site located in the algal-covered area near the main tidal channel facing the lagoon opening. The lowest Fisher  $\alpha$  index values were noted at almost all sites in the innermost northern portion of the la-

agoon covered *Salicornia* meadows. The high and low Fisher- $\alpha$  values are consistent with the maximum and minimum species richness values at nearly all sites.

Shannon (H) values vary between 0.0 and 2.4; again, the highest value was observed at site TR4-3 (H = 2.4) and the lowest Shannon value (H = 0.0) was recorded at TR4-4 and 0.1 at site TR1-4. Berger-Parker dominance index values ( $\max pi$ ) range between 0.3 and 1.0. Shannon (H) and dominance index values (D) are in general accordance with species richness values (see Table 2).

### 3.4. Cluster analysis

Cluster analysis (Q-mode) analyzing the similarity, composition and abundance of foraminifera at individual sample stations was performed with percent-abundance data to obtain additional environmental information and included all taxa. Results of the Q-mode analysis revealed the presence of 3 clusters (A–C; Fig. 3). The resulting dendrogram shows that each cluster occupies different areas of Mahrés Lagoon, and that these cluster areas coincide with the major habitats of the lagoon.

Cluster A comprises the sample sites that are located at the extreme margins of the lagoon covered by *Salicornia* meadows (TR1-2, TR1-4, TR4-1, TR4-4). It is these peripheral sample stations that are located at highest tidal elevations, are subject to the greatest salinity fluctuations, and they intermittently go dry during low tides. Cluster A sample sites are strongly dominated by *Trochammina inflata*, the only agglutinated taxon present. The range of species richness and Fisher  $\alpha$  diversity index values in cluster A is between 1 and 6 and 0.1 and 1.0, respectively. Cluster B occurs throughout the innermost northern core of Mahrés Lagoon (TR1-1, TR1-3, TR2-2, TR2-3, TR2-4, TR3-1, TR3-2, TR3-3, TR3-4, TR4-2) and is mainly dominated by species of the hyaline-perforate genus *Ammonia*. Species richness and Fisher  $\alpha$  diversity index values in cluster B range between 3 and 11 and 0.5 and 2.2, respectively. Cluster C comprises a sample site situated in the southernmost central region of the lagoon (TR4-3) and another site located at the northwesternmost inner margin (TR2-1). Cluster C is dominated by species of *Ammonia* and also contains some miliolids. Agglutinated foraminifera at these sites are rare. The values of the Fisher  $\alpha$  diversity index and the species index of this cluster range from  $\alpha = 2.2$  to 4.3 and from 11 to 18 respectively.

### 3.5. Ternary diagrams

Ternary plot data were calculated on the basis of relative percent abundances of the three wall types in polythalamous foraminifera (hyaline-perforate, porcelaneous, and agglutinated) and were conducted to validate the groups provided by cluster analysis and by high FNs ( $\geq 470$ ). To illustrate matching grouping characteristics, the diagram was marked with color-coded signatures for the sites of the respective clusters. Sampling points with particularly high numbers of individuals per gram of sediment were additionally circled in bold. The diagram shows a division into two groups (groups 1 and 2) and an overall dominance of agglutinated (group 1) and hyaline-perforate taxa (group 2). It also reveals that the samples from two samples from group 2 contained slightly higher numbers of porcelaneous taxa than the other samples of group 2. The relative number of agglutinated taxa was substantially higher in samples belonging to group 1, a suite of samples that fully matches cluster 1 from the Q-mode analysis. This group includes sample stations located at highest tidal elevations at the extreme peripheral margins where the sites are covered by *Salicornia* meadows (Fig. 4).

## 4. Discussion

The Gulf of Gabes and its associated coastal wetlands are considered highly productive areas, contributing about 40 percent of Tunisia's total fish production (DGPA 2015). Numerous recent studies on modern shallow-water benthic foraminifera have provided essential contributions and information on the species richness, habitat structures, and evolution coastal environments along the coast of Tunisia (BLANC-VERNET et al. 1979; BEN HAMAD et al. 2018; HAMAD et al. 2019; ZAÏBI et al. 2011; ZAÏBI et al. 2016; BEN KHALIFA et al. 2019; DAMAK et al. 2019; KAMOUN et al. 2019; KAMOUN et al. 2020; KAMOUN et al. 2022a; KAMOUN et al. 2022b). This work has contributed to a better understanding of the evolution of the Tunisian coast, a coastal environment that has undergone significant changes over the last 6000 years due to tectonic, climatic, and anthropogenic forcing (JEDOUÏ et al. 1998; MORHANGE & PIRAZZOLI 2005; MARQUER et al. 2008; ANZIDEI et al. 2011; ZAÏBI et al. 2016; BÉJAOUÏ et al. 2019). Our study of living benthic foraminifera from the relatively small lagoon of Mahrés provides further

insights into the structuring of foraminiferal faunas, the distribution and abundance of indicator species, and their dependence on habitats. Analysis of the numerical abundance, species richness, and dominance of individual taxa revealed comparatively low-diverse assemblages of living benthic foraminifera. In general, the Mahrés Lagoon assemblages can be divided into two groups: (1) The first group is located at the margin and at the extreme distal end of the lagoon and is characterized by a high concentration of foraminifera and assemblages with low diversity on sandy and muddy substrates covered by *Salicornia* meadows. This group is strongly dominated by the agglutinated foraminifer *Trochammina inflata*. (2) The second group is found in the inner central parts of the lagoon and at sample stations oriented toward the mouth of the lagoon and is dominated by species of *Ammonia*. The foraminiferal faunas within this group contain much fewer living specimens but are relatively more diverse. They can be found in deeper tidal channels, on sandy substrates, and in partially vegetated areas.

Low species richness and diversity indices (1–18 species, Fisher  $\alpha = 0.1$  and 4.3, Shannon H values = 0.0 and 2.4) typically define foraminiferal faunas at individual lagoon sites with high dominance values (max  $\pi = 0.2$  and 1.0). The sample points at the peripheral area and the distal lagoon sites exhibit the lowest diversity values. These stations, positioned at the highest tidal range, are subjected to significant fluctuations in salinity and temperature. Lagoon areas that do not experience extreme fluctuations or remain submerged during low tides exhibit marginally higher diversity, albeit still low.

*Trochammina* and other agglutinated faunas are known to dominate areas with extreme tidal conditions, as evidenced by numerous studies (CULVER 1990; PATTERSON 1990; HAYWARD & TRIGGS 1994; HORTON 1999; WOODROFFE et al. 2005; LANGER & LIPPS 2006; LANGER et al. 2016; FIORINI et al. 2019; FAJEMILA et al. 2020; FAJEMILA et al. 2022; SARIASLAN & LANGER 2021). These findings have proven invaluable in the interpretation of past environments.

While the peripheral, higher areas of the lagoon are predominantly inhabited by *Trochammina*, the central inner areas and those towards the opening of the lagoon are dominated by *Ammonia*. These areas are also subject to the effects of the tides, although less clearly. In the tidal channels, the inflowing seawater is permanently retained, but the associated habitats are also subject to evaporation and the associated temperature and salinity fluctuations. Some of these areas



(sandflats) actually dry out completely at extremely low tide, and thus differ from the *Salicornia*-covered lagoon areas that retain a residual moisture around their dense root systems. Like *Trochammina*, various species of *Ammonia* cope well with such stress conditions (LANGER 1993; KOUKOUSIOURA et al. 2011; KOUKOUSIOURA et al. 2012; HAYWARD et al. 2021 and references therein).

However, during the studies of the living fauna of Mahrés Lagoon, it is noticeable that the distributional range of *Trochammina inflata* remains restricted to the very narrowly defined area of the higher peripheral areas of the lagoon and that they are either not transported at all or only in very small proportions from their habitats. The restricted distribution of *Trochammina* is likely influenced by the abundant and extensive colonization of dense *Salicornia* meadows and the low tidal range in the lagoon. Spatial dispersal and transport out-of-habitat are likely impeded by both factors. In the Mahrés Lagoon, *Trochammina* retains its distribution and remains within its restricted habitat, allowing the fauna to document significant ecological information applicable to paleoecological and environmental studies.

A lateral and out-of-habitat distribution is more probable for the tidal channels and sample stations located at the lagoon entrance. This inference is supported by the increased diversity, alterations in the percentages of wall structural groups, and the presence of characteristic marine species (e.g. *Lobatula lobatula*, *Nonion* sp. 1, and *Peneroplis pertusus*). However, the dominant presence of the genus *Ammonia* in the foraminiferal fauna signifies typical intertidal and shallow water conditions.

The introduction of fully marine foraminifera species is presumably mainly via the wide opening of the lagoon in the south. As the wetlands of Tunisia are frequently visited by migratory birds (HAMZA & SELMI 2015), avian-mediated transport via the feet of birds cannot be excluded (LIPPS 1982; CULVER & LIPPS 2003).

Apart from single individual of *Peneroplis pertusus*, no other symbiont-bearing foraminifera were found in the material investigated. Specimens of the genus *Amphistegina*, a taxon of large foraminifera that quickly dispersed from the eastern to the central Mediterranean after the opening of the Suez Canal (LANGER & HOTTINGER 2000; LANGER 2008; LANGER et al. 2012; LANGER et al. 2013; LANGER & MOUANGA 2016; GUASTELLA et al. 2019; GUASTELLA et al. 2021; GUASTELLA et al. 2023; RAPOSO et al. 2023), were also

absent. Yet, this species in particular spread deep into the Gulf of Gabes at a very early stage and subsequently established large and permanent populations throughout the region (BLANC-VERNET et al. 1979; EL KATEB et al. 2018; STULPINAITE et al. 2020). It is likely that the extreme conditions of the lagoon, combined with the absence of extensive seagrass beds or algal turfs, successfully prevented this species from invading the lagoon. At the same time, this possibly indicates that the sandspit effectively prevents the invasion of fully marine species into the lagoon.

## 5. Conclusions

Analysis of the distribution of living foraminifera in the lagoon of Mahrés (Gulf of Gabes, Tunisia) shows a clear spatial differentiation of the faunas depending on habitat and tides. Dense *Salicornia* meadows in the highest intertidal zone contain predominantly agglutinated foraminifera of *Trochammina*. In the central areas of the lagoon and at the sampling stations towards the mouth of the lagoon, mainly hyaline-perforated species of the genus *Ammonia* are found. The spatial separation is reflected in multiple lines of independent evidence including cluster, species richness, diversity, and abundance analyses. The lateral and vertical separation of faunas correlates with the distribution of habitats, the density of salt marsh vegetation and the exposure to the vertical tidal gradient. Vertical zonation is fixed to narrowly defined boundary areas, where even small differences in elevation, as little as a few centimeters can result in remarkable differences in foraminiferal composition. The clear faunal differences seen in these areas suggest that no faunal exchange, out-of-habitat transport or large-scale dispersal occurs across these boundaries. Therefore, the foraminiferal assemblages found in these areas are likely to be deposited in situ and preserve vital information for reconstructing past environmental conditions. The lateral and vertical partitioning of assemblages is here attributed primarily to tidal elevation, a convenient metric that integrates a number of factors. Future research would therefore benefit from including data on the frequency and duration of tidal inundation, soil moisture, pore water salinity, soil redox potential, sulfide and organic matter concentrations. The distribution and abundance patterns, the presence of indicator taxa, along with the evidence of exceptionally low transport rates across habitats, provide novel insights into the reconstruction

of coastal fossil habitats. This holds particular significance for the rapidly changing Tunisian coast, impacted by climate, sea-level changes, and tectonic activity.

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# Declaration of Authorship

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