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Larger Symbiont-bearing Benthic Foraminiferal Assemblages in Shelf Sediments of Andaman-Nicobar Archipelago

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Authors' contributions

This work was carried out in collaboration among all authors. Author MM did the sample collection, sample analysis, identification of foraminifera, data analyses and manuscript. Authors RB and PMM did the research plan, sample collection and manuscript preparation. Author JRP did the statistical analysis. Authors AR, CJ and PJR did the sample collection, isolation of foraminifera, sediment sample processes and review of literature. Authors ADS and ASM did the scanning electron microscopic photograph and discussions. All authors read and approved the final manuscript.

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Original Research Article

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ABSTRACT

The endosymbionts bearing larger benthic foraminifera (LBF) is among the important faunal group of coral reef ecosystems. They are extensively studied globally to understand coral reefs' health prospects. This paper aimed to document the number of species belongs LBF that existed in the shelf sediments of Andaman and Nicobar Islands (ANI). To know the species composition between shallow (~10 m) to deeper transect (~50 m). In addition, the distribution and diversity of LBF from present study compared with earlier reported data from other geographical locations of the Indian Ocean. A total of 26 LBF species were identified in 26 sediment samples from 13 locations, which was the highest richness of LBF among the studies reported earlier from 35° E to 93° E (west to east) of Indian Ocean. However, other than ANI the Gulf of Mannar and Red Sea showed more species richness (16 species from each) and lowest richness was found at Chagos Archipelago and Arabian Gulf (4 species each). Two assemblages found in the study corresponded with the two targeted- sample transects of ~10 and ~50 m those are the assemblage I *Calcarina spenglerii* group and the assemblage II *Calcrarina mayori* group from the depth transect respectively.

Keywords: Species richness; coral reef; algal symbionts; mesophotic environments.

1. INTRODUCTION

Coral reefs are biodiverse and economically valuable marine ecosystems [1,2]. Shallow-water and mesophotic coral reefs occur within subtropical and tropical regions (~30°S–30°N), living on the seafloor within the photic zone [3,4]. Reef ecosystems are often called rain forests of the oceans based on their immense biodiversity; they can harbor 32 out of 34 described phyla that occur in marine habitats [5]. Yet coral reefs are well developed and extend to the greatest depths in very clear, nutrient-poor (oligotrophic) waters where sufficient light for photosynthesis can reach depths in excess of 100 m [6-9].

Benthic foraminifera that host algal endosymbionts and grow to larger sizes than most other benthic protozoans are often informally referred to as larger benthic foraminifera (LBF). The LBF are important calcifiers, contributing substantially to reef sediments [10-13]. The LBF can be long lived compared to most other shallow-dwelling foraminifera, growing slowly over the course of months to a year or more to reach diameters usually in excess of 1 mm and commonly >1 cm. Because they host symbiotic algae, they generally require predictably clear water, especially those living at depths >20 m [14,15]. With suitable light intensities and limited availability of dissolved inorganic nutrients (e.g., ammonia, nitrite, nitrate and phosphate), the photosynthetic algal symbionts can produce photosynthate (i.e., simple sugars and lipids) well in excess of the inorganic nutrients that are available for algal growth. Instead, the algae excrete their excess photosynthate to the host, providing the host with energy for calcification, metabolism, and reproduction, while feeding by the host provides essential nutrients for growth of the host and the algae [16,17].

Since the late Paleozoic, LBF have been common components of carbonate biofacies, especially throughout the Cenozoic [18,19]. The LBF are widely used as stratigraphic tools [20-22], as well as paleoenvironmental indicators [23,24]. The latter interpretations have been based in part upon ecological studies of modern LBF [25-28] that have revealed that specific assemblages and morphologies can be used to interpret paleodepth and other paleoenvironmental factors [23,24].

The definition of LBF has varied substantially through time and across studies. Originally, the term referred to fossil taxa that were large in size and sufficiently complex in internal morphologies that they required examination in oriented thin sections to identify them, and that were useful in biostratigraphic research (Drooger [29], and references therein). Their likely dependence on algal endosymbionts when alive was not originally recognized. Moreover, this definition did not include the Amphisteginidae nor the

Peneroplidae, despite their common occurrence in Cenozoic fossil LBF assemblages [23, 30].

In the 1970s and 1980s, researchers began to recognize that many of the largest foraminifera, which live in reef and carbonate-shelf environments where they are important contributors to sediments, host algal endosymbionts [31,32]. This understanding greatly enhanced the utility of such foraminifera as paleoenvironmental indicators. Recognition that *Amphistegina* spp. host algal endosymbionts, are important sediment producers, and are amenable to study in culture, resulted in some researchers including them in the informal LBF functional group. More recently, with greater emphasis on algal symbiosis than on size or carbonate production, even peneroplids that are quite small (e.g., *Monalysidium* spp.) are being considered LBF by some authors [33].

As currently used, extant LBF include members of the orders Miliolida and Rotaliida, with several families that host algal symbionts represented in each order. Among the Miliolida, there are families that host diatoms (Alveolinidae), dinoflagellates (Soritidae), chlorophytes (Soritidae, Peneroplidae), and rhodophytes (Peneroplidae) [31,32]. Among the Rotaliida, diatoms are the predominant algal-symbiont group.

Species recognized as LBF can be found on oceanic banks, continental margins and island-shelf margins throughout most of the warm-temperate, subtropical and tropical latitudes where sufficient light for photosynthesis reaches the sea floor to depths of at least several meters [15,34,35]. However, taxonomic comparisons of LBF assemblages have been influenced by several trends. As noted above, what taxa have been categorized as LBF has varied widely through time. Moreover, whether the taxa have been identified conservatively by taxonomic “lumpers” or separated more finely by “splitters” has influenced the number of species reported in any specific study. Finally, technology has played a key role, first with improved optics and scanning electron microscopy and, more recently, such applications as micro-CT scanning [36,37] and molecular genetics [38].

A global total of 76 species of extant LBF has been recognized in very recent publications Förderer et al. [33] estimated a total of 68 species for Indo-Pacific Ocean including Red Sea and Persian Gulf, to which [39] added three newly described *Marginopora* species. At least five species are restricted to the Atlantic Ocean [40]. The 76 species are recognized as belonging to six families: Alveolinidae, Peneroplidae, Soritidae, Amphisteginidae, Calcarinidae and Nummulitidae (though not including the Asterigerinidae, which host diatom symbionts and are comparable in size to, or larger than, Peneroplidae). Distributions of modern LBF in various regions have been reported by numerous authors, which [33] utilized to model LBF diversity trends, concluding that the highest LBF diversity (54 species) can be found in the Philippines, which is the centre of the Coral Triangle and centre of coral diversity [41].

The Andaman-Nicobar Archipelago also has been identified as a hotspot of biodiversity that deserves attention and preservation [42]. We found relatively few previous studies that reported modern LBF taxa in this region Yuvaraja and Ramanujam [43,44]. reported eight species from the South Andaman and Neil Island, while Muruganantham et al. [45] and Tripati [46] reported 16 species each from the South Andaman and Great Nicobar Islands respectively. Moreover, these studies were not based upon systematic sample collection and did not reveal the ecological and environmental significance of the LBF reported. The goal of our study was to sample and assess LBF assemblages along a north-south traverse from the Northern Andaman to Car Nicobar Island, to assess species richness of taxa we considered to be LBF, and to compare assemblage occurrences between ~10 and ~50 m depth transects. This study also conducted a comprehensive comparison of the distribution and diversity of LBF from the existing literature and within the Indian Ocean, focusing on the western region from 93°E to 35°E.

1.1 Study Area

The Andaman-Nicobar Archipelago in the Northern Indian Ocean (6−14° N and 92−93° E) represents the emergent portion of the Arakan Yoma Ridge (Fig. 1). This ridge is the northern extent of the island arc that is bordered on the west by the Sumatra-Andaman subduction zone [47]. To the west of the Archipelago is the Bay of Bengal, to the east is the younger Andaman Sea. The unique biodiversity and endemism of the Archipelago ranges from indigenous human tribes and unique terrestrial biotas to mega diversity in the marine flora and fauna. Coral reefs include fringing reefs on the eastern side and barrier-reef development to the west.

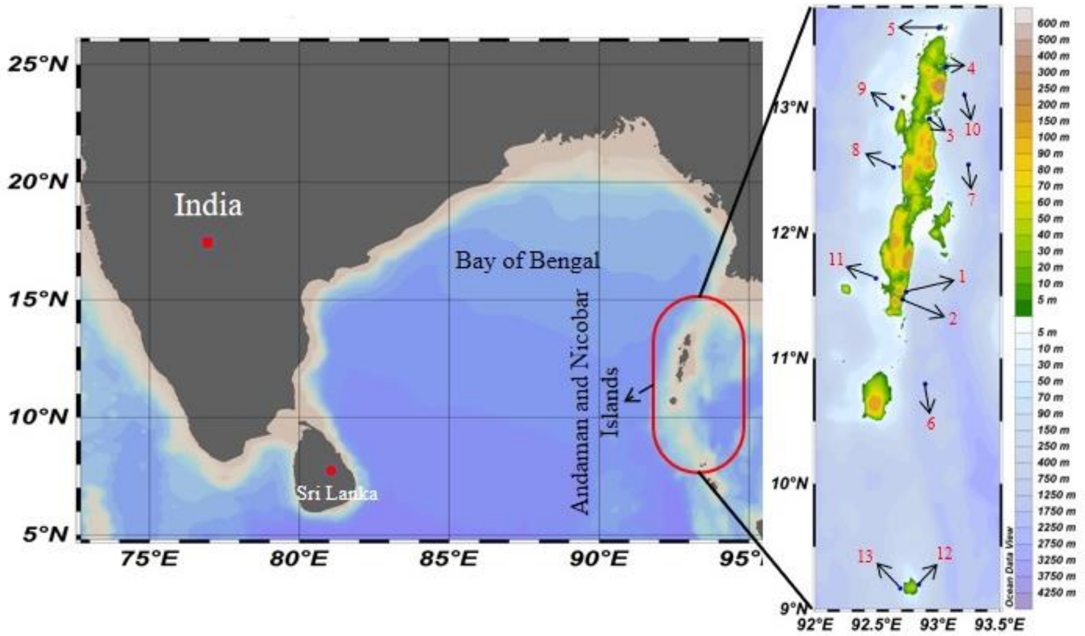

Fig. 1. Map of the Andaman and Nicobar Islands with sampling locations

The Andaman group of islands are separated from the Nicobar Islands at 10° N by a channel (known as the middle channel) that is 150 km wide and 732 m deep. As a result, the terrestrial fauna and flora are represented by separate provinces: The Indo-Burma Biodiversity Hotspot is recognized in the Andaman Islands, while the Sundaland Hotspot biota are found in the Nicobar Islands [48]. Marine biodiversity has close affinity with the Indo-Malayan and Indo-Chinese regions [49]. Two additional passages connect the Andaman Sea with the Bay of Bengal and the equatorial Indian Ocean, the northern channel at 15° N, and the southern channel at 06° N. The Andaman Sea is also connected with the South China Sea through the Malacca Strait [47,50].

The archipelago is influenced by both the southwest and northeast Indian monsoons; average rainfall is ~3000 mm/year. During the winter, surface currents in the Andaman Sea flow to the southwest, driven by north-easterly winds. In summer, westerly winds drive currents towards the northeastern part of the Andaman Sea from the Indian Ocean [51]. The climate of the islands can be classified as three seasons, based on rainfall. The southwest monsoon (May–October) produces heavy rainfall, strong winds and frequent cyclones. During the northeast monsoon (November–December), rainfall is more moderate. The dry season (January–April) is characterized by minimal rainfall, reduced winds and waves, and consistently calm environmental conditions. High humidity, about 80%, occurs throughout the year. Annual temperature varies from 22.5−32.5° C, averaging slightly higher in the southern Nicobar Islands than in the northern Andaman Islands. Similarly, the average salinity of 32.0−33.5‰ increases to the south. The average primary productivity of the Andaman Sea is 273 mgC/m^2/day, indicating an oligotrophic environment [52]. The area selected for this study extends from the North Andaman (13°N) to the South Car Nicobar (9°N) (Fig. 1).

2. MATERIALS AND METHODS

We collected 2 sediment samples from each location (one as replicate) of a total of 13 locations and altogether 26 samples. Therefore, ~100 g of sediment was chosen for foraminiferal studies and 50 gm for other sedimentary and geochemical work from each location. While the samples belonging to 10 m depth were collected by SCUBA diving during the coral reef drilling program in March-2018; whereas the 50 m depth was sampled through McIntryre Grab during the 355th voyage of Sagar Sampada (FORV), in January-2016. The sediments collected for foraminifera studies were divided into two aliquots each 50 g and one stored as an archive and another used for the present study. The sediments were washed using tap water to remove the particles <63 μm and air-dried at room temperature. The dried sediments were sieved to separate the >500 µm and > 63µm. All the available live larger benthic foraminifera (based on the appearance of symbiotic colors on the specimens) specimens were picked using a stereoscopic binocular microscope from the >500 µm sediment fractions. In addition, we also examined 2-3 g sediments of <500 µm and >63µm fractions was essential to finding specimens of the Peneroplidae. The identified specimens were mounted on micropaleontological slides and some selected specimens were illustrated using scanning electron microscopy to aid species identification. The number of specimens counted from replicate samples converted as average numbers (Table 1). Data were analyzed using the statistical software PRIMER-6 [53] to determine species richness (S), number of LBF per 50 g (N), the Margalef Richness Index (D), the Pilou Equitability Index (J'), and the Shannon-Weiner Diversity Index (H'), and to carry out cluster analysis by stations, using Bray Curtis similarity of square-root transformed species-abundance data.

3. RESULTS

Twenty six species of LBF were identified among 2051specimens considered to have been alive at the time of collection (Table 1) along the Andaman-Nicobar Archipelago (Fig. 1). Eleven species from the Order Miliolida were found, including three belonging to the Family Soritidae, six species of Peneroplidae and two species of Alveolinellidae. The remaining 15 species belonged to the Order Rotaliida, including five species of Amphisteginidae, four species of Calcarinidae, and six species of Nummulitidae. The absolute abundance was high in the families (Fig. 2) were noticed in Calcarinidae (759) followed by Amphisteginidae (399), Peneroplidae (199), Nummulitidae (123), Soritidae (27) and Alveolinellidae (13) in the 10 m depth, though in the 50 m depth it was found as the Nummulitidae (235) was more abundant followed by Amphisteginidae (166), Calcarinidae (121), Soritidae (6) and Alveolinellidae (3). However, the Peneroplidae was absent in this regime.

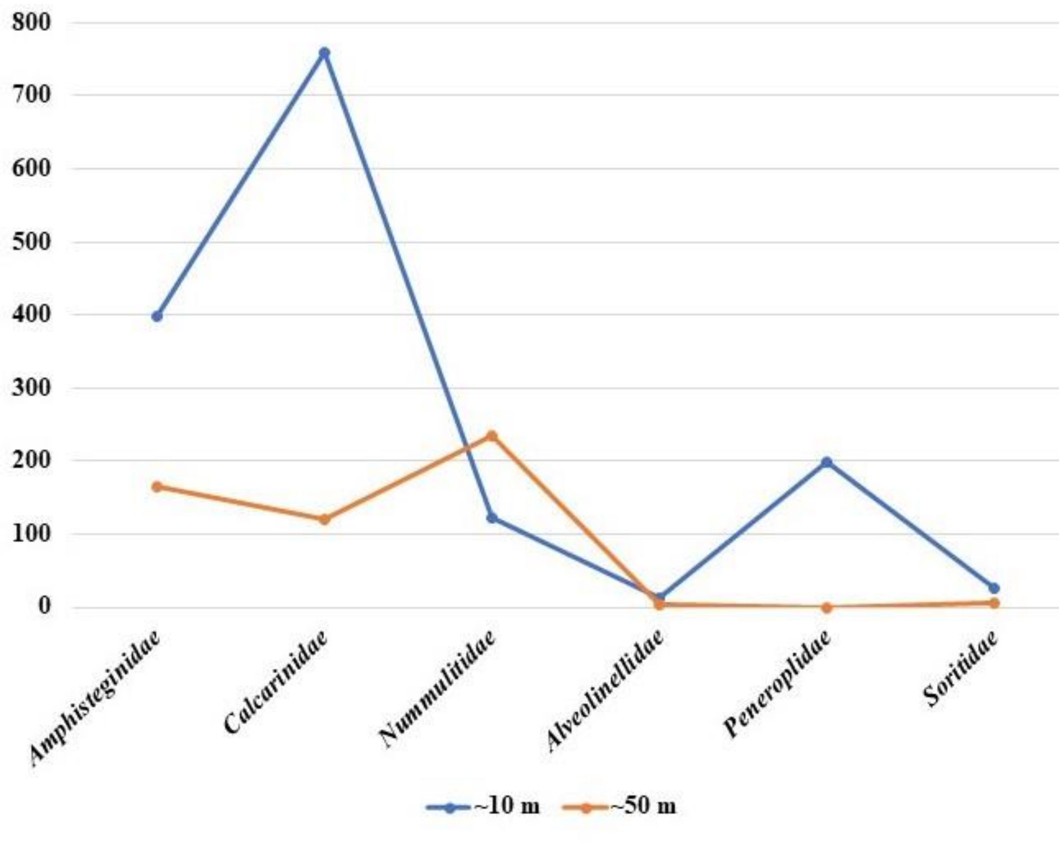

Fig. 2. Family wise absolute abundance in both ~10 and ~50 m Depths

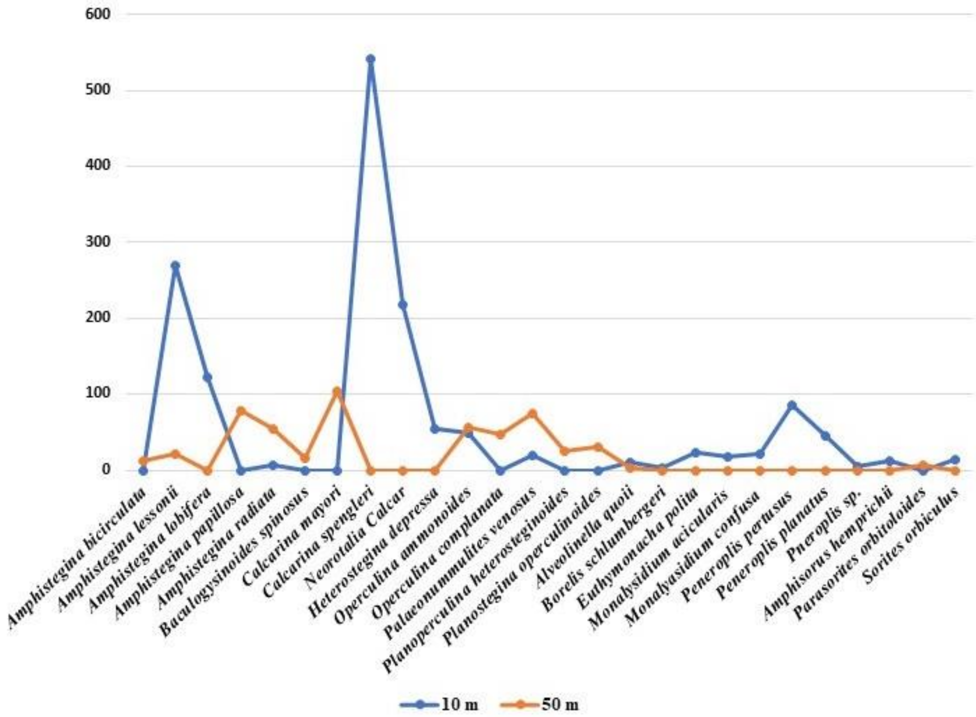

Fig. 3. Absolute abundance of LBF in both ~10 and ~50 m depths

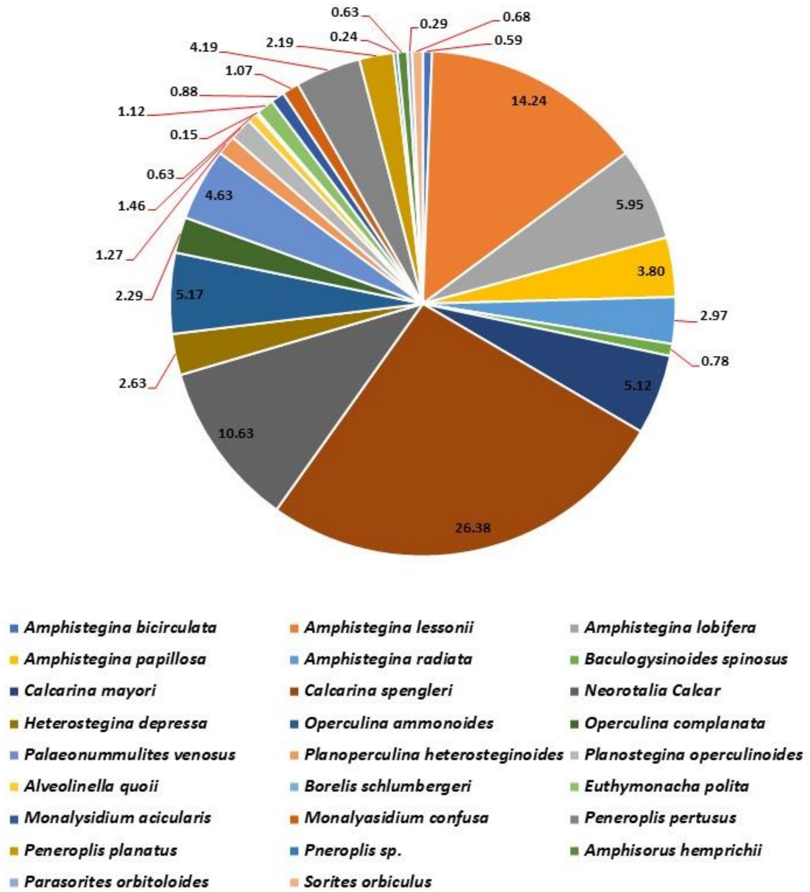

Fig. 4. Relative abundance of LBF in overall study

Table 1. Larger benthic foraminiferal species counts by sample (LA=Little Andaman, SA=South Andaman, MA=Middle Andaman, NA=North Andaman, CN= Car Nicobar, E = Andaman Seaside of the island chain, W = Bay of Bengal side of the island chain)

Family	**Amphisteginidae**					**Calcarinidae**				**Nummulitidae**						**Alvelolinellidae**		**Peneroplidae**					**Soritidae**				
Species	***Amphistegina bicirculata***	***Amphistegina lessonii***	***Amphistegina lobifera***	***Amphistegina papillosa***	***Amphistegina radiata***	***Baculogypsinoides spinosa***	***Calcarina mayori***	***Calcarina spengleri***	***Neorotalia calcar***	***Heterostegina depressa***	***Operculina ammonoides***	***Operculina complanata***	***Palaeonummulites venosus***	***Planoperculina heterosteginoides***	***Planostegina operculinoides***	***Alveolinella quoii***	***Borelis schlumbergeri***	***Euthymonacha polita***	***Monalysidium acicularis***	***Monalysidium confusa***	***Peneroplis pertusus***	***Peneroplis planatus***	***Peneroplis* sp.**	***Amphisorus hemprichii***	***Parasorites orbitolitoides***	***Sorites orbiculus***	**Total**
1-SA (10 m) E	0	76	49	0	0	0	0	170	40	15	10	0	0	0	0	0	0	7	18	11	32	14	0	0	0	7	449
2-SA (8 m) E	0	63	0	0	0	0	0	198	66	12	18	0	8	0	0	0	1	10	0	7	19	8	0	0	0	0	410
3-MA (07 m) E	0	92	17	0	0	0	0	132	80	0	21	0	12	0	0	0	2	6	0	4	23	13	0	0	0	0	402
4-NA (10 m) E	0	30	56	0	0	0	0	27	32	21	0	0	0	0	0	3	0	0	0	0	0	10	5	0	0	0	184
5-NA (10 m) E	0	9	0	0	7	0	0	14	0	6	0	0	0	0	0	7	0	0	0	0	12	0	0	13	0	7	75
6-LA (48 m) E	0	4	0	26	17	0	33	0	0	0	0	2	4	0	8	3	0	0	0	0	0	0	0	0	0	0	97
7-MA (50 m) E	0	8	0	0	21	0	0	0	0	0	0	19	26	0	0	0	0	0	0	0	0	0	0	0	0	0	74
8-MA (56 m) W	0	0	0	17	0	0	0	0	0	0	22	1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	50
9-NA (67 m) W	0	0	0	0	0	0	0	0	0	0	0	0	17	13	14	0	0	0	0	0	0	0	0	0	0	0	44
10-NA (63 m) E	12	0	0	0	9	0	20	0	0	0	4	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	53
11-SA (64 m) W	0	3	0	0	7	0	0	0	0	0	15	9	0	13	8	0	0	0	0	0	0	0	0	0	6	0	61
12-CN (49 m) E	0	7	0	22	0	0	27	0	0	0	0	14	12	0	0	0	0	0	0	0	0	0	0	0	0	0	82
13-CN (50 m) W	0	0	0	13	0	16	25	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	70
Total	**12**	**292**	**122**	**78**	**61**	**16**	**105**	**541**	**218**	**54**	**106**	**47**	**95**	**26**	**30**	**13**	**3**	**23**	**18**	**22**	**86**	**45**	**5**	**13**	**6**	**14**	**2051**

In the ten sediment samples collected from the ~10 m target depth immediately offshore from the Andaman Islands, 18 species from the six families were identified. The Peneroplidae produced the most species (6). *Amphistegina lessonii* and *Calcarina spengleri* tests were found in all five samples; *Neorotalia calcar*, *Heterostegina depressa*, *Peneroplis pertusus* and *P. planatus* were each found in four samples. *Calcarina spenglerii* (541 specimens), *Amphistegina lessonii* (270), *Neorotalia calcar* (218) and *A. lobifera* (122) were the most abundant species (Fig. 3) found in the ~10 m samples.

Sixteen sediment samples were collected from the 50-m target depth, including two samples from Car Nicobar and six from Andaman. Overall, these samples were quite variable, yielding 13 species belonging to five families (Table 1). The Nummulitidae, representing five species, made up nearly half (235) of the 531 specimens found in these samples. The most abundant species (Fig. 3) overall were *Calcarina mayorii* (105 specimens), *Amphistegina papillosa* (78), *Palaeonummulites venosus* (75), *Operculina ammonoides* (57) and *Amphistegina radiata* (54). *Palaeonummulites venosus* and *O. complanata* were found in twelve of the sixteen samples. Specimens found in eight samples, in order of abundance, were *Calcarina mayorii, A. radiata*, *Operculina ammonoides, A. papillosa*, and *A. lessonii*, though the last accounted for only 22 specimens overall. Other species that occurred in at least four samples were *Planostegina operculinoides* and *Planoperculina heterosteginoides. Amphistegina bicirculata* (29 specimens), *Baculogypsinoides spinosus* (20) and *C. spengleri* (16) and *Alveolinella quoii* (3) were each found in two samples. *Planostegina operculinoides* and *Planoperculina heterosteginoides* were identified only from the sites off the Andaman Islands. The relative abundance (Fig. 4) found in overall study was dominated with *Calcarina spenglerii* (26.38%) followed by *Amphistegina lessonii* (14.24%) and *Neorotalia Calcar* (10.63%).

Statistical analysis was used to further describe the density, diversity, species richness and equitability of the LBF (Table 2). The density of LBF was 2–22 specimens cm^{-2}. The Shannon-Wiener Diversity Index (H) ranged from 1.12–2.03, the Margalef Species Richness Index (D) from 0.70–1.80 and Pielou's Equitability Index (J) varied from 0.68–0.97.

To further understand for the relationship among the stations, cluster analysis was utilized (Bray Curtis Similarity Index), and it has (Fig. 5) emphasized that a total of 3 major groups based on the abundance of LBF at on or above 50% similarity level. Group I from four

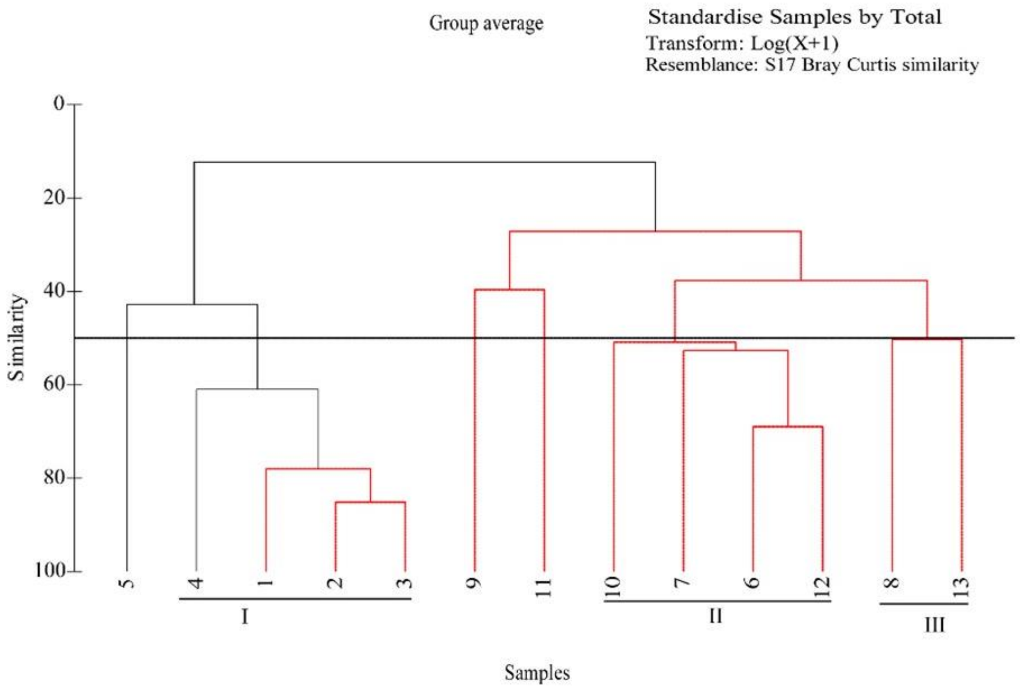

Fig. 5. Dendrogram showing relative similarity among the stations

Table 2. Summary of statistics for each sample (S = number of species, N = number of specimens identified, D = Margelef's Richness Index, J' = Peilou's Equitablity Index, H' = Shannon Weiner Diversity Index)

Sample	S	N	D	J'	H'
1	12	449	1.80	0.79	1.97
2	11	410	1.66	0.69	1.65
3	11	402	1.67	0.76	1.83
4	8	184	1.34	0.87	1.82
5	8	75	1.62	0.98	2.03
6	8	97	1.53	0.81	1.68
7	4	74	0.70	0.95	1.32
8	4	50	0.77	0.81	1.13
9	3	44	0.53	0.99	1.09
10	6	53	1.26	0.88	1.57
11	7	61	1.46	0.95	1.85
12	5	82	0.91	0.94	1.51
13	4	70	0.71	0.98	1.36

~10 m stations showed 60% average similarity. *Calcarina spengleri, A. lessonii* (21%), *N. calcar, A. lobifera, P. pertusus* and *P. planatus* were the most abundant members of the group. The other shallow site, Station 5, was an outlier from this group due to the occurrence of lower abundance of LBF. Group II included 4 stations from ~50 m sites (6,7,10 and 12), with an average similarity of 42%. The five dominant species were *C. mayori*, *P. venosa*, *A. radiata*, *O. complanata* and *A. papillosa*. A third group of two ~50 m stations (8 and 13), with an average similarity of 48%, had two dominant species, *O. ammonoides* and *A. papillosa*. Two other deeper stations (9 and 11) showed less similarity due to low abundance and dominance of Nummulitidae species *P. heterosteginoides* and *P. operculinoides*. Overall, common species *A. lessonii*, *A. radiata*, *O. ammonoides*, *P. venosus* and *A. quoii* were found in samples from both ~10 and ~50 m sites.

4. DISCUSSION

The 26 sediment samples collected across an ~450 km^2 area of the Andaman-Nicobar Archipelago yielded 26 species of LBF belonging to six families. This number of species is somewhat lower that the ~39 species reported from northwestern Pacific reefs and reefs of Indonesian Archipelago [27,54] and is about half the 54 species reported for the Coral Triangle region and Philippines [33]. However, the number of species that we found was undoubtedly limited by our sampling. In particular, collection of only ten sediment samples at ~10 m depth clearly undersampled for the shallow-dwelling, reef-associated taxa. As Stephenson et al. [55] demonstrated in samples from the Florida reef tract (western Atlantic), most reef-dwelling foraminifera live on firm or hard substrata, not in mobile sediments, regardless of whether they host algal symbionts. Also, as Baker et al. [40] demonstrated, the shallowest habitats (<5 m) occur in a wider range of environmental conditions than deeper shelf environments, and a greater diversity of habitats can support a greater diversity of taxa. Thus, we undoubtedly missed species that live in reef flats, patch reefs, and shallow reef-margin environments. Nonetheless, our data support the hypothesis of greater diversity in shallow habitats, as we recorded 18 species in 10 samples, compared to sixteen samples from ~50 m depths, which yielded 13 species.

The inclusion of small peneroplids as LBF did increase species numbers compared to results from earlier studies of LBF, which did not include tiny genera such as *Monalysidium*. We primarily found the smaller peneroplids in the 63−500 µm size fraction of the sediment samples.

Thus, while we recorded a higher diversity of LBF than previous reports from the central and western Indian Ocean, and adjacent seas (Table 3), other factors must be considered when making comparisons. Such factors range from what sampling methods were employed, what depths were sampled, and what specimens were included in counts (e.g., only those known to be collected live, those presumed to have been collected live, all well preserved specimens, all specimens identifiable to genus). Classification considerations also are inherent to such comparisons, including what species were defined as larger benthic foraminifera, whether the researchers involved in identifications tended to be taxonomic "splitters" or "lumpers", and when the studies were conducted relative to recent species descriptions, especially those in association with studies of phylogenetic relationships.

Table 3. Comparison of LBF taxa reported in studies from the western Indian Ocean [1 = Present Study, 2 = Gulf of Mannar Islands [78], 3 = Lakshadweep Islands [79, 80], 4 = Maldive Islands [81], 5 = Chagos Archipelago [82], 6 = Mozambique Coast [65], 7 = Zanzibar Islands [83], 8 = Kenya Coast [84], 9 = Somalia Coast [85], 10 = Arabian Gulf [86], 11 = Red Sea [64] and 12 = Bahrain Coast [87]]

Sl.No	Species	1	2	3	4	5	6	7	8	9	10	11	12
1	*Alveolinella quoii*	+	+	---	+	---	--	---	---	---	---	---	---
2	*Amphisorus hemprichii*	+	---	+	---	+	---	+	+	---	---	+	---
3	*Amphisorus duplex*	---	---	---	---	---	---	+	+	---	---	---	---
4	*Amphistegina bicirculata*	+	---	---	+	---	---	+	---	---	---	---	---
5	*Amphistegina lessonii*	+	+	+	+	+	---	+	+	+	+	+	---
6	*Amphistegina lobifera*	+	+	---	+	---	---	+	---	+	---	---	---
7	*Amphistegina madagascariensis*	---	---	+	---	---	---	---	---	---	---	---	---
8	*Amphistegina papillosa*	+	+	---	---	---	---	+	---	---	---	---	---
9	*Amphistegina radiata*	+	+	+	+	---	---	+	+	+	---	---	---
10	*Amphistegina* sp.	---	---	---	+	---	---	---	---	---	---	---	---
11	*Amphistegina* sp1	---	---	---	---	---	+	---	---	---	---	---	---
12	*Baculogypsina spinosus*	+	---	---	---	---	---	---	---	---	---	---	---
13	*Borelis pulchra*	---	---	+	---	---	---	---	---	---	---	---	---
14	*Borelis schlumbergeri*	+	+	---	---	---	+	+	---	---	+	+	---
15	*Borelis* sp.	---	---	---	---	---	---	---	---	---	---	+	---
16	*Calcarina* sp1.	---	---	---	+	---	---	---	---	---	---	---	---
17	*Calcarina mayori*	+	---	---	---	---	---	---	---	---	---	---	---
18	*Calcarina spengleri*	+	+	---	---	---	---	---	---	---	---	---	---
19	*Coscinospira hemprichii*	---	---	---	---	---	+	---	---	---	---	+	+
20	*Coscinospira* sp.	---	---	---	---	---	---	---	---	---	---	---	+
21	*Euthymonacha polita*	+	---	---	---	---	+	---	---	---	---	---	---
22	*Heterostegina depressa*	+	+	+	+	+	+	+	+	+	---	+	---
23	*Laevipeneroplis inornatus*	---	+	---	---	---	---	---	---	---	---	---	---
24	*Marginopora vertebralis*	---	---	+	---	---	---	---	---	---	---	---	---
25	*Monalysidium acicularis*	+	---	---	---	---	---	---	---	---	---	---	---
26	*Monalysidium confusa*	+	---	---	---	---	---	---	---	---	---	---	---
27	*Neorotalia calcar*	+	+	+	---	---	+	+	---	+	---	+	---
28	*Operculina ammonoides*	+	+	---	+	+	---	+	---	+	---	---	---
29	*Operculina complanata*	+	---	---	---	---	---	---	---	---	+	+	---
30	*Operculina discoidalis*	---	---	---	---	---	---	+	---	---	---	---	---
31	*Pararotalia calcar*	---	---	---	---	---	---	---	+	---	---	---	---
32	*Parasorites orbitoloides*	+	---	---	---	---	---	---	---	---	---	---	---
33	*Palaeonummulites venosus*	+	---	+	+	---	---	+	---	---	---	---	---
34	*Peneroplis arietinus*	---	---	+	---	---	---	---	---	---	---	+	+
35	*Peneroplis planatus*	+	+	---	---	---	+	---	+	---	---	+	+
36	*Peneroplis pertusus*	+	+	+	---	---	---	---	+	---	+	+	+
37	*Peneroplis proteus*	---	---	---	---	---	---	---	---	---	---	+	---
38	*Peneroplis bradyi*	---	---	---	---	---	---	---	---	---	---	+	---
39	*Peneroplis* sp.	+	---	---	---	---	---	---	---	---	---	---	---
40	*Planoperculina heterosteginoides*	+	---	---	---	---	---	---	---	---	---	---	---
41	*Planostegina operculinoides*	+	---	---	+	---	---	---	---	---	---	---	---

Sl.No	Species	1	2	3	4	5	6	7	8	9	10	11	12
42	*Soritus marginalis*	---	+	+	---	---	---	---	---	---	---	+	---
43	*Soritus orbiculus*	+	+	---	---	---	+	+	---	---	---	+	---
44	*Soritus* sp.	---	---	---	---	---	---	---	---	---	---	+	---
45	*Soritus* sp1	---	---	+	---	---	---	---	---	---	---	---	---
46	*Soritus variablis*	---	---	---	---	---	+	---	---	---	---	---	---

The relatively few samples available from each location and depth also limited our ability to statistically compare our samples relative to location. For example, species recorded in only one or two samples probably reflect natural patchiness or local conditions, and not necessarily biogeographic differences between assemblages from the Andaman Islands compared to the Car Nicobar sites. The second factor is water transparency; especially at depths >30 m, small differences in the proximity to terrestrial runoff or topographic upwelling can influence whether LBF species requiring very low-light can survive at a 50 m or 100 m location [15, 27]. We conclude that the depth trends we found are robust, with porcelaneous (miliolid) taxa primarily found in shallow samples, while the various members of the rotaliid families show the well-known depth zonation of these taxa.

The Miliolida: Miliolid foraminifera produce high magnesium-calcite tests, whose wall structure includes a combination of calcite needles, rod, lath or plate-shaped crystals that produce a translucent to opaque structure [56-58]. Many of the estimated 36 species of living Miliolida that host algal symbionts [45, 33] and those foraminifera have morphologic features that are considered adaptations to allow light to reach the algal symbionts, while maintaining strength of the test [59, 60]. The inherent opacity of the porcelaneous test wall, combined with structural limitations, tend to limit the depth distributions of such Miliolida. We recorded 11 species, representing three families, Alveolinellidae, Peneroplidae and Soritidae, of which specimens of only two species*, A. quoii* and *Parasorities orbitolitoides*, were found in any samples that came from >10 m depth. The limited number of species that we recorded was probably the consequence of not sampling at depths <10 m and their associated habitats.

Alveolinid fossils appeared in the upper Cretaceous [61] Two species of Alveolinellidae, *A. quoii* and *B. sclumbergeri*, were recorded in our samples. *Alveolinella quoii* is a large fusiform species that occurs throughout the western Pacific and the eastern Indian Ocean, with limited records beyond the Maldive Islands and northern Indian Ocean [33, 34, 45]. This species has been recorded living on reef slopes at depths of 5–60 m [27, 62] We found living specimens in two samples from ~10 m and one sample from 48 m. *Borelis schlumbergeri* is smaller in size and is well known from throughout the Indo-Pacific [33, 40, 63]. The depth distribution of this species has been reported from 8 m [64] to 45 m, and as living abundantly at 25–35 m [25]. We found only three specimens in two samples from ~10 m depth.

The fossils of family Peneroplidae known from late Cretaceous [61]. We identified six species from this family, all from samples collected at ~10 m depth and primarily from the 63–500 µm grain-size fractions. The smallest species, *Euthymonacha polita* was identified from 3 samples. It has been reported depths of 5–20 m [44, 65–67], with a distribution ranging from the eastern Pacific to the western Indian Ocean [33]. We also found two species of *Monalysidium.* The species *M. acicularis* occurs throughout the tropical Indo-Pacific [33] to depths of 40 m [68]. We found 18 specimens in only one ~10-m sample. *Monalysidium confusa* was previously reported from the Philippines and New Caledonia [33, 68] and from the 15 m depth of Andaman Sea [67]. We found specimens in three of our ~10 m samples. The genus *Peneroplis* was represented by three species in our study. *Peneroplis pertusus* occurs circumtropically [33, 40, 45] at depths ranging from 0–40 m [27, 45, 67–69] We found living specimens in four samples from ~10 m depth. *Peneroplis planatus* was identified in four ~10 m samples; this species is also well known from throughout the tropical Indo-Pacific, though it has not been reported previously from the central Indian Ocean from Lakshadweep, Maldives and Chagos Islands [33, 45, 70] *Peneroplis planatus* has been reported as living from the inter-tidal to 40 m depth [27, 68, 69]. A morphospecies identified as *Peneroplis* sp. was similar to *P. pertusu*s, but it has a single large aperture with multiple apertural teeth. We found five specimens in one ~10 m sample.

The Family Soritidae, found since late Oligocene [61], includes relatively large, discoid taxa. This family was represented by three species from three different genera, two of which host dinoflagellate symbionts. *Sorites orbiculus* is a shallow-dwelling [27], circumtropical [71] species; we found specimens in two ~10 m samples. *Amphisorus hemprichii* is also broadly distributed throughout the tropical Indo-Pacific [33], reportedly as deep as 70 m, but most commonly at <30 m [27, 45, 68]. We found 13 live specimens from one sediment sample from ~10 m depth. *Parasorites orbitolitoides* which hosts chlorophyte symbionts, is the deepest living member of the Soritidae. This species has been reported from throughout the Indo-west Pacific region, though reports are lacking from the Lakshadweep Islands in the western Indian

Ocean [33, 70]. Living specimens have been reported from depths of 10–90 m [27, 28, 62, 71]. We found specimens showing some chlorophyte greenish colour in a 64 m sample.

The Rotaliida: In the Order Rotaliida, 35 extant species that host diatom endosymbionts and that are considered LBF have been identified worldwide, belonging to the families Amphisteginidae, Calcarinidae and Nummulitidae [33,72]. We found 15 of these species in our samples from the Andaman-Nicobar Archipelago. In this section, we discuss these taxa by family and, within the families, by their depth trends, from shallow- to deeper-dwelling species. In general, our findings are consistent with depth trends reported by Hohenegger [27] for LBF within 64 m.

The family Amphisteginidae is known since the Eocene Epoch [73]. We identified five species of the genus *Amphistegina* Members of this genus in the Indo-Pacific are well known to exhibit light-related depth zonation and trends in test shape. The robust *A. lobifera* thrives at the shallowest depths, followed in order by *A. lessonii, A. radiata, A. bicirculata*, and *A. papillosa*, the latter often recorded from depths >100 m [26–28, 74]. *Amphistegina lobifera* has been reported to depths of 45 m or more but lives most abundantly at depths <20 m [26–28,74]. We found this species in three samples from ~10 m. *Amphistegina lessonii* commonly co-occurs at shallow depths with *A. lobifera* and at intermediate depths with *A. radiata* and *A bicirculata* [26, 27,74]. We found *A. lessonii* to be the dominant species in the ~10 m samples, and they occurred in low numbers in four of the ~50 m depth samples. The largest, biconvex test-bearing member of this family, *A. radiata* has been reported from the western Pacific to the western Indian Ocean and Red Sea, though it has not been reported from Lakshadweep Island, Chagos or the Seychelles islands [33, 45, 70]. The species has been reported from depths of 5–95 m, most abundantly in the 20–50 m depth range [26–28, 62, 74]. We recorded *A. radiata* in one samplesof ~10 m depth and four samples from ~50 m depth. The much less common *A. bicirculata* strongly resembles very flat *A. lessonii* specimens in dorsal view but exhibits an inner circular arrangement of chamber walls in ventral view, when viewed with a light microscope. *Amphistegina bicirculata* occurs throughout most of the Indo-Pacific, at least as far east as Hawai'i [26] and in the northern Indian Ocean and Gulf of Aqaba. The species has not been reported from the Philippines, the eastern tropical Pacific Ocean or the islands of the western Indian Ocean [33, 45]. *Amphistegina bicirculata* has been found alive at depths from 20–130 m, but most abundantly at depths from ~30–70 m depth [28, 62, 74]. We found this species in only one sample at 63 m. The deepest-dwelling species of the genus is *A. papillosa*, which is characterized by a relatively small, papillated, flattened-biconvex test. It occurs abundantly in low light, usually relatively deep habitats in the western Pacific and Indian Ocean (e.g., Madagascar, Mozambique) and Red Sea, but has not been reported from central Indian Ocean islands such as Lakshadweep, Maldives, Chagos and Seychelles [33, 45, 70]. While living specimens have been reported at depths ranging from 10–150 m, this species tends to be most common in the 50–130 m depth range [27, 28, 62, 74]. We found specimens from 48–56 m depths.

Star-shaped LBF with canaliculated spines belong to the Family Calcarinidae and members of this family are found since Late Cretaceous time [58]. A total of 14 species representing four genera have been identified primarily from the western Pacific and eastern Indian Ocean; we found four of those species belonging to three genera. *Neorotalia calcar* is the most broadly distributed species of this family, and as it is also found in the western Indian Ocean [33, 35,39, 45]. Specimens are characterized by elongated and pointed chambers with canaliculated spines, and it commonly lives in shallow waters associated with macroalgae [58]. We found this species relatively abundant in four of the five samples from ~10 m depth. The genus *Calcarina* includes two species that tend to occur at shallow to intermediate euphotic depths. We identified *Calcarina spengleri*, which bears long spines on the terminus of its chambers in all the five samples from ~10 m depth. This species has been reported from intertidal to 45 m depths, with abundance noted at 15–25 m [37, 54, 62]. The largest species, *Baculogypsinoides spinosus* has been reported from 5–85 m depth, with peak abundance at ~55–65 m [27,28, 74]. Tripaty [46] reported it from Great Nicobar Island and we found representatives in only one samples, at 52 m depths, off Car Nicobar. The calcarinid species that we found most abundantly and consistently in the deeper samples was *C. mayori*, which is characterized by a relatively small test. This species has been reported from 3–70 m depth, and most abundantly down to 40 m depth [28, 54]. This was the most abundant species that we found in the ~50 m depth samples (20%) from 4 samples.

The Family Nummulitidae is widely known from Paleogene carbonates [75] and is represented by 15 extant species. Though most are restricted to the Indo-Pacific region, *Heterostegina depressa* occurs circumtropically [33, 34, 69, 74]. In our samples from the Andaman-Nicobar Archipelago, we identified six species belonging to five genera. Because most of these species are well adapted to low-light environments, they can live in well-shaded environments in shallow water as well as in much deeper habitats [76]. For example, *Heterostegina depressa* has been found from intertidal sites to >100 m depths, but most abundantly at 20–30 m [26, 27, 77, 76]. We found this species in four ~10 m samples out of five. We found both *Operculina ammonoides* and *Palaeonummulites venosus* in samples from the ~10 and ~50 m depths. Both are widespread tropical Indo-Pacific species [33, 34], that have been reported from depths of ~10 m to more as much as 90 m, with peak abundances at ~40–50 m [27, 74]. *Operculina complanata* is a somewhat deeper-dwelling species reported only from the Indo-west Pacific [33, 45]. We found specimens in samples from eight sites from 10–67 m. Previous studies have reported this species from 20–150 m depth, with peak abundances at ~50 m [28, 62]. *Planoperculina heterosteginoides* has been previously reported only from sites in the core area of Indo-west Pacific region [33, 45]. Most recently Tripati [46] reported it from Nicobar samples, consistent with our findings from the Andaman region. The species has previously been reported from 50–130 m depth [27, 28, 62, 74]. We found it only in two samples from 64 and 67 m depths. *Planostegina operculinoides* has also been reported mostly from a limited range in the Indo-west Pacific [33, 58]. Living specimens were reported from depths of 15 to >100 m [27, 28, 62, 74], and most abundantly at ~80 m depth. We found *P. operculinoides* in three samples from the ~50 m sites.

5. CONCLUSION

- ❖ Twenty-six LBF species were recorded for reefs of the Andaman-Nicobar Archipelago, which is somewhat higher than diversities reported for western Indian Ocean reefs, slightly lower than diversities of Japan and Indonesian reefs, and roughly half the number of LBF species reported in the Coral Triangle region.
- ❖ All species identified in this study are well-known Indo-west Pacific taxa.
- ❖ *Calcarina spenglerii*, *Amphistegina lessonii, Neorotalia calcar,* and *Amphistegina lobifera* dominated in the samples from ~10 m depth
- ❖ *Calcarina mayori, Palaeonummulites venosus, Amphistegina papillosa* and *Operculina ammonoides* were characteristic of samples from ~50 m depth.
- ❖ Representatives of the Miliolida were primarily found in the 63–500 µm sediment fractions from ~10 m samples; *Peneroplis pertusus*, *Peneroplis planatus* and *Parasorites orbitolitoides* were also found in some >500 µm sediment fractions.
- ❖ *Baculogypsinoides spinosus* was only found in samples from Car Nicobar.
- ❖ Because we only sampled sediment from ~10 m or deeper, and many LBF live primarily on phytal or hard substrata, we likely missed some species, especially taxa that live in nearshore and back-reef habitats.
- ❖ We recommend further systematic sampling of reef and other nearshore habitats associated with the islands of the Andaman-Nicobar Archipelago, especially samples from back-reef, reef-flat, and shallow fore-reef environments, to more completely enumerate the LBF species, their habitats, and their depth distributions.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Whitaker, R. Endangered Andaman. Department of Environment. *Government of India*. 1985, *51p.*
2. Wilkinson, C. Status of Coral Reefs of the World. *Australian Institute of Marine Science, Townsville, Australia.* 2004, *1, 301p.* https://www.icriforum.org/sites/default/files/scr2004v1-all.pdf
3. Miththapala, S. Coral Reefs: Coastal Ecosystems Series Colombo, Sri Lanka: *Ecosystems and Livelihoods Group Asia.* 2008, *IUCN.* 1, 1–36. http: //www.iucn.org/coastalinfo/.
4. Kahng, S.E.; Copus, J.M.; Wagner, D. Mesophotic coral reef ecosystems, *in* Rossi, S. (Ed.), Marine Animal Forests. Springer, Cham, Switzerland, 2017, pp. 1–22. https://doi.org/10.1007/978-3-319-21012-4_4.
5. Wilkinson, C. Status of Coral Reefs of the World. Australian Institute of Marine Science, Townsville, Australia. 2002, 1, 1–31. http://www.vliz.be/imisdocs/publications/213235.pdf
6. Hallock, P.; Schlager, W. Nutrient excess and demise of coral reefs and carbonate platform. PALAIOS. 1986, 1, 389–398. http://dx.doi.org/10.2307/3514459.
7. Hinderstein, L.M.; Mar, J.C.A.; Martinez, F.A.; Dowgiallo, M.J.; Puglise, K.A.; Pyle, R.L.; Zawada, D.G.; Appleldoorn, R. Theme session on “Mesotrophic coral ecosystem: Characterization, ecology and management. Coral Reefs. 2010, 29, 247–251. https://doi.org/10.1007/s00338-010-0614-5.
8. Bongaerts, P.; Frade, P.R.; Hay, K.B.; Englebert, N.; Latijnhouwers, K.R.W.; Bak, R.P.M.; Vermeij, M.J.A.; Hoegh-Guldberg, O. Deep down on a Caribbean reef: Lower mesophotic depths harbor a specialized coral endosymbiont community. Sci. Rep. 2015, 5, 1–9. https://doi.org/10.1038/srep07652.
9. Lesser, M.P.; Slattery, M.; Mobley, C.D. Biodiversity and functional ecology of mesophotic coral reefs. Ann. Rev. Ecol. Syst. 2018, 49, 49–71. https://doi: 10.1146/annurev-ecolsys-110617-062423.
10. Mckee, E.D.; Chronic, J.; Leopold, E.B. Sedimentary belts in lagoon of Kapingamaringi Atoll. Bulletin of the American Association of Petroleum Geologists, 1959, 43, 501–562.
11. Hallock, P. Production of carbonate sediments by selected large benthic foraminifera on two Pacific coral reefs. J. Sediment. Petrol. 1981a, 51, 467–474. https://doi.org/10.1306/212F7CB1-2B24-11D7-8648000102C1865D.
12. Doo, S.S.; Hamylton, S.; Finfer, J.; Byne, M. Spatial and temporal variation in reef-scale carbonate storage of large benthic foraminifera: A case study on One Tree Reef. Coral Reefs. 2017, 36, 293–303. https://doi.org/10.1007/s00338-016-1506-0.
13. Prazeres, M.; Martínez-Colón, M.; Hallock, P. Foraminifera as bioindicator of water quality: The FoRAM Index Revisited. Environ. Pollut. 2019, https://doi.org/10.1016/j.envpol.2019.113612.
14. Hallock, P. Why are larger foraminifera large? Paleobiology. 1985, 11, 195–208. https://doi.org/10.1017/S0094837300011507.
15. Hallock, P. Fluctuation in trophic resource continuum: A factor in global diversity cycles? Paleoceanogr. Paleoclimatol. 1987, 2, 457–471. https://doi.org/10.1029/PA002i005p00457.
16. Hallock, P. Algal symbiosis: A mathematical analysis. Mar. Biol. 1981b, 62, 249–255. https://doi.org/10.1007/BF00397691.
17. Dubinsky, Z.; Frank, I.B. Uncoupling primary production from population growth in photosynthesizing organisms in aquatic ecosystems. Aquat. sci. 2001, 63, 4–17. https://doi.org/10.1007/PL00001343.
18. Beavington-Penney, S.J.; Racey, A. Ecology of extant nummulitids and large

benthic foraminifera: Application in paleoenvironmental analysis. Earth Sci Rev., 2004, 67, 219–265. https://doi.org/10.1016/j.earscirev.2004.02.005.

19. Pomar, L.; Beceta, J.; Hallock, P.; Mateu-Vicens, G.; Basso, D. Reef building and carbonate production modes in the west-central Tethys during the Cenozoic. Mar Pet Geol. 2017, 83, 261–304. http://doi:10.1016/J.MARPETGEO.2017.03.015.
20. Serra-Kiel, J.; Hottinger, L.; Caus, E.; Drobne, K.; Ferrández, C.; Jaurhi, AK.; Less, G.; Pavlovec, R.; Pignatti, J.; Samso, J.M.; Schaub, H.; Sirel, E.; Strougo, A.; Tambareau, Y.; Tosquella, J.; Zakrevskaya, E. Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. Bulletin de la Société Géologique de France. 1998, 169, 281–299.
21. Molina, E.; Torres-Silva, A.I.; Coric, S.; Briguglio, A. Integrated biostratigraphy across the Eocene/Oligocene boundary at Noroña, Cuba, and question of the extinction of orthophragminids. Newsl. Stratigr. 2016, 49, 27–40. https://doi:10.1127/nos/2015/0069.
22. Papazzoni, C.A.; Cosovic, V.; Briguglio, A.; Drobne, K. Towards a calibrated larger foraminiferal biostratigraphic zonation: Celebrating 18 years of application of the shallow benthic zones. PALAIOS. 2017, 32, 1–4. http://doi:dx.doi.org/10.2110/palo.2016.043.
23. Hallock, P.; Glenn, E.C. Larger foraminifera: A tool for paleoenvironmental analysis of Cenozoic carbonate facies. PALAIOS. 1986, 1, 55–64. https://doi:10.2307/3514459.
24. Mateu-Vicens, G.; Pomer, L.; Ferrandez-Canadell, C. X Nummulitic banks in the upper Lutution "Buil level", Ainsa basin, south central Pyrenean Zone: The impact of internal waves. Sedimentology. 1986, 59, 527–552. https://doi: 10.1111/j.1365-3091.2011.01263. x.
25. Hottinger, L. Distribution of larger Peneroplidae, *Borelis* and Nummulitidae in the Gulf of Elat, Red Sea. Utrecht Micropaleontological Bulletins. 1977, 15, 35–109.
26. Hallock, P. Distribution of selected species of living algal symbionts bearing foraminifera on two Pacific coral reefs. J. Foraminiferal Res. 1984, 14, 250–261. https://doi.org/10.2113/gsjfr.14.4.250.
27. Hohenegger, J. Coenoclines of larger foraminifera. Micropalontology. 2000, 46, 127–151. https://www.jstor.org/stable/i265494
28. Hohenegger, J. Depth coenoclines and environmental considerations of western Pacific larger foraminifera. J. Foraminiferal Res. 2004, 34, 9–33. https://doi.org/10.2113/0340009.
29. Drooger, C.W. Radial foraminifera, morphometrics and evolution. Verhandelingen der Koninkligke Nedarlandse Akademie van Wetenschappen, Afd. Natuurkunde, Erste Reeks, Amsterdam. 1993, 41, 241p.
30. Hallock, P.; Glenn, E.C. Paleoenvironmental analysis of foraminiferal assemblages, a tool for recognizing depositional facies in lower Miocene reef complexes. J. Paleontol. 1985, 59, 1382–1394. https://www.jstor.org/stable/1304951.
31. Hallock, P. Symbiont-bearing foraminifera, *in* Sen Gupta, B. K. (Ed.), Modern Foraminifera. Kluwer Press, Amsterdam. 1999, pp. 123–139.
32. Lee, J.J. Algal symbiosis in larger foraminifera. Symbiosis. 2006, 42, 63−75.
33. Förderer, M.; Rodder, D.; Langer, M.R. Patterns of species richness and centre of diversity in the modern Indo-Pacific larger foraminifera. 2018, Sci Rep. 8, 1–9. https://doi.org/10.1038/s41598-018-26598-9.
34. Langer, M.R.; Hottinger, L. Biogeography of selected larger benthic foraminifera. Micropaleontology. 2000, 46, 105–126. https://www.jstor.org/stable/1486184.
35. Langer, M.R. Foraminifera from the Mediterranean and the Red Sea, in: Por, F.D. (Ed.), Aqaba, Eilat: The Improbable Gulf, Environment Biodiversity and Preservation. Magnes Press, Jerusalem. 2008, pp. 397–415. ISBN 978-965-493-380-3. 463 pp.
36. Gőrőg, A.; Szinger, B.; Toth, E.; Viszkok, J. Methodology of microcomputer tomography on Foraminifera. Paleontol. Electron. 2012, 15, 1–15. https://doi.org/10.26879/261
37. Renema, W. Morphological diversity in the foraminiferal genus Marginopora. PLoS ONE. 2018a, 13, 1–24.

https://doi.org/10.1371/journal.pone.0208158.
38. Holzmann, M.; Pawlowski, J. An updated classification of rotaliid foraminifera based on ribosomal DNA phylogeny. Mar. Micropaleontol. 2017, 132, 18−34. 10.1016/j.marmicro.2017.04.002.
39. Renema, W. Terrestrial influence as a key driver of spatial variability in large benthic foraminiferal assemblage composition in the Central Indo-Pacific. Earth Sci Rev. 2018b, 177, 514–544. https://doi.org/10.1016/j.earscirev.2017.12.013.
40. Baker, R.D.; Hallock, P.; Moses, E.F.; Williams, D.E.; Ramirez, A. Larger foraminifers of the Florida reef tract, USA: Distribution patterns on reef-rubble habitats. J. Foraminiferal Res. 2009, 39, 267–277. https://doi.org/10.2113/gsjfr.39.4.267.
41. Hoeksema, B.W. Delineation of the Indo-Malayan centre of maximum marine biodiversity: The Coral Triangle in biogeography, in: Renema, W. (Ed.), Time and Place: Distribution, Barriers and Islands: Springer, Dordrecht. 2007, pp. 117–178.
42. Balakrishnan, M.; Srivastava, R.C.; Pokhriyal, M. Biodiversity of Andaman and Nicobar Islands. Biobytes, 2008, 3, 9–12. https://doi=10.1.1.548.2444&rep=rep1&type=pdf
43. Yuvaraja, P.M.; Ramanujam, N. Distribution of benthic and planktonic foraminifers in South Andaman, India. Asian j. mar. sci. 2013a, 1, 24–26.
44. Yuvaraja, P.M.; Ramanujam, N. Distribution of benthic foraminifers in Neil Island, South Andaman, India. Afr J Geo Sci Res. 2013b, 1, 4–6.
45. Muruganantham, M.; Ragavan, P.; Mohan, P.M. Diversity and distribution of living larger benthic foraminifera from coral reef environments, South Andaman Island, India. J. Foraminiferal Res. 2017, 47, 252–257. https://doi.org/10.2113/gsjfr.47.3.252.
46. Tripati, S.K. Symbiont-bearing foraminifera from inner shelf area of Great Nicobar Island, Andaman Sea: Coral retrieval. Indian J. Mar. Sci. 2018, 47, 629–634. http://nopr.niscair.res.in/handle/123456789/44120.
47. Chatterjee, A.; Shankar, D.; McCreary, J.P.; Vinayachandran, P.N.; Mukherjee, A. Dynamics of Andaman Sea circulation and its role in connecting the equatorial Indian Ocean to the Bay of Bengal. J. Geophys. Res. 2017, 122, 3200–3218. https://doi.org/10.1002/2016JC012300.
48. Ramakrishna, Mondal, T.; Raghunathan, C.; Raghuraman, R.; Sivaperuman, C. New records of Scleractinian corals in Andaman and Nicobar Islands. Rec. Zool. Surv. India, Occ. Paper No. 2010, 321 :1-144.
49. Smith, M. The Reptilia and Amphibia of the Malay Peninsula from the isthumus of Kra to Singapore, including the adjacent islands. Bulletin of Raffles Museum. 1930, 3, 1–149. https://doi.org/10.5962/bhl.title.10813.
50. Raju, D.V.R.; Gouveia, A.D.; Murthy, C.S. Some physical characteristics of Andaman Sea waters during winter. Indian J. Mar. Sci. 1981, 10, 211–218. http://nopr.niscair.res.in/handle/123456789/39079.
51. Saidova, K.M. Benthic Foraminifera community on the Andaman Sea (Indian Ocean). Mar. Biol. 2008, 48, 561–567. https://doi:10.1134/S0001437008040073.
52. Qazim, S.Z.; Anzari, Z.A. Food components of Andaman Sea. Indian J. Mar. Sci. 1981, 10, 276–279. http://nopr.niscair.res.in/handle/123456789/39094.
53. Clarke, K.R.; Ainsworth, M. A method of linking multivariate community structure to environmental variables. Mar. Ecol. Prog. Ser. 1993, 92, 205–219. https://doi: 10.3354/meps092205.
54. Renema, W. Habitat selective factors influencing the distribution of larger benthic foraminiferal assemblages over the Kepulauan Seribu. Mar. Micropaleontol. 2008, 68, 286–298. doi: 10.1016/j.marmicro.2008.06.002.
55. Stephensen, C.M.; Hallock, P.; Kelmo, F. Foraminiferal assemblage indices: A comparision of sediment and reef rubble samples from Conch Reef, Florida, USA. Ecol. Indic. 2015, 48, 1–7. http://dx.doi.org/10.1016/j.ecolind.2013.02.009.
56. Blackman, P.D.; Todd, R. Mineralogy of some foraminifera as related to their classification and ecology. J. Paleontol. 1959, 33, 1–15. https://www.jstor.org/stable/1300802.
57. Towe, K.M.; Cifelli, R. Wall ultrastructure in the calcareous foraminifera: Crystallographic aspects and a model for

calcification. J. Paleontol. 1967, 41, 742–762. https://www.jstor.org/stable/1302055.

58. Loeblich, A.J.; Tappan, H. Foraminiferal Genera and Their Classification. Van Rostrand Reinhold, New York. 1987, 2114 p.
59. Hottinger, L. Comparative anatomy of elementary shell structures in selected larger foraminifera, in: Hedley, R.H., Adams, C.G. (Eds.), Foraminifera. Academic Press, New York. 1978, 3, pp. 203–266.
60. Hallock, P.; Röttger, R.; Wetmore, K. Hypotheses on form and function in foraminifera, in: Lee, J.J., Anderson, O.R. (Eds.), Biology of the Foraminifera. Academic Press, New York. 1991, pp. 41–72.
61. Boudagher-Fadel, M.K. Evolution and geological significance of larger benthic foraminifea. UCL Press, University College London. 2018, 704p. https:// doi.org/ 10.14324/ 111.9781911576938
62. Renema, W. Large foraminifera from the deep photic zone of mixed siliciclastic-carbonate shelf off Kalimantan, Indonesia. Mar. Micropaleontol. 2006, 58, 73–82. 10.1016/j.marmicro.2005.10.004.
63. Bassi, D.; Braga, G.C.; Di-Domenico, G.; Pignatti, J.; Abramovich, S.; Hallock, P.; Koenen, J.; Kovács, Z.; Langer, M.R.; Pavia, G.; Iryu, Y. Paleobiogeography and evolutionary patterns of the lager foraminifer *Borelis* De Montfort (Borelidae). Pap. Palaeontol. 2019, 7, 377–403. https://doi.org/10.1002/spp2.1273.
64. Madkour, H.A.; Ali, M.Y. Heavy metal in the benthic foraminifera from the coastal lagoons, Red Sea, Egypt: Indicators of anthropogenic impact on environment (Case Study). Environmental Geology. 2009, 58, 543–553. https://doi:10.1007/s00254-008-1529-0.
65. Langer, M.R.; Thissen, J.M.; Makled, W.A.; Weinmann, A.E. The foraminifera from the Bazaruto Archipelago (Mozambique). Neues Jahrb Geol Palaontol. 2013, 267, 155–170. https://doi: 10.1127/0077-7749/2013/0302.
66. Meric, E.; Yokes, M.B.; Avsar, N.; Dincer, F. Main introduction way of Indo-Pacific and Red Sea originated benthic foraminifers to the Eastern Mediterranean. International Int. j. environ. Geoinformatics. 2015, 2, 7–14. https://doi.org/10.30897/ijegeo.303555.
67. Mohan, P.M.; Muruganantham, M.; Sachithanandam, V.; Srinivasulu, S.; Kasilingam, K. Foraminifera, *in* Kailash, C., and Raghunathan, C. (Eds.), Faunal Diversity of Biogeographic Zones Islands of India. Zoological Survey of India, Kolkata. 2019, pp. 15–44.
68. Debenay, J.P. A guide to 1000 foraminifera from south-western Pacific: New Caledonia. Publications Scientific du Museum, Paris. 2012, 378p. https://doi: 10.2113/gsjfr.43.3.314.
69. Renema, W. Larger foraminifera on reefs around Bali (Indonesia). Zoologische Verhandelingen Leiden. 2003, 345, 337–366.
70. Saraswati, P.K. Symbiont bearing benthic foraminifera of Lakshadweep. Indian J. Mar. Sci. 2007, 36, 351–354. http://hdl.handle.net/123456789/62.
71. Holzmann, M.; Hohenegger, J.; Hallock, P.; Piller, W.E.; Pawlowski, J. Molecular phylogeny of large miliolid foraminifera (Soritaceae Ehrenberg, 1839). Mar. Micropaleontol. 2001, 43, 57–74. https://doi.org/10.1016/S0377-8398(01)00021-4.
72. Renema, W.; Troelestra, S.R. Larger foraminifera distribution on a mesotrophic carbonate shelf in southwest Sulawesi Indonesia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 2001, 175, 125–146. https://doi.org/10.1016/S0031-0182(01)00389-3.
73. Todd, R. Smaller foraminifera of Late Eocene age from Eua, Tonga. Geological survey professional paper; United States Government Printing Office. 1970, 640, 1–51.
74. Hansen, H.J.; Buchardt, B. Depth distribution of *Amphistegina* in the Gulf of Elat. Utrecht Micropaleontological Bulletin. 1977, 15, 205–224.
75. Hehenegger, J.: Yardonova, E.; Hatta, A., Remarks on West Pacific Nummulitidae (Foraminifera). Journal of Foraminiferal Research. 2002, 30, 3–28.
76. Renema, W. Large foraminifera in low-light environments, in: Loya, Y., et al. (Eds.), Mesophotic Coral Ecosystem. Coral Reefs of the World, Springer, Dordrecht. 2019, pp. 553–561. https://doi.org/10.1007/978-3-319-92735-0_31.
77. Yordanova, E.K.; Hohenegger, J. Taphonomy of larger foraminifera: Relationship between living individuals and empty tests on flat reef slopes (Sesoko

Island, Japan). Facies. 2002, 46, 169–204. https://doi.org/10.1007/BF02668080.

78. Sheeba, M.; Mohanraju, T. Distribution of benthic foraminifera around six coral Islands of Tuticorin, Bay of Bengal. World J. Zool. 2017, 12, 22–29. http://doi: 10.5829/idosi.wjz.2017.22.29.

79. Rao, K.K.; Sivadas, P.; Narayanan, B.; Jayalakshmy, K.V.; Kutty, M.K. Distribution of foraminifera in the certain Islands of Lakshadweep Archipelago, Arabian Sea. Indian J. Mar. Sci. 1987, 16, 161–178. http://drs.nio.org/drs/handle/2264/6024

80. Gadi, S.D.; Vidya, P.; Mustak, M.S.; Rajashekhar, K.P. Foraminifera of Lakshadweep Archipelago, Arabian Sea. Proceedings of Zoological Society, 2015, 69, 217−224. https://doi 10.1007/s12595-015-0150y.

81. Parker, J.H.; Gischler, E. Modern foraminiferal distribution and diversity in two atolls from the Maldives, Indian Ocean. Mar. Micropaleontol. 2011, 78, 30–49. http://doi: 10.1016/j.marmicro.2010.09.007.

82. Murray, J.W. Larger foraminifera from Chagos Archipelago: Their significance for Indian Ocean biogeography. Mar. Micropaleontol. 1994, 24, 43–55. https://doi.org/10.1016/0377-8398(94)90010-8.

83. Thissen, J. The foraminifera of the Zanzibar Archipelago (Tanzania, East Africa). Dissertation, Rheinischen Friedrich-Wilhelms-Universitatat Bonn. 2014, 225p. http://hss.ulb.uni-bonn.de/2015/3866/3866.pdf.

84. Chasen, S.A. Foraminifera of the Kenya coastline. J. Foraminiferal Res. 1981, 11, 191–202. https://doi.org/10.2113/gsjfr.11.3.191.

85. Pignatti, J.; Frezza, V.; Benedetti, A.; Carbone, F.; Accordi, G.; Matteucci, R. Recent foraminiferal assemblages from mixed carbonate-siliciclastic sediments of southern Somalia and Eastern Kenya. Ital. J. Geosci. 2012, 131, 47–65. http://doi 10.3301/IJG.2011.22.

86. Cherif, O.H.; Al-Ghadban, A.N.; Al-Rifaiy, I.A. Distribution of foraminifera in the Arabian Gulf. Micropaleontology. 1997, 43, 253–280. https://doi.org/10.2307/1485827.

87. Amao, A.O.; Kaminski, M.A.; Setoyama, E. Diversity of foraminifera in a shallow restricted lagoon in Bahrain. Micropaleontology. 2016, 62, 197–211. https://www.jstor.org/stable/26645516.

Appendix I. Species identified from 13 locations of ~10 and ~50 m depth in the Andaman and Nicobar Islands with the reference that illustrates the species

Amphistegina bicirculata Larsen, 1976	Hohenegger [82], Fig. 5 (3)
Amphistegina lessonii d'Orbigny in Deshayes, 1830	Hohenegger et al. [31], Fig. 19
Amphistegina lobifera Larsen, 1976	Hohenegger [27], Fig. 8
Amphistegina papillosa Said, 1949	Hohenegger [27], Fig. 8
Amphistegina radiata (Fichtel & Moll, 1798)	Hohenegger et al. [31], Fig. 20
Baculogypsinoides spinosus Yabe & Hanzawa, 1930	Hohenegger [82], Fig. 6 (9)
Calcarina mayori Cushman, 1924	Renema (2002), Pl, 5 Fig. 5-6
Calcarina spengleri (Gmelin, 1791)	Renema & Hohenegger (2005), pl. 1,2
Neorotalia calcar (d'Orbigny in Deshayes, 1830)	Hohenegger et al. [31], Fig. 21
Heterostegina depressa d'Orbigny, 1826	Hohenegger et al. [31], Fig. 30
Operculina ammonoides (Gronovius, 1781)	Hohenegger et al. [31], Fig. 28
Operculina complanata (Defrance in Blainville, 1822)	Hohenegger [31], Fig. 6
Palaeonummulites venosus (Fichtel & Moll, 1798)	Hohenegger et al. [31], Fig. 29
Planoperculina heterosteginoides Hottinger, [25]	Hohenegger [31], Fig. 6
Planostegina operculinoides (Hofker, 1927)	Tripathi [46] Pl. 3, Fig. 4
Alveolinella quoii (d'Orbigny, 1826)	Hohenegger et al. [31], Fig. 13
Borelis schlumbergeri (Reichel, 1937)	Madkour and Ali [64], Fig. 3 (1&2)
Euthymonacha polita (Chapman, 1900)	Langer et al., (2013) Fig. 7 (23&24)
Monalysisdium acicularis (Batsch, 1791)	Debenay [68] p. 112
Monalysidium confuse (McCulloch, 1977)	Debenay [68] p. 112
Peneroplis pertusus (Forsk˚al in Niebuhr, 1775)	Hohenegger et al. [31], Fig. 9
Peneroplis sp. Montfort, 1808	Loeblich and Tappan, [58] p. 379
Peneroplis planatus (Fichtel& Moll 1798)	Hohenegger et al. [31], Fig. 8
Amphisorus hemprichii Ehrenberg [71]	Hohenegger et al. [31], Fig. 16
Parasorites orbitolitoides (Hofker, 1930)	Hohenegger et al. [31], Fig. 14
Sorites orbiculus (Forsk˚al in Niebuhr, 1775)	Hohenegger et al. [31], Fig. 15

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