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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 paleoenvironmental 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 & Coppejahns, 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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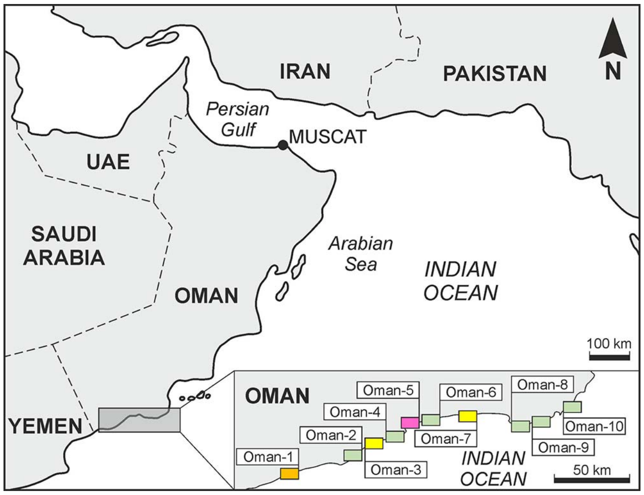

FIGURE 1. Sampling area along the southern coast of Oman with sampling sites enclosed in a rectangle. The colour coding corresponds to the four habitat types outlined in the text (ocher = harbour, yellow = sand bay, green = phytal-associated habitat, and purple = mangrove-lined bay inlet).

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 semidiurnal with a daily range averaging 1.5–2 m, and a maximum range of ~3 m (Al-Hatrushi 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 (Mughsail 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 uninerуis* 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-µm 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 α, Shannon's H', Simpson's Index of Diversity (SID); Fisher et al., 1943; Murray, 1973). Fisher α 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 α 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	Mughsail 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 = 261–999 individuals), whereas only smaller amounts were available from sandy bays (N = 205–347), 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

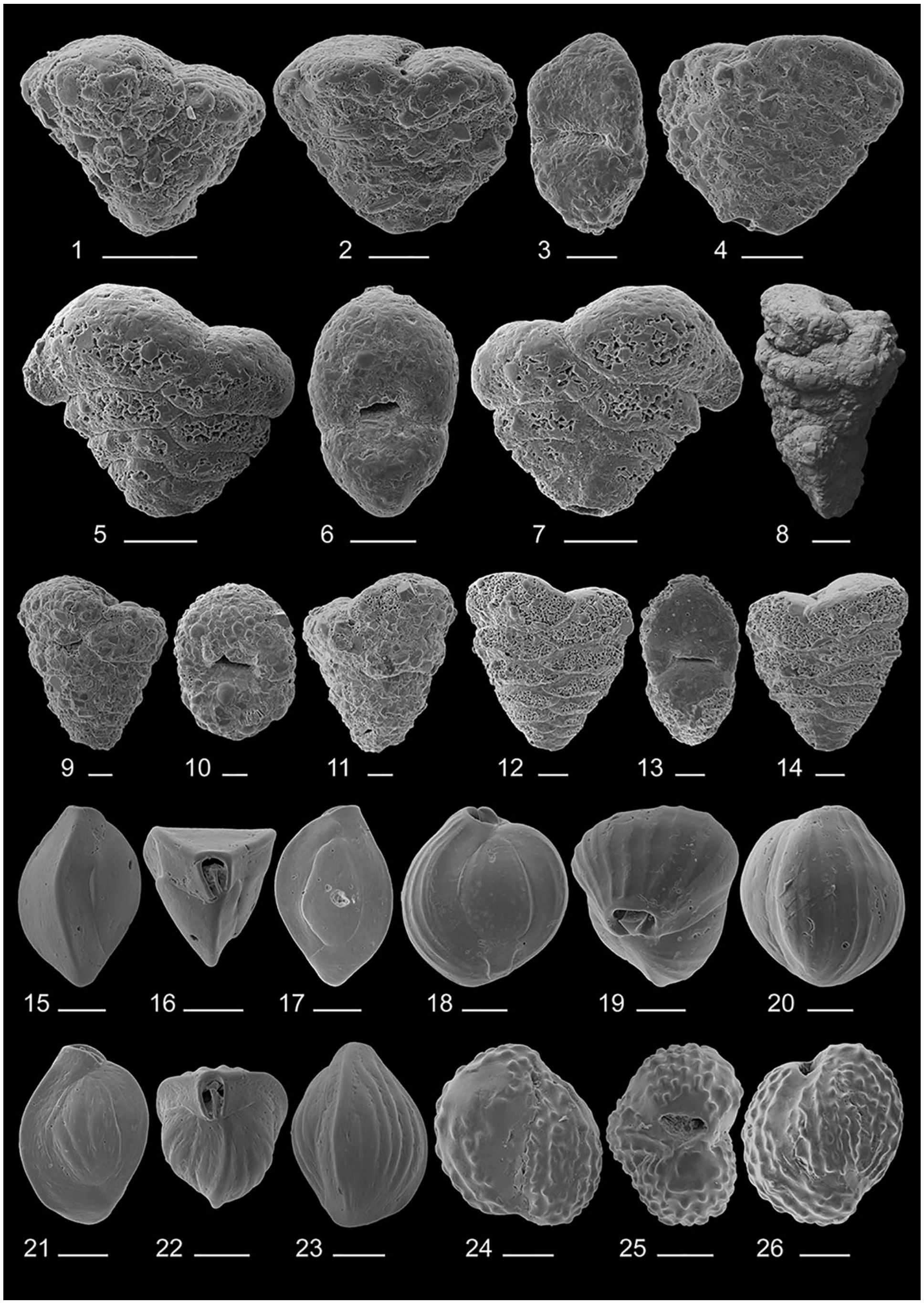

FIGURE 3. Benthic foraminifera from the southern coast of Oman. **1–4** *Textularia pseudosolita* Zheng, 1988. **5–7** *Textularia* sp. 2. **8** *Pseudogaudryina* sp. **9–11** *Textularia agglutinans* Seguenza, 1862. **12–14** *Textularia* sp. 1. **15–17** *Triloculina affinis* d'Orbigny, 1852. **18–20**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

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 α index values between 3.5 and 6.8 (Fig. 9). Fisher α 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

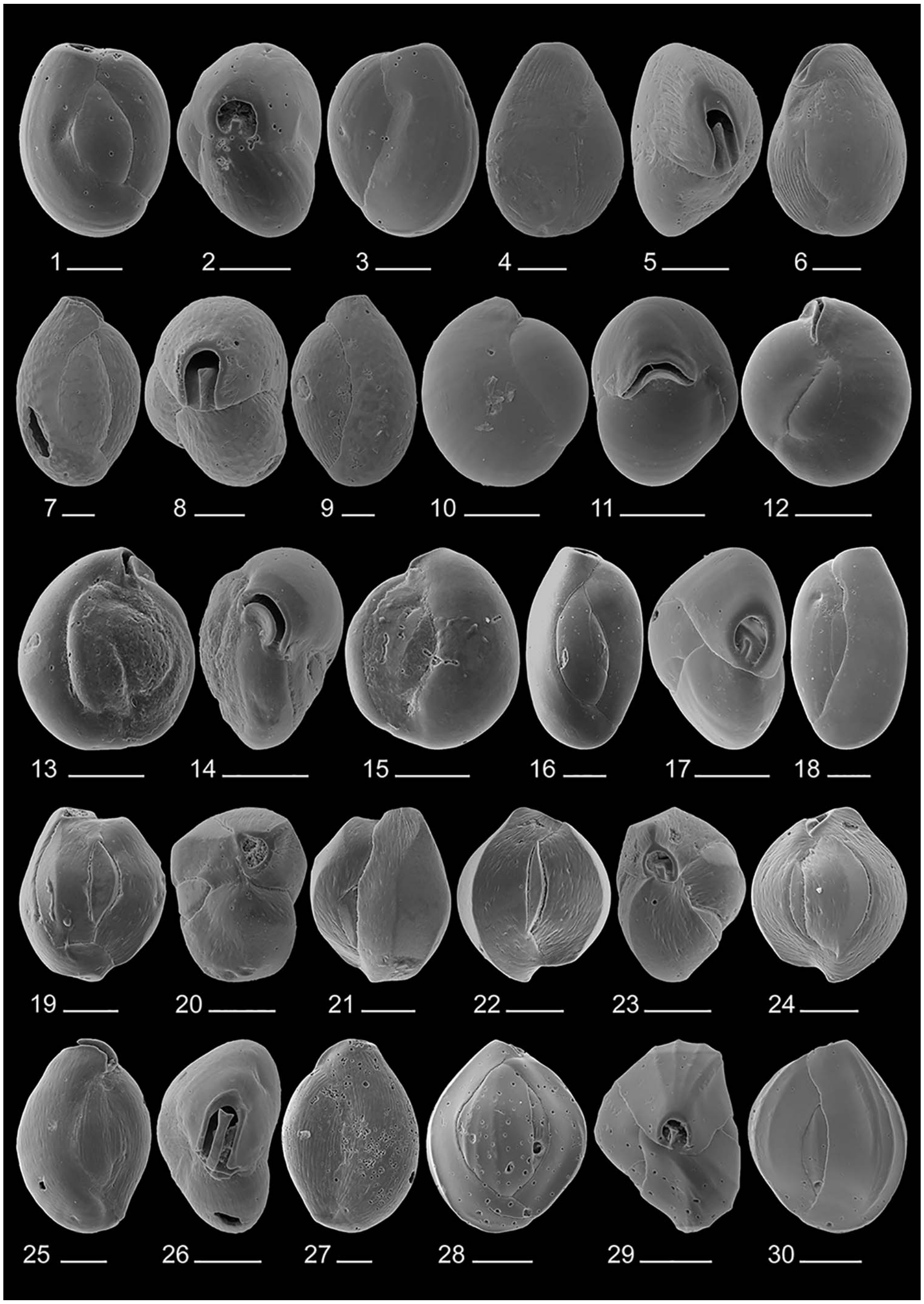

FIGURE 4. Benthic foraminifera from the southern coast of Oman. **1–3** *Pseudotriloculina* sp. 1. **4–6** *Pseudotriloculina* sp. 2. **7–9** *Pseudotriloculina* sp. 3. **10–12** *Milionella circularis* (Bornemann, 1855). **13–15** *Sigmamiliolinella australis* (Parr, 1932). **16–18** *Quinqueloculina 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 μm.

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 α 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).

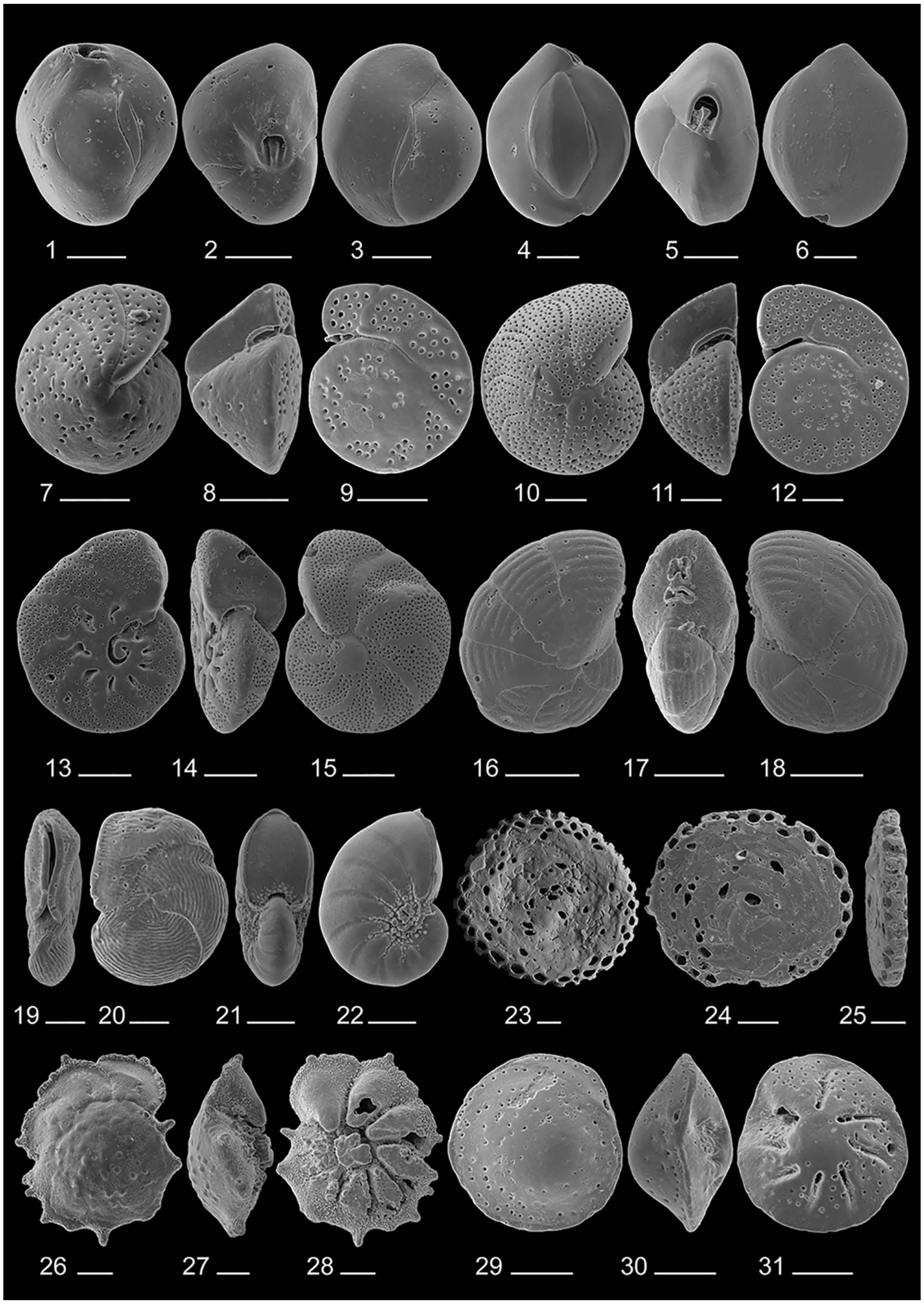

FIGURE 5. Benthic foraminifera from the southern coast of Oman. **1–3** *Quinqueloculina* sp. 3. **4–6** *Quinqueloculina* sp. 4. **7–9** *Cibicides refulgens* Montfort, 1808. **10–12** *Cibicides* sp. **13–15** *Hanzawaia* cf. *H. nipponica* Asano, 1944. **16–18** *Peneroplis pertusus* (Forsskål in 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** *Lamellodiscorbis* sp. 1. Scale bar = 100 μm.

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*

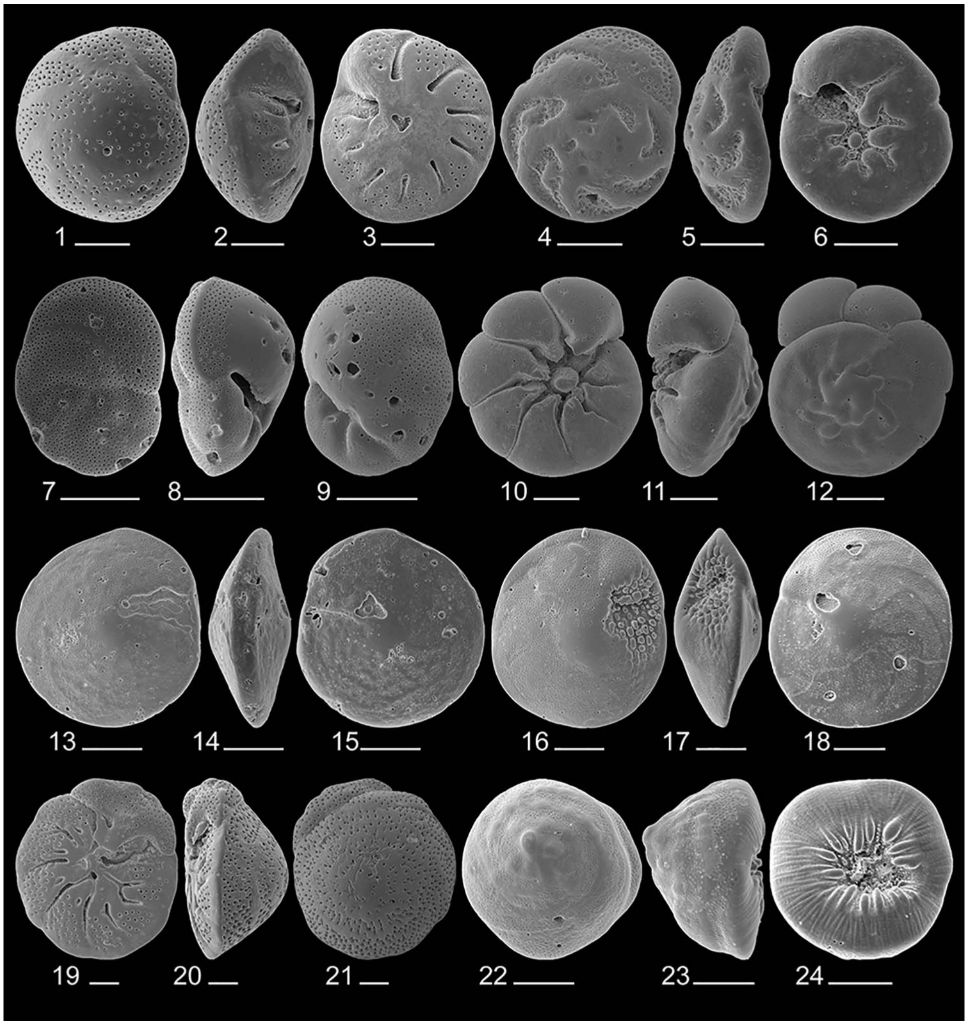

FIGURE 6. Benthic foraminifera from the southern coast of Oman. **1–3** *Pararotalia calcariformata* McCulloch, 1977. **4–6** *Rosalina* aff. *R. orientalis* (Cushman, 1925). **7–8** *Baggina* sp. **10–12** *Ammonia amurensis* Shchedrina, Mayer, 1975. **13–15** *Amphistegina radiata* (Fichtel, Moll,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

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 α 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

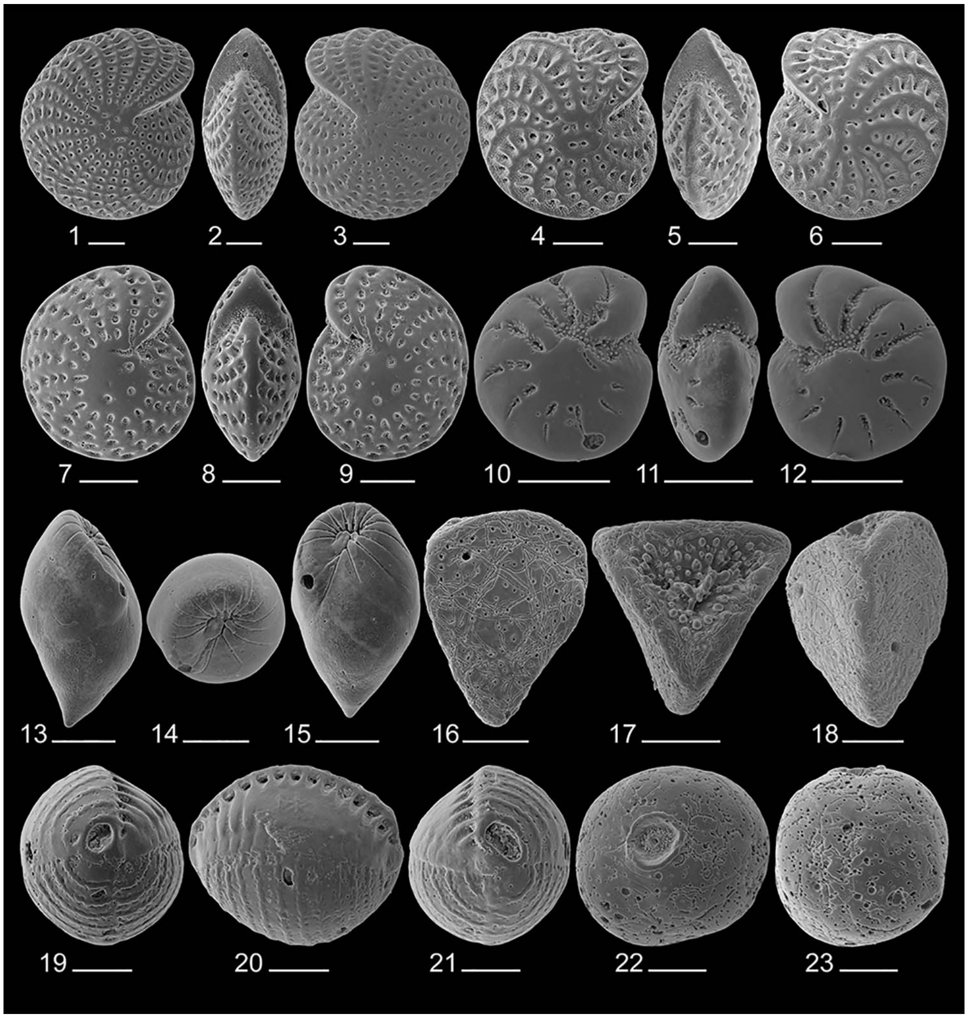

FIGURE 7. Benthic foraminifera from the southern coast of Oman. **1–3** *Elphidium* cf. *craticulatum* (Fichtel & Moll, 1798). **4–6** *Elphidium* cf. *limbatum* (Chapman, 1907). **7–9** *Elphidium* sp. 1. **10–12** *Elphidium* sp. 2. **13–15** *Elongobula milletti* (Cushman, 1933). **16–18** *Fijiella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

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

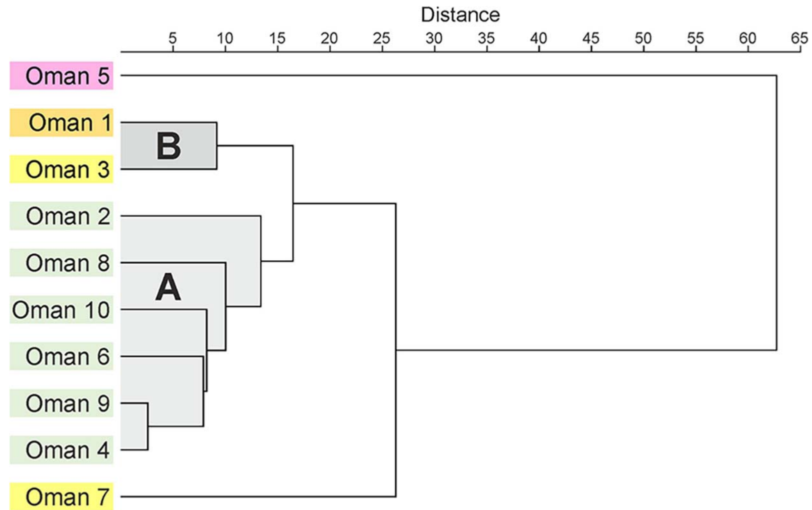

FIGURE 8. Cluster dendrogram showing Cluster A and B flanked by two outliers. The colour coding corresponds to the four habitat types outlined in the text and caption of Figure 1.

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).

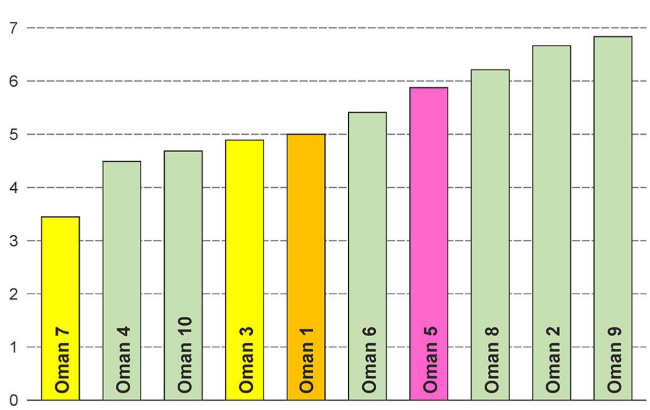

FIGURE 9. Fisher α values in shallow-water habitats along the coast of Oman. The colour coding corresponds to the four habitat types outlined in the text and caption of Figure 1.

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 α 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
*Ammonia amurensis**	0	3	17	44	0	31	23	27	75	4
Amphistegina lessonii	15	50	37	55	5	35	10	42	78	26
Amphistegina radiata	53	47	51	161	0	91	4	55	311	79
Baggina sp.	0	0	0	0	1	0	0	0	0	0
Borelis schlumbergeri	19	4	10	8	0	9	0	4	3	5
Cibicides refulgens	3	3	0	7	4	7	1	5	36	0
Cibicides sp.	17	14	7	33	12	17	10	14	61	5
*Elongobula milletti**	2	1	0	2	0	2	0	0	3	0
Elphidium cf. *craticulatum*	1	0	0	0	0	0	0	0	0	0
Elphidium cf. *limbatum*	185	8	83	40	8	51	10	37	116	13
Elphidium sp. 1	1	1	0	8	0	27	3	10	18	5
Elphidium sp. 2	0	0	0	0	0	0	8	0	0	0
Fijiella simplex	0	1	0	0	0	0	0	0	0	0
Glabratellina kermadecensis	0	6	3	10	8	2	0	2	16	4
Hanzawaia cf. *H. nipponica*	0	0	0	0	4	0	0	3	0	0
Lamellodiscorbis sp. 1	7	7	1	19	4	13	0	9	12	10
Lamellodiscorbis sp. 2	10	0	0	0	0	0	0	2	8	0
Milionella circularis	0	0	0	0	1	0	0	0	0	0
Nonion sp.*	4	3	4	1	4	6	10	3	6	9
Pararotalia calcariformata	5	18	20	45	2	49	209	72	53	34
Peneroplis pertusus	4	8	0	5	0	18	4	5	14	0
Pseudogaudryina sp. 1	0	0	0	0	3	0	0	0	1	0
Pseudotriloculina echinata	0	0	1	0	0	1	0	3	4	0
Pseudotriloculina sp. 1	0	0	0	0	0	0	0	1	1	1
Pseudotriloculina sp. 2	0	0	1	0	0	0	0	0	0	0
Pseudotriloculina sp. 3	0	0	1	0	0	0	0	0	0	0
Quinqueloculina aff. *multimarginata* type 1	4	4	0	0	0	1	0	0	34	0
Quinqueloculina aff. *multimarginata* type 2	50	6	30	20	21	30	28	29	45	34
Quinqueloculina seminula	4	8	5	8	4	14	20	6	17	8
Quinqueloculina sp. 1	0	0	0	0	0	0	0	0	0	1
Quinqueloculina sp. 2	2	1	1	0	0	7	0	0	6	2
Quinqueloculina sp. 3	0	0	3	0	0	8	1	0	17	2
Quinqueloculina sp. 4	0	0	0	0	0	0	0	0	14	0
Rosalina aff. *R. orientalis*	0	2	0	1	5	2	0	1	4	0
Sigmamiliolinella australis	0	7	6	5	32	24	1	2	23	17
Siphoninoides laevigatus	1	0	0	0	0	0	0	0	0	0
Sorites orbiculus	2	1	8	2	3	9	0	3	7	2
Textularia agglutinans	0	0	3	2	1	0	5	5	2	0
Textularia pseudosolita	0	0	0	0	0	0	0	0	6	0
Textularia sp. 1	2	2	0	0	0	4	0	0	4	0
Textularia sp. 2	0	0	0	0	0	0	0	0	1	0
Triloculina affinis	0	0	0	1	0	0	0	2	1	0
Triloculina fichteliana	0	0	0	0	0	0	0	0	1	0
Triloculina sp. 1	0	0	0	0	0	0	0	1	1	0
Vertebratlina striata	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
Amphistegina, %	17,3	47,3	30,1	45,3	4,1	27,5	4,0	28,3	38,9	40,2
Pararotalia, %	1,3	8,8	6,8	9,4	1,6	10,7	60,2	21,0	5,3	13,0
Cibicides, %	5,1	8,3	2,4	8,4	13,1	5,2	3,2	5,5	9,7	1,9
Elphidium, %	47,7	4,4	28,4	10,1	6,6	17,0	6,1	13,7	13,4	6,9
Ammonia, %	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 α 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 α = 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 α = 3.5–4.9). Moderate species richness and Fisher α values were recorded from the semi-enclosed harbour and muddy mangrove bay habitats (18–22 species, Fisher α = 5.0–5.8; Table 2). Species richness and Fisher α 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 α 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

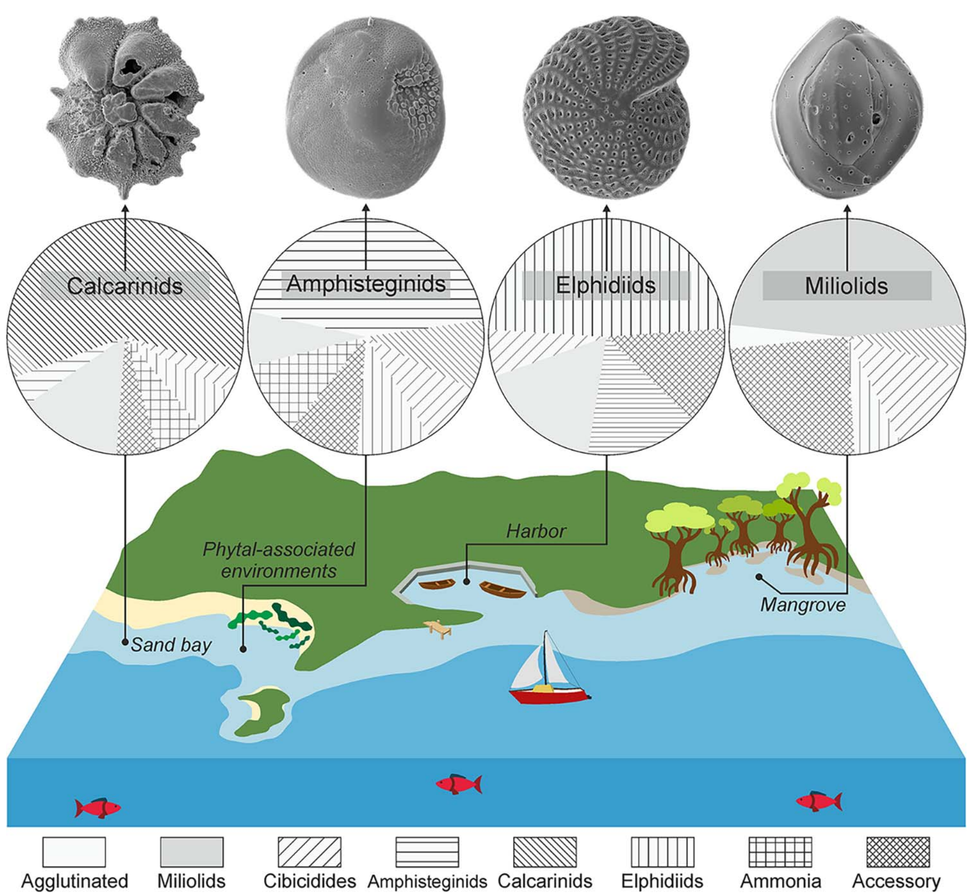

FIGURE 10. Schematic illustration of shallow-water habitats off the coast of Oman with circle diagrams showing average percentage values of individual groups of shallow-water benthic foraminifera.

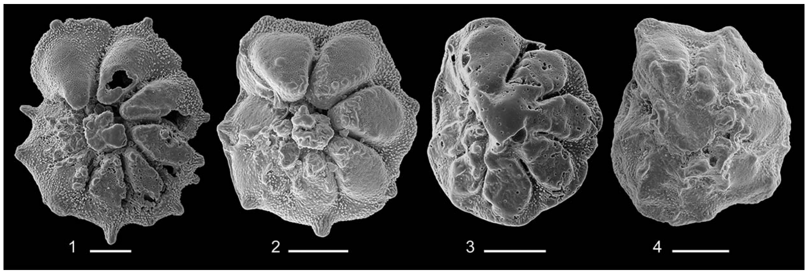

FIGURE 11. Preservation stages and categorization of foraminiferal tests: 1) well preserved, 2) moderately-well preserved, 3) abraded and broken, 4) fully damaged, broken and abraded.

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 (cibicidiids; 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 (allogromiids, saccaminids, hormosinaceans, bathysiphonids, hippocrepinaceans; 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

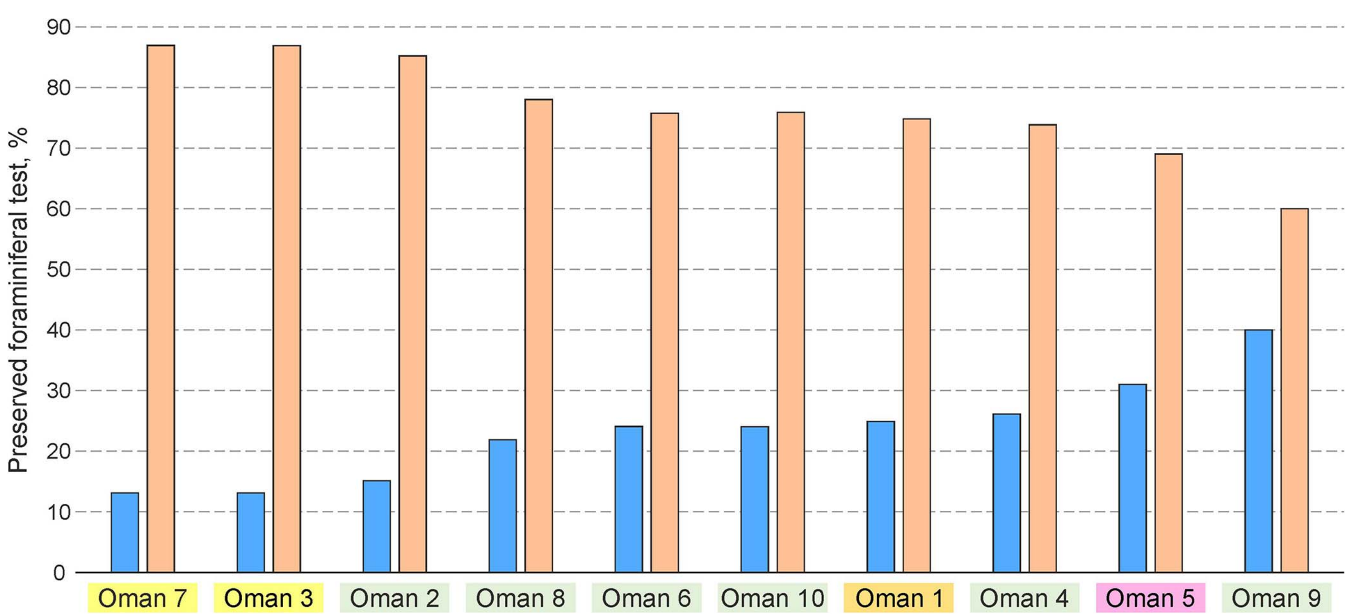

FIGURE 12. Percent abundance bar diagram showing the relation of well and moderately-well (blue) preserved versus abraded/broken and fully damaged (brown) foraminiferal tests in shallow-water habitats along the southern coast of Oman. Coloured sample site numbers refer to sand (yellow), harbour (brown), 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 α ≤4.9), high dominance (*Pararotalia calcariformata* – 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 α ≤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 α ≤6.8), but generally higher than in sand bays. Diverse and heterogenous 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 α ≤5.8), but higher than in sand bays. Abundant smaller miliolids (~47%), moderate amounts of amoniiid, cibicidiid (13.1%), and elphidiid (6.5%) taxa. Agglutinated foraminifera contribute ~3% to the total assemblage, calcarinid and other LBF with low amounts (≤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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