

## Larger benthic foraminifera and their distribution patterns on the Spermonde shelf, South Sulawesi

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A systematic description of the distributional pattern of 20 species of larger benthic foraminifera on the Spermonde Archipelago and their relation with environmental parameters is presented. Around 13 islands transects at the exposed and leeward slope were sampled.

Apart from parameters like substrate type, hydrodynamic energy and light intensity (directly related to depth) also nutrient availability and environmental stability determine the distribution over the shelf. Some of the species, and especially the calcarinids, are less specialised to some of these parameters than in other areas.

*Elphidium craticulatum*, showing chloroplast husbandry, is an important fauna component.

### Introduction

During most of the Cenozoic, larger benthic foraminifera contributed much to the carbonate production on tropical shelves (Hallock, 1981b; 1997). At the Great Barrier Reef, sediment contained up to 35% dry weight of larger foraminifera in the inter-reef and reef sediments (Scoffin & Tudhope, 1985; Yamano et al., 2000). By volume, Cenozoic limestones may consist of up to 80% larger foraminifera (Hallock, 1981b). Modern-day equivalents to the depositional setting of these environments can be found on shallow carbonate platforms with a barrier reef system, such as the Spermonde Archipelago, South Sulawesi, Indonesia.

Due to their symbiotic nature, larger foraminifera are restricted to areas within the photic zone that are low in nutrients (Hallock, 1987). Large, benthic foraminifera harbour four main types of symbionts: chlorophytes, rhodophytes, diatoms and dinoflagellates. Each foram species houses only one of these four types. Because each symbiont type uses its own range of the light spectrum, the foraminifera hosts are restricted in their depth distribution. Chlorophytes (using green light) are restricted to the shallowest areas, diatoms and dinoflagellates can live in the deepest settings.

Some of the diatom- and dinoflagellate-bearing foraminifera have a very open host-symbiont relationship. One foram species may host up to 20 different diatom species at a time, but this number is restricted to only one in a certain population in a particular depth range (Lee & Anderson, 1991). Since, each diatom species has its own depth preference, switching between various symbionts enables the host species to be less restricted in depth range.

Larger foraminifera can regulate the amount of light reaching their symbionts in two ways, finding shelter in shaded areas (for example between seagrass or macro-

algae leaves) or by moving their symbionts inside the shell away from the light. The latter method requires a dark non reflecting surface, such as rubble covered by algae or seagrass leaves (Hottinger, 1997).

Hydrodynamic energy and light intensity may both be reflected in the shell morphology of the benthic forams (Hallock et al., 1991). Foraminifera build more robust shells in high energy environments, whereas in quiet environments thin-walled shells dominate. Especially in miliolids, which show an opaque porcelaneous wall structure, thick-walled species produce structures like windows and pores to enhance light penetration through the shell (Hallock et al., 1991).

Both water turbulence and light level tend to reduce with depth. In order to utilise low light intensities, deep living symbiont-bearing foraminifera tend to maximise the surface to volume ratio. Complex internal structures improve both test strength and light availability for the symbionts and are found in many, but not all, species of larger foraminifera (Hallock, 1985; Hallock et al., 1991).

Because of their long life span, larger foraminifera favour stable conditions. The association with symbionts increases the metabolic rate and calcification of larger foraminifera in periods that light is available to the symbionts. Light penetration into the water column varies annually with the season. During the dry season, larger foraminifera might receive enough light, whereas during the wet monsoon, light penetrates less deep into the photic zone. In such situation, the symbiont is not profitable anymore to the host, since it demands energy and shelter but gives nothing in return.

Recent studies on ecological parameters affecting the distribution of larger symbiotic foraminifera have been focused on oligotrophic reef areas. These are characterised by low terrestrial influx, low nutrient levels and consequently little plankton in the water column and a relatively deep photic zone.

Hottinger (1977, 1983, 1988) showed that the distribution of larger foraminifera in the Gulf of Aqaba, is determined by sediment structure, light intensity, water energy and food availability. Hohenegger (1994) and Hohenegger et al. (1999) studied the occurrence of 21 species of larger foraminifera near Okinawa (Ryukyu islands, Japan) in terms of light intensity, water movement and substrate type. They found that each species showed its own characteristic distribution with respect to these parameters.

At both areas a depth zonation pattern was found for larger foraminifera. Other studies dealing with ecological parameters of living larger foraminifera were only done at Palau and Hawaii (Hallock, 1984) and Palau (Hohenegger, 1996). A few other studies dealt with only a limited number of species. For example, Lipps & Severin (1986) described the occurrence of *Alveolinella quoyii* in Madang lagoon.

Hallock (1987, 1988) indicated the importance of nutrient levels on the diversity and distribution of larger foraminifera in both time and space. She showed that the absence of a deep euphotic assemblage in the Caribbean and at some areas in the Indo-Pacific is related to relatively high nutrient levels. Species specialised in oligotrophic conditions are large, with a high surface to volume ratio. To reach such a size, a long growth period (possibly several years) of favourable circumstances is needed. Oligotrophic regions show more stable conditions, allowing the occurrence of specialised deep water species. In contrast, in coastal areas with much fluvial run off, which is an important nutrient source the deepest part of the photic zone is usually not available

for large, long-living foraminifera due to the light limitations during the wet monsoon.

Cenozoic strata rich in larger foraminifera that have been deposited in coastal areas with some terrigenous run-off such as the Tonasa-formation in Sulawesi (Wilson, 1996; Wilson & Bosence, 1996) and the Eocene deposits of Nanggulan on Java make up an important part of Cenozoic deposits in the tropics.

However, no recent equivalents to these areas have been studied with regard to the occurrence of larger benthic foraminifera. In the present study, the larger, symbiont-bearing foraminifera occurring on a mesotrophic shelf are described. Their cross-shelf depth distributions are compared with published data.

### Area

The Spermonde Archipelago is situated on a shallow carbonate shelf bordered in the east by the south-western peninsula of Sulawesi and in the west by the Makassar Strait. The shelf is approximately 40 km wide and increases gradually in depth until a maximum depth of about 60 m is reached just before the discontinuous barrier (fig. 1). Cay-crowned reefs and shoals occur in rows parallel to the coast. In the outershelf area these reefs remain submerged and do not develop cays. Cay crowned reefs

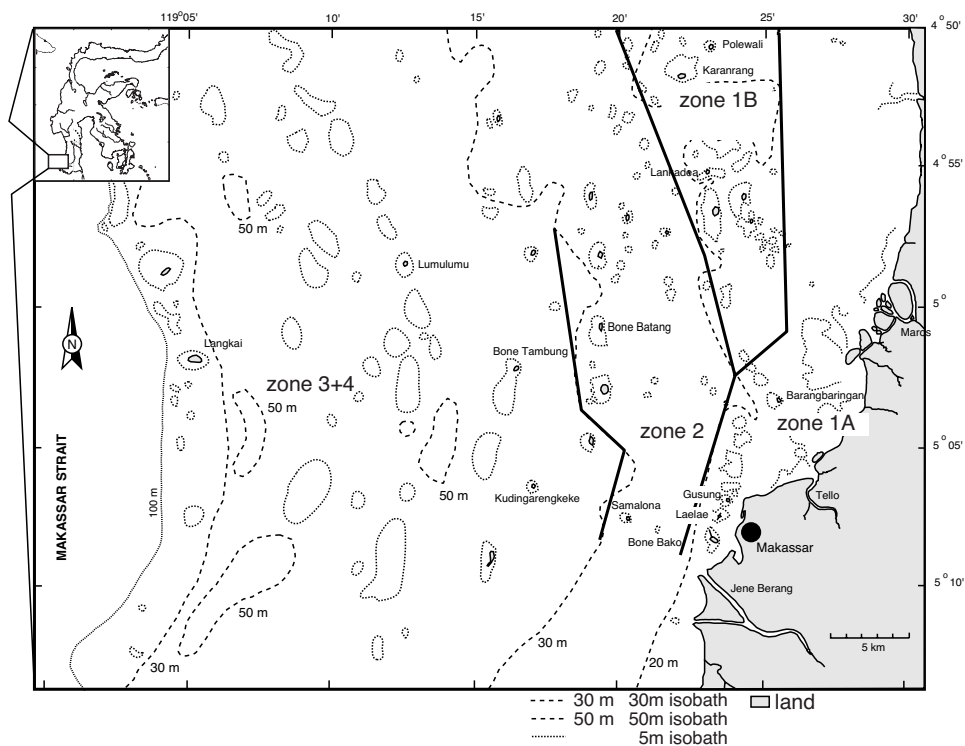


Fig. 1. Map of the research area showing all reefs that have been visited during this study. Self sampling zones: 1a: Southern Near Shore, 1b: Northern near shore; 2: Mid Shelf; 3+4: Outer Shelf.

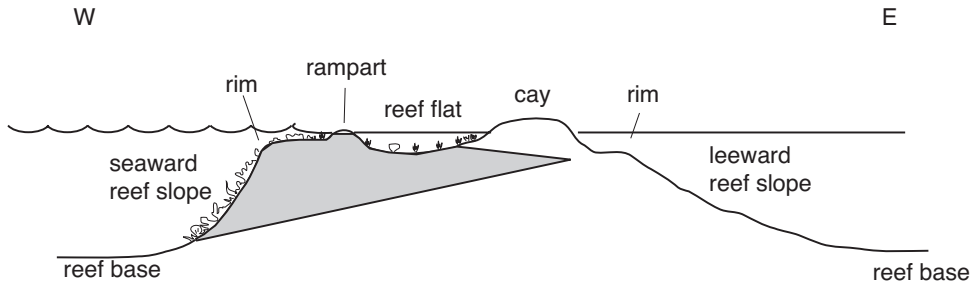


Fig. 2. Schematic section through a typical sand cay reef as found in the Spermonde Archipelago. Elements used in the text are indicated. Scale differs for each island and area. Coral cover reaches about 30 m depth in zone 3+4, but only a maximum of 6 m in zone 1A. Shaded area indicates the extend of the coral cover on the north and south sides of the reefs.

develop in seas with high hydrodynamic energy. Reef debris is swept on the reef flat, usually forming shingle ramparts, bordering a shallow reef flat at the exposed side, and an island on the leeward side (Guilcher, 1988). The reef flat in between the coral rubble rampart and island usually is very shallow (not more than 0.5 m at low tide). The reef flanks at the windward side are covered with dense coral growth, while the leeward reef slope consists of a sandy slope (fig. 2).

At the Spermonde Archipelago, the shape of the reefs is determined by a monsoon system with the highest hydrodynamic energy during the wet north-west monsoon from November until March; in this period the wave energy is combined with oceanic swell coming from the Pacific (Umbgrove, 1929; Umbgrove, 1930; de Klerk, 1983). In the dry season, south-eastern winds are weaker because the area is sheltered by the mainland and the influence of oceanic swell is less (Hoeksema, 1990).

Two major rivers flow onto the southern part of the Spermonde shelf, i.e. the Maros in the north and the Jene Berang in the south. The discharge of the Jene Berang is the largest of the two, and it does not only contain erosion products from the volcanic drainage area, but also waste of the sewer system of Makassar, a city with over a million inhabitants. The Maros is much smaller and its discharge is mainly derived from a carbonate rich drainage area. Fluvial influence on the shelf is restricted to a zone extending four kilometres from the coast (Storm, 1989). In this zone, nutrient levels, silt and sand content are higher, limiting visibility measured by secchi discs to only 5 m depth in the dry and 2.5 m in the wet season (Erfteemeijer, 1993). Salinity is slightly lower during the dry season in this zone (31-32‰ compared to 35-36‰ in the outershelf areas (Erfteemeijer, 1993)). During the rainy season, coastal salinity decreases with 10-15‰ in the surface water and the nutrient levels are about 2-3 times higher than during the fair weather season (Erfteemeijer, 1993). The waters outside this first shelf zone all show comparable nutrient levels that do not vary throughout the year (Erfteemeijer, 1993).

Further than four kilometres offshore, the sediments contains 75-85% carbonate, increasing to 85-95% around the barrier (Verheij, 1993). Secchi depth increases going off shore, reaching its maximum value (30 m) during the dry season around Lankai, on the barrier reef at the shelf margin (Erfteemeijer, 1993). During the wet season high

turbidity and terrigenous input decreases light penetration, with secchi depth half those of the in dry season (Verheij, 1993).

Coral rubble and sandy substrates are the most important substrates for larger benthic foraminifera in the Spermonde Archipelago. Areas with a dense cover of sea-grass and macroalgae, which are an important substrate for larger foraminifera in other Indo-Pacific areas are rare. Coral rubble covered by coralline algae is the main substrate on the western slopes of the reef, where it is found in between living corals. At some places, rubble avalanches, caused by the seasonal storms and the oceanic swell provide abundant substrate for larger foraminifera. Especially at reefs in the outershelf, living coral cover can be very dense at 12-24 m, and very little illuminated substrate is available for larger foraminifera. Sandy substrate is present on the reef flat, the leeward reef slope and the reef base. On the reef flat, sand pockets between patches of living corals usually show wave ripples. These moving sands are not suitable substrate for larger foraminifera because of continuous burying, breakage and transport out of the area.

On the basis of geography, geomorphology and distance to the shore, the Spermonde was divided into four shelf zones (van Vuuren, 1920). These zones differ in biotic and abiotic parameters (de Klerk, 1983; Moll, 1983; Hoeksema, 1990; Erftemeier, 1993). Not all authors use the same zonation. Moll (1983) ignored the first zone, whereas Verheij (1993) combines the second and third zone. Hoeksema (1990), using free-living corals, recognises all four zones. In the present study a slightly modified zonation is used, clarifying the terrestrial impact on the distribution of larger foraminifera. In order to compare results, the classification of the shelf zones resembles those given by Van Vuuren (1920) and Hoeksema (1990). Zone 1A (Southern Near Shore area) is bounded by the 20 m isobath and within 4 km from the shore, while zone 1B (Northern Near Shore area) is also bordered by the 20 m isobath, but the islands are more than 4 km from the shore. Zone 2 (Midshelf area) has a maximum depth between 20 m and 30 m, all other islands were situated in the combined zone 3+4 (Outershelf area).

## Methods

Foraminifera samples were taken (August-November 1997), by hand during SCUBA diving down to a depth of 33m. All suitable substrate was collected from a circular sampling area of 1000 cm<sup>2</sup> and taken to the laboratory. The samples were sun-dried after which the foraminifera were detached from their substrate. All samples were sieved over a 0.5 mm sieve before sorting. We counted the larger foraminifera that were sampled alive. They could easily be recognised as being alive at the moment of sampling since they differed from dead tests by their symbiont colour.

186 samples have been collected at the leeward (east) and seaward (west) sides of 13 reefs (named on fig. 1) at 3 m depth intervals. Of these samples, 182 contained living larger foraminifera. Three islands were sampled in the Southern Near Shore, Northern Near Shore and Midshelf zones, and four islands were sampled in the Outershelf zone (table 1).

Presence/absence data are used to determine ecological preferences of species. A

Table 1. Samples taken in the Spermonde area, 0 = sample taken, but did not contain larger foraminifera, 1 = sample taken containing larger foraminifera, 2 = two samples taken containing larger foraminifera.

depth	1A				1B				2											3+4																			
	2	3	6	9	12	3	6	9	12	15	1	1.5	2	3	4	6	9	12	15	18	21	24	27	1	2	3	4	6	7	9	10	12	15	18	21	24	27	30	33
<b>exposed</b>																																							
Laelae		1	1	1	1																																		
Gusung		1	1	1	0																																		
Baranberingan	1	1	1	1	0																																		
Polewali						1	1	1	1	1																													
Karanrang						1	1	1	1	1																													
Lankadea						1	1	1	1	1																													
Bone Baku														1	1	1	1	1	1	1	1	1	1																
Samalona														2	2	1	1	1	1	1	1	1	1	1															
Bone Batang														1	1	1	1	1	1	1	1	1	1																
Kudingareng Keke																																							
Bone Tambung																																							
Lumulumu																																							
Langkai																																							
<b>leeward</b>																																							
Laelae		1	1	1	0																																		
Gusung		1	1	1	0																																		
Baranberingan																																							
Polewali						1	1	1	1	1																													
Karanrang						1	1	1	1	1																													
Lankadea						1	1	1	1	1																													
Bone Baku																																							
Samalona														1	1	1	1	1	1	1	1	1	1																
Bone Batang														1	1	1	1	1	1	1	1	1	1																
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Bone Tambung																																							
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Langkai																																							

species is considered present if at least five specimens occur in a sample of 200-300 specimens. The presence/absence data are compared with the random distribution in all samples on the parameters leeward slope vs seaward slope and firm vs. sandy substrate using a chi square test.

In addition, grab samples have been taken in three transects over the Spermonde shelf. These samples often showed a disturbed sediment-water surface, and therefore could not be used to obtain quantitative data. However, during sampling the presence of large species on top of the grabs has been recorded. This provided additional information on the maximum depth at which some of the species occur.

**Results**

On both the leeward and exposed sides of zone 3+4 reef slopes, densities were slightly higher than in the other areas (fig. 3), reaching up to 6 foraminifera cm<sup>-2</sup>. Except for the Southern Near Shore zone (1A), highest densities were found in the deepest (reef base) samples. Due to depth variations of the shelf bottom around reefs, this pattern is not clear in the Midshelf zone (2). Reef base samples contain 4-6 foraminifera cm<sup>-2</sup>, slope samples 1-3 specimens cm<sup>-2</sup>.

At the Northern Near Shore (1B), Midshelf (2) and Outershelf (3+4) zones, the maximum depth at which larger foraminifera were observed, was in the deepest samples taken of the transects (15 m at the Northern Near Shore, 24-27 m at the Midshelf and 33 m at the Outershelf zone). The Outershelf area grab samples showed that the maximum depth at which larger foraminifera lived was 40 m. In the Southern Near Shore area larger foraminifera were only observed in the shallowest samples (down to 6-9 m), and were absent on the reef base (samples taken down to 12 m).

In total 21 larger foram species have been found. They will be discussed systemat-

Table 2. Chi square values and the falsification change of the null hypothesis that the samples in which a species occurred was the same as the total set of samples analysed. The fourth and seventh column gives an indication which slope direction (E= Exposed, L= Leeward) or substrate type (H= solid, Z= soft) is over-represented.

soort	chi-square	P	E<>L	chi-square	P	H<>Z
<i>Operculina ammonoides</i>		2		1,0	<0.001	Z
<i>Nummulites venosus</i>		11,7			<0.005	Z
<i>Alveolinella quoyii</i>						
<i>Amphistegina papilosa</i>	5,43	<0.05	E	8,10	<0.005	Z
<i>Elphidium craticulatum</i>	9,39	<0.005	E			
<i>Dendritina ambigua</i>	4,45				<0.05	Z
<i>Parasorites orbitolitoides</i>	27,0				<0.001	Z
<i>Calcarina gaudichaudii</i>	42,0	<0.001	E	21,8	<0.001	H
<i>C. hispida</i>						
<i>Baculogypsinoides spinosus</i>	25,6	<0.001	E			
<i>Peneroplis pertusus</i>						
<i>Spirolina arietina</i>						
<i>Neorotalia calcar</i>	22,9	<0.001	L			
<i>Peneroplis planatus</i>	19,9	<0.001	L			
<i>Laevipeneroplis proteus</i>						
<i>Amphisorus hemprichii</i>	33,9	<0.001	E	35,0	<0.001	H
<i>Amphistegina radiata</i>	64,0	<0.001	E	33,5	<0.001	H
<i>Heterostegina depressa</i>	40,5	<0.05	E	35,0	<0.001	Z
<i>Sorites orbiculus</i>						

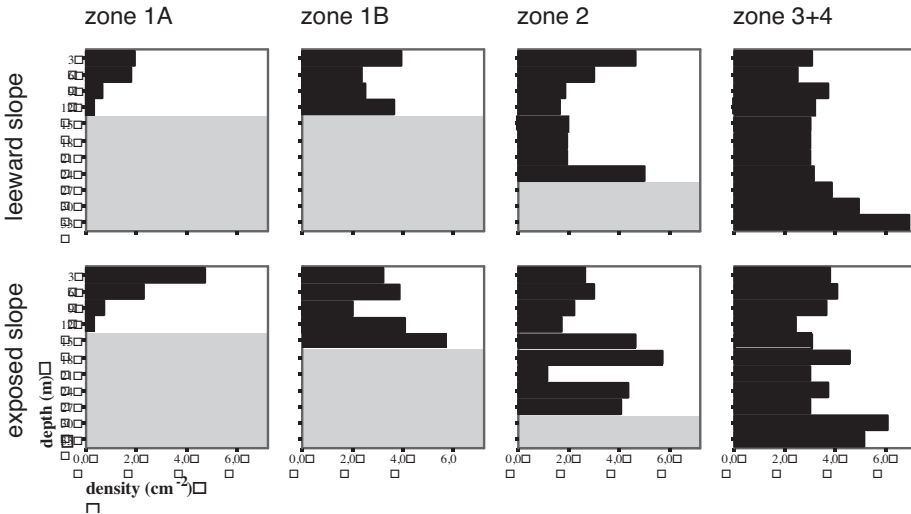


Fig. 3. Bar diagram showing the average density of larger benthic foraminifera on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

ically in the following section. Per species, a short description with the most important characters and symbiont type will be presented, with remarks on occurrence at the Spermonde Shelf and comparative distribution data from other areas reported in the literature.

**Systematic account**  
**Suborder Miliolina**  
**Family Peneroplidae**  
*Peneroplis planatus* (Fichtel & Moll, 1798)  
 (fig. 7a, b)

**Description.**— Test very thin and flat, planispiral and involute. Chambers in last whorl rapidly increase in width with nearly constant height, giving test flaring appearance. Last whorl shows some derolment, which in some specimens even may cause loss of contact with the former whorl in the last few chambers. Chambers with fine striae on outer surface.

**Affinities.**— The much rarer *Peneroplis pertusus* (Forskål, 1775) is evolute, with a marked umbilicus and no widening in the last whorl. The striae on the chamber walls are coarser. Both species differ from *Dendritina* species by the linear arrangement of multiple circular to oval apertures.

**Symbiont type.**— Rhodophyte, *Porphyridium purpureum* (Lee & Anderson, 1991; Leutenegger, 1984).

**Distribution.**— *P. planatus* is the most abundant peneroplid of this study with densities up to 0.7 cm<sup>-2</sup>. It occurred significantly (chi-square test,  $p < 0.001$ , table 2) more abundant on the leeward reef slopes than on the exposed slopes. *P. planatus* did not show a clear preference for substrate type. Samples with a high abundance of this species were often taken in the vicinity of the seagrass *Halophylus ovalis*. Although no

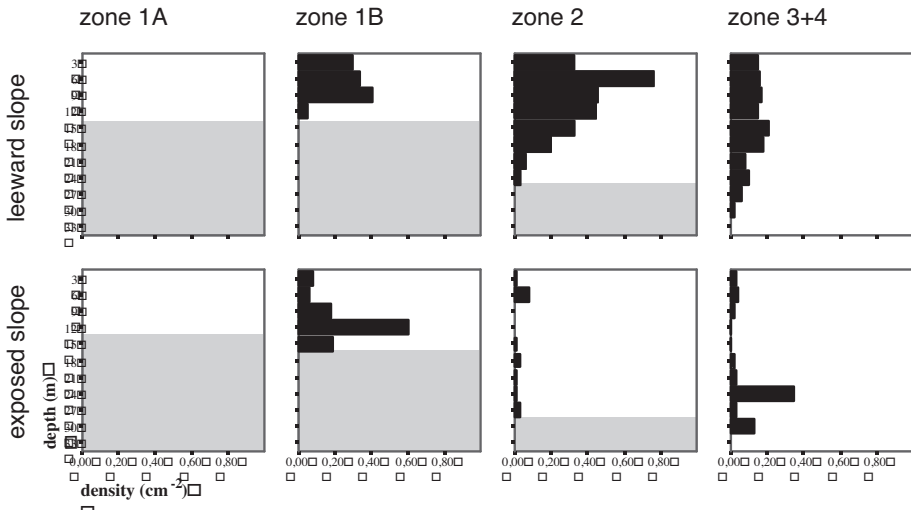


Fig. 4. Bar diagram showing the average density of *Peneroplis planatus* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.



specimens were seen living on seagrass leaves, some were found attached to its root system. The highest densities have been found at 3-12 m depth in the Northern Near Shore and Midshelf area (fig. 4), in the Outer Shelf Zone, the maximum depth at which *P. planatus* was found is 30 m.

Discussion.— Just like at the Spermonde (fig. 4), at Okinawa, life specimens were found at 0-30 m depth, with the highest density in the upper 10 m (Hohenegger et al., 1999), but Hallock (1984) observed it at Palau from 1-5 m depth only.

Hohenegger (1994, 1996) recorded this species living attached to fine algal mats on solid substrates, where they find shelter against turbulence. The high light requirements and position of the apertures in the shell prevent *P. planatus* to live attached to large macroalgae (Hohenegger, 1994). Hohenegger et al. (1999) state that 'sandy substrates are clearly avoided', because *P. planatus* can not attach to the sediment and will be buried or swept away. In this study substrate preference is markedly different from that at Okinawa.

Troelstra et al. (1996) found abundant peneroplids (*P. pertusus* and *P. planatus*) on reefs in the Outershelf zone, where they lived preferentially epiphytic on algae and seagrasses from 1-21 m. Due to the unavailability of the preferential habitat known from other areas, *Peneroplis planatus* has moved to a different habitat at the Spermonde Archipelago.

*Dendritina ambigua* (Fichtel & Moll, 1798)  
(fig. 7c, d)

Description.— Test planispiral and involute. *Dendritina* differs from *Peneroplis* by its dendritic aperture. Test surface very finely striate with small pores in depressions between the striae, the striae are slightly oblique to the sutures. The shell is involute, sometimes showing a very small umbilical depression. In large specimens, last 2-4 chambers flaring.

Affinities.— The congeneric *D. zenghae* Ujuie at the Spermonde Archipelago is more evolute, always showing a clear umbilicus and a smooth surface. Last whorl in large specimens is flaring, increasing in size and arched, so that it has a flattened periphery. Large specimens of *Dendritina* can be mistaken for *Laevipeneroplis proteus* (d'Orbigny, 1839), which has a larger umbilicus, a row of pores on the aperture surface and chlorophytic symbionts (Leutenegger, 1984) (fig. 7e, f).

Symbiont type.— Rhodophyte, *Porphyridium purpureum* (Lee & Anderson, 1991; Leutenegger, 1984).

Distribution.— On the Spermonde Shelf, *D. ambigua* showed a significant preference for sandy sediments (chi square test,  $p < 0.05$ , table 2) as well, but no preference for either leeward or seaward slope was found. *D. ambigua* is found at depths ranging from 10-30 m in reef base samples and in some shallower samples on the leeward side around reefs all over the shelf, except in the southern near shore area (fig. 5). It usually occurred in areas on the shelf bottom where organic detritus and algae accumulated.

*D. zenghae* was only found in two samples in very low densities. It was photographed at the reef base of several Midshelf and Outershelf reefs, together with *Assilina ammonoides* and *Parasorites orbitoloides* (fig. 24d, e).

*L. proteus* was found in one sample taken at the west side of the Outershelf reef

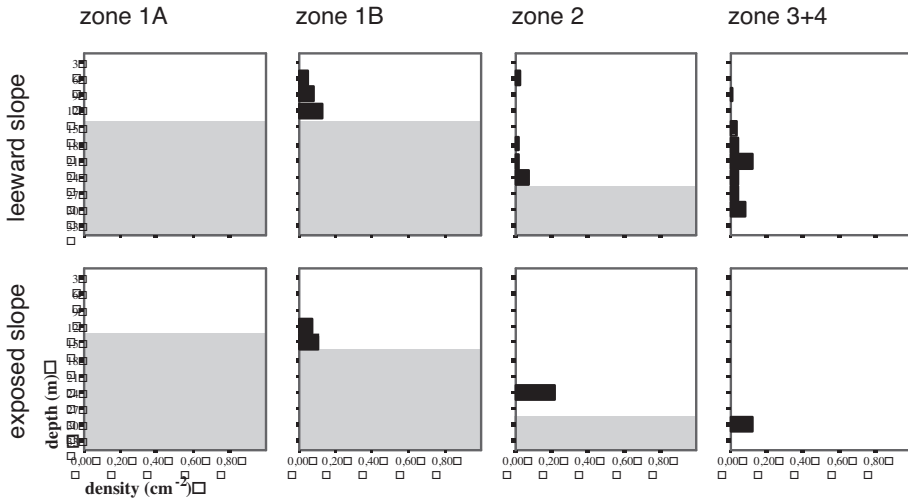


Fig. 5. Bar diagram showing the average density of *Dendritina ambigua* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

Lankai at 2m depth, where it co-occurred with *Amphisorus hemprichii* on macro-algae that were attached to coral rubble in a very highly hydrodynamic setting.

Discussion.— Next to *P. planatus*, the only other abundant peneroplid in the Spermonde Archipelago is *D. ambigua*. Both *Dendritina* species have previously only been reported alive from Okinawa, where *D. zhengae* occurred at 10-50 m and *D. ambigua* at 10-30 m with a maximum density at 20m. At Okinawa *D. ambigua* showed a significant preference for sandy substrates as well (Hohenegger, 1994; Hohenegger et al., 1999).

The depth distribution at the Spermonde Archipelago is similar to that at Okinawa. This species lives predominantly on stable sands in relatively quiet areas at the reef base. On the higher parts of the reef slopes and reef flat, the substrate is to regularly disturbed.

**Family Soritidae**

*Parasorites orbitolitoides* (Hofker, 1930)

(fig. 7g, h)

Description.— Test round, flat, and smooth. Its height hardly increases towards the periphery. First few chambers peneropline, later chambers annular. All chambers divided into chamberlets. Small, round apertures occur in one or two rows in a groove at the periphery (Loeblich & Tappan, 1988).

Affinities.— Because of its green colour and delicate appearance, this species is easily distinguished from other Soritidae.

Symbiont type.— Chlorophytic algae (Hallock & Peebles, 1993).

Distribution.— In the Spermonde area, a similar distribution pattern as for *D. ambigua* is found. *P. orbitolitoides* has a significant preference for soft substrate (table 2). The chlorophyte symbionts limit the depth distribution to shallow areas.

All samples in which *P. orbitolitoides* was found were taken at the reef base, with

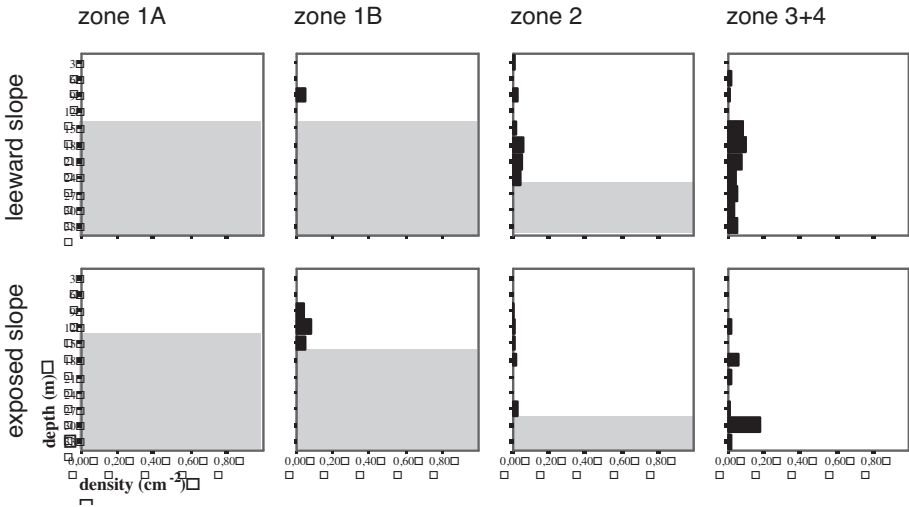


Fig. 6. Bar diagram showing the average density of *Parasorites orbitolitoides* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

highest densities in the Northern Nearshore and Midshelf zones (fig. 6). Here it occurred most abundantly at places with organic detritus accumulations, which occasionally covered the sides of the foraminifera (fig. 24f). In the Outershelf zone, off Lankai, *P. orbitolitoides* was also found on a gently declining leeward slope.

Discussion.— Unlike at the Spermonde, *P. orbitolitoides* has been reported from both solid and sandy substrates. Hohenegger et al. (1999) found a significant preference for sandy substrates at Okinawa, where *P. orbitolitoides* was found at 10-70 m depth. Hallock & Peebles (1993) found *P. orbitolitoides* living on coral rubble at 15-30 m depth in the Florida Keys. In the Gulf of Aqaba this species lives at 0-50 m on hard substrates and epiphytic on macro-algae (Hottinger, 1977). Due to its chlorophyte symbionts, *P. orbitolitoides* needs rather high light intensities. With its thin test walls and fragile test this species can not stand in high energy settings, but it can live in relatively deep water compared to other chlorophyte bearing species. At the Spermonde Shelf, this is only in areas without coral cover, restricting this species to soft substrate.

*Sorites orbiculus* (Forskål, 1775)  
(fig. 10a, b)

Description.— Discoidal test, initial few chambers planispiral evolute, at an early stage succeeded by annular ones. Aperture form a single row of openings with protruding rims and 8-shaped apertures resulting from cross like oblique stolons (Loeblich & Tappan, 1988).

Affinities.— Superficially similar to *Amphisorus hemprichii*. The test is thinner and the apertural face differs (see description of both species). The test of *Sorites orbiculus* is much smaller than that of *Amphisorus hemprichii*. Underwater, *S. orbiculus* is greyish brown, while *A. hemprichii* has a greenish blue colour. Dried specimens of *A.*

*hemprichii* are dark red-brown, while *S. orbiculus* remains greyish brown.

Symbiont type.— Dinoflagellate, *Symbiodinium* spec. (Leutenegger, 1977; Lee & Anderson 1991).

Distribution.— *S. orbiculus* was found regularly, but always in very low densities at the Spermonde Archipelago (usually 1-5 specimens per sample). *S. orbiculus* did not show any preference for substrate type or slope direction (table 2). Troelstra et al. (1996) found this species living abundantly on *Enhalus* seagrass-leaves, especially on the reef flat. Furthermore they state that this species is hardly found on solid substrates. The low abundance of *Enhalus* on the reef flat during the present study, explains why we found much lower numbers of *S. orbiculus* than Troelstra et al. (1996).

Discussion.— This species has been reported as epiphytic on sea grasses and macro-algae (Hohenegger, 1996; Troelstra et al., 1996), usually in shallow water (0-30 m, Hohenegger, 1994).

Unlike some other species, this species is not able to shift to another substrate when its preferred habitat is not present. According to Hohenegger et al. (1999) *S. orbiculus* prefers more structured surfaces when it occurs on solid substrates. The coral rubble at the Spermonde show rather smooth surfaces. This might explain the abundance of *A. hemprichii* (preferring smooth surfaces) over *S. orbiculus* on coral rubble.

*Amphisorus hemprichii* Ehrenberg, 1839  
(fig. 10c, d)

Description.— *A. hemprichii* is the largest soritid found at the Spermonde Archipelago, reaching almost 1.5 cm in diameter. Test biconcave with thickened rims, aperture of numerous pores on the peripheral margin, elongated across the margin, and aligned in two alternating rows (Loeblich & Tappan, 1988). The test usually shows some radial lining on the test, especially in larger specimens.

Affinities.— see *Sorites orbiculus*.

Symbiont type.— Dinoflagellate, *Symbiodinium* spec.

Distribution.— *A. hemprichii* significantly prefers solid substrates (chi square test,  $p < 0.001$ , table 2) and the exposed reef slopes (chi square test,  $p < 0.001$ , table 2) in the Spermonde Archipelago. It was observed attached to large boulders by a protoplasm sheath to prevent detachment and breakage (fig. 24h). Around the margin, sediment grains were found stuck to this sheath. Large specimens occasionally occurred on soft substrate at the reef base. Its depth distribution depends on the distance to the shore (fig. 7); the more offshore, the deeper the range of the reef slope and the deeper the lowest depth limit of the species. In the Southern Near Shore area, in the proximity of large river outlets, it does not occur despite the availability of suitable substrate. Around reefs in the Northern Near Shore zone, *A. hemprichii* only occurred in the shallowest samples. At the Midshelf and Outershelf zones *A. hemprichii* occurs almost as deep as the maximum depth of the suitable substratum (18 m at the west side of Lankai), or over 20 m depth (e.g. 22 m at Karang Kassi reef, 21 m at Bone Tambung reef). In the Northern Near Shore zone, large specimens of *A. hemprichii* were also found at the reefbase, in between seagrass (*Halophilus*).

Discussion.— This species has been reported from firm substrate, irrespective of depth from the reef crest until 60 m depth (Hohenegger, 1994; Hohenegger et al.,

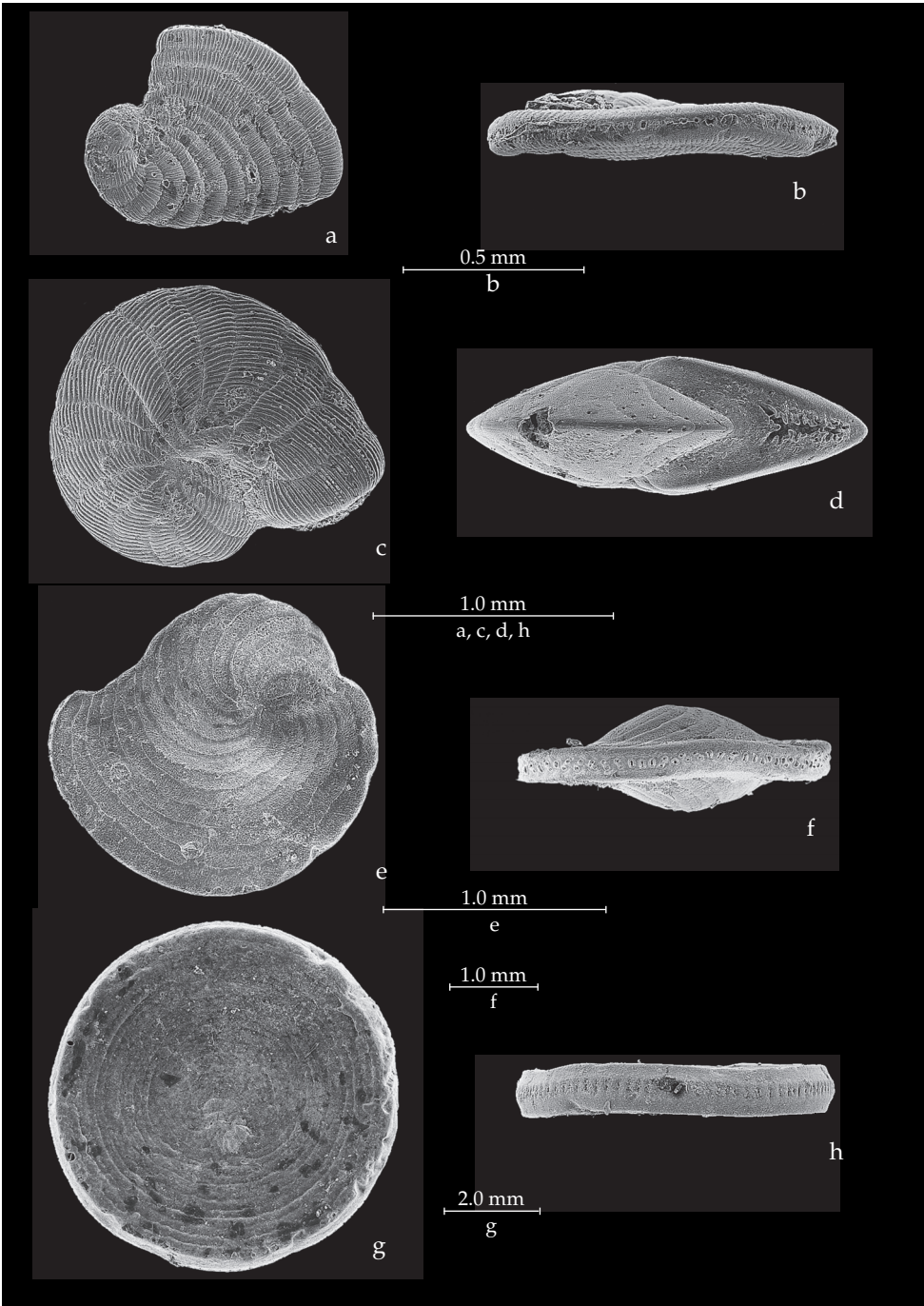


Fig. 7a, b: *Peneroplis planatus*. c, d: *Dendritina ambigua*. e, f: *Laevipeneroplis*. g, h: *Parasoritis orbitolitoides*.

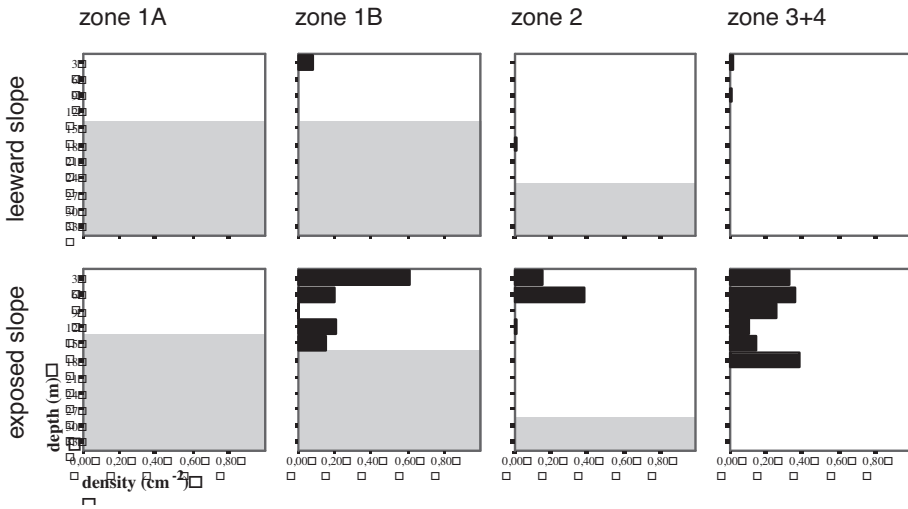


Fig. 8. Bar diagram showing the average density of *Amphisorus hemprichii* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

1999; Troelstra et al., 1996). Hohenegger, 1996, reported *A. hemprichii* from Palau at 0-10 m depth only.

Troelstra et al. (1996) found this species in high density on solid substrate in shallower water, often in places with high wave energy. At the Gulf of Aqaba, Hottinger (1977) found *A. hemprichii* living from 0-20 m mainly epiphytic on *Halophila* leaves and various algae.

In general, the habitat of this species can best be typified as highly illuminated regions in the uppermost slope and fore reef crest (Hohenegger et al., 1999). The distribution at SW Sulawesi is rather similar to that at other areas. At Okinawa it did not occur at the highly energetic upper reef crest, where *Marginopora vertebralis* was more abundant. The latter species does not occur on the Spermonde Shelf. *A. hemprichii* is found on solid substrates in the upper reef crest as well, and also in the very wave-exposed slope of Lankai. In these areas, irregularly shaped tests occur (fused, cork screw-shaped tests, test with parts perpendicular to the main disc). Toler & Hallock (1998) found high frequencies of shell malformations in stressed populations of *Amphistegina*. The irregular shaped tests might indicate that *Amphisorus* lives at the limits of its potential at the shallow exposed side of Lankai.

**Family Alveolinidae**

*Alveolinella quoyii* (d’Orbigny, 1826)

(fig. 10e)

Description.— Large fusiform miliolid (up to 1.5 cm) with many small, round pores on apertural face.

Affinities.— It is distinguished from all other foraminifera in the Spermonde by its fusiform shape. Specimens of *Borelis*, the only other extant alveolinid genus, have a single row of apertures on the apertural face.

Symbiont type.— Diatoms, *Fragliaria shiloi* and other species (Leutenegger, 1984, Lee & Anderson, 1991).

Distribution.— *A. quoyii* is a rare species at the Spermonde Archipelago. *A. quoyii* was regularly seen at the reef base and base of slope area, usually in low densities on sandy substrates at 18-24 m depth.

Discussion.— *A. quoyii* has been found living on highly structured firm substrates in well illuminated, high energy settings at 3-12 m depth (Lipps & Severin, 1986). Hohenegger (1994) and Hohenegger et al. (1999) report a wider distribution of this species, down to 50 m depth on both sandy and solid substrates. It is often observed in high energy environments, where it lives in sheltered crevices in boulders and rubble, as well as in low energy environments on sandy substrates below the wave base (Hohenegger et al., 1999). *A. quoyii* has been found in a wider environment outside the Spermonde Archipelago than within the Spermonde, where it does not occur in shallow water settings on solid substrates. This might be because the solid substrate in this area is not as structured and the coral rubble does not provide enough shelter during storms.

**Suborder Rotalida**  
**Family Amphisteginidae**  
**Genus *Amphistegina***

The genus *Amphistegina* is characterised by a low trochospiral, lenticular and inequally biconvex test, that can be bi-involute or partially evolute on the spiral side. Chambers are strongly arched at the periphery (Loeblich & Tappan, 1988).

*Amphistegina lessonii* d'Orbigny, 1826  
(fig. 10f)

Description.— Test flat involute trochospiral. Umbilical side thicker than the spiral side (Hohenegger, 1999). Dorsal septa radial, curving backwards at about 2/3 of shell radius. Ventral septa sinusoidal.

Affinities.— *A. lessonii* is most easily confused with *A. lobifera*. This latter has lobate septa, visible on both sides of large specimens, but difficult to see in smaller specimens (Hohenegger et al. 1999). *A. lobifera* is more globular and its margins are round, while the periphery of *A. lessonii* is angular.

Symbiont type.— Diatoms, *Nitzschia frustulum* var. *symbiotica* and other species (Leutenegger et al., 1984; Lee & Anderson, 1991).

Distribution.— *A. lessonii* is the most abundant larger foraminifera in the area. It occurs in almost all samples, but the highest densities have been found on shallow, soft substrates (down to 25 m depth) (fig. 9). The maximum depth at which *A. lessonii* occurred varied from 9 m at Lae Lae to 30-33 m around the Midshelf reefs (fig. 9). This pattern is similar to what Troelstra et al. (1996) reported, but they found much higher densities on the reef flat.

Discussion.— *A. lessonii* shows a very broad depth range in the Indo Pacific from 0-90 m (Hohenegger et al., 1999), with highest densities around 10-25 m (Hallock, 1984; Hohenegger, 1996). It has been reported to have either a preference for sandy (Hallock, 1984) and solid substrate (Hollaus & Hottinger, 1997). Hansen & Buchardt

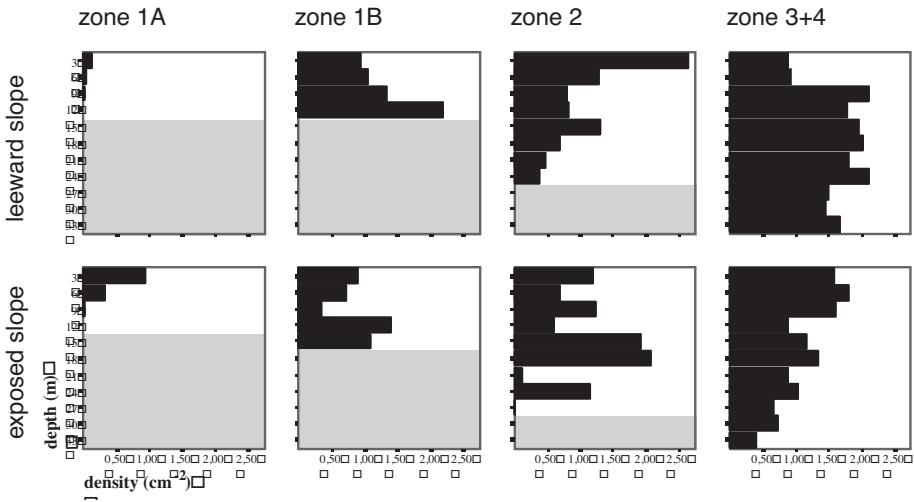


Fig. 9. Bar diagram showing the average density of *Amphistegina lessonii* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

(1977) found *A. lessonii* (empty shells and living specimens combined) from 0-85 m in the Gulf of Aqaba.

In the Spermonde, *A. lessonii* has no preference and is found on all substrates. Compared to other species, the shell shape of *A. lessonii* is adapted to living on sandy substrates that are moved by waves (Hohenegger et al., 1999). On the soft substrate at the leeward slope, *A. lessonii* is the most common species.

*Amphistegina lobifera* Larsen, 1880  
(fig. 10h)

Description.— *A. lobifera* is very similar to *Amphistegina lessonii*, from which it is distinguished because of its lobate septa. This is especially clear in large specimens, and more difficult to see in smaller specimens (Hohenegger et al., 1999). Axial sections of this species are more rounded than in *A. lessonii*.

Affinities.— see *A. lessonii*.

Symbiont type.— Diatoms, *Nitzschia frustulum* var. *symbiotica* and other species (Leutenegger et al., 1984; Lee & Anderson, 1991).

Distribution.— *A. lobifera* was the rarest *Amphistegina*-species found. It only occurred in the shallowest samples, on both the eastern and western reef sides (fig. 11). No specimen was recorded from deeper than 12 m. The depth range of this species does not vary much between the four shelf zones, where it was found on both solid and soft substrates. On coral rubble, this species occurs below larger boulders covered with red algae. Here, *A. lobifera* occurred mainly on the sides, the largest specimens living closer to the boulder edges than small specimens.

Discussion.— The highest densities of *A. lobifera* have been found at very shallow depths (Hallock, 1984; Hohenegger, 1994; Hohenegger, 1996; Hohenegger et al., 1999).

Because of its thick shell, this species can live in the highest light-energy levels of



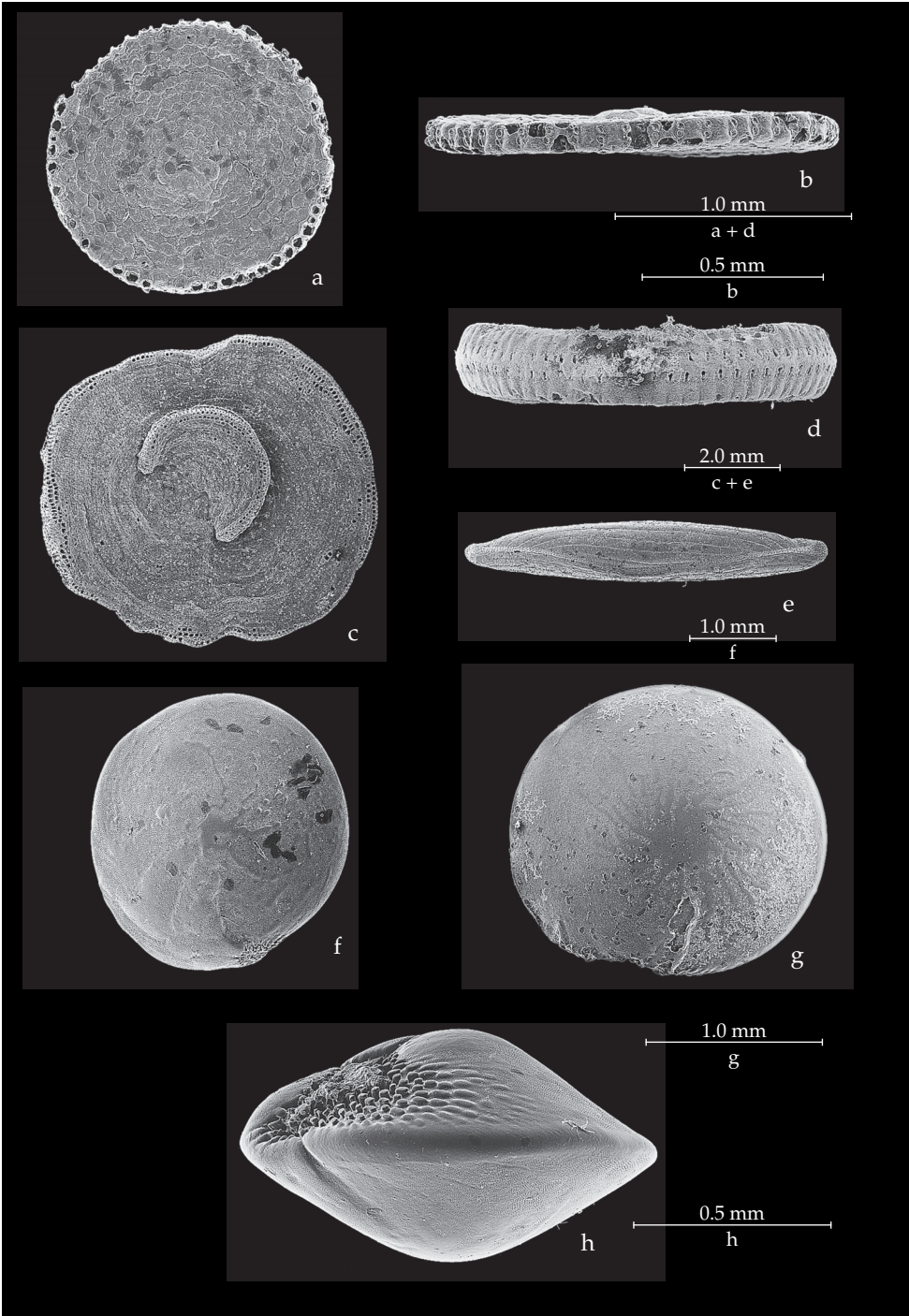


Fig. 10a, b: *Sorites orbiculus*. c, d: *Amphisorus hemprichii*. e: *Alveolinella quoyii*. f: *Amphistegina lessonii*. g: *Amphistegina radiata*. h: *Amphistegina lobifera*.

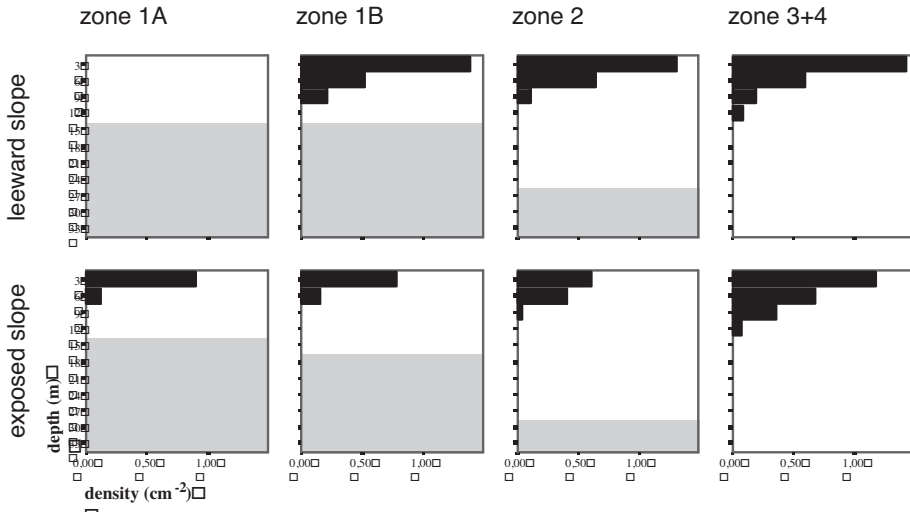


Fig. 11. Bar diagram showing the average density of *Amphistegina lobifera* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

all species of *Amphistegina* (Hallock, 1981a). *A. lobifera* had the best ability to attach to solid surfaces in order to withstand high hydrodynamic energy (Hallock, 1981a; Hohenegger et al., 1999). Similar to Hohenegger (1994) we did not find *A. lobifera* (or any other larger foraminifera) in high energy sands on the reef flats. *A. lobifera* was found on sheltered sandy substrates and in sheltered places between coral rubble covered by algae.

*Amphistegina radiata* (Fichtel & Moll, 1798)  
(fig. 10g)

Description.— Large biconvex tests, both sides showing radial orientation of the septa, turning backwards at about 2/3 of chamber height (Hohenegger, 1999).

Affinities.— The most similar species in the Spermonde Archipelago is *A. papillosa*, which is much smaller and flatter.

Symbiont type.— Diatoms, *Nitzschia frustulum* var. *symbiotica* and other species (Leutenegger et al. 1984; Lee and Anderson, 1991).

Distribution.— In the Spermonde Archipelago this species is found at 2-33 m depth (fig. 12). *A. radiata* significantly (table 2) preferred both firm substrates and the western slope of the reefs. At shallow depths specimens occur hidden between coral rubble, especially the smaller ones. *A. radiata* does not replace *A. lessonii* with depth, but is rather characteristic for solid substrates. *A. radiata* is more abundant in the 2-30 m depth range on solid substrate, while *A. lessonii* is dominant on soft substrates at the same depths.

Discussion.— *A. radiata* has been recorded from intermediate depths at solid substrates (Hohenegger et al., 1999; Troelstra et al., 1996). Hohenegger et al. (1999) explained its absence in shallow waters at the reef crest by its lesser ability to attach to the substrate than *A. lessonii* and *A. lobifera* because of small apertural fields. In the

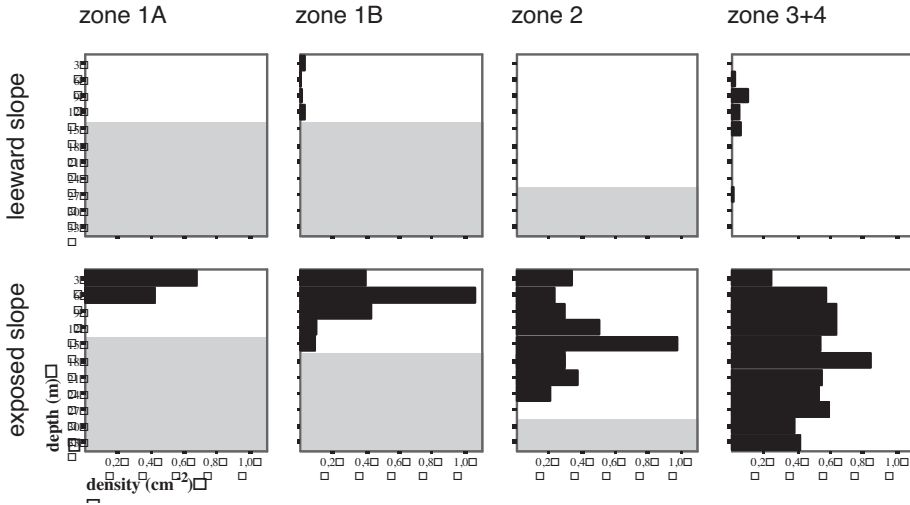


Fig. 12. Bar diagram showing the average density of *Amphistegina radiata* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

same area, Hohenegger (1994) found *A. radiata* on both solid and soft substrates in the shallow part of the range, and predominantly on soft substrates at greater depths. At Palau Hallock (1984) found that *A. radiata* replaced *A. lessonii* with depth.

At the Spermonde shelf, *A. radiata* and *A. lessonii* are found in the same depth range. *A. radiata* is found on the exposed side, while *A. lessonii* occurs both on the leeward side and the exposed side. Especially larger specimens of *A. radiata* are found abundantly on the surface of coral rubble (fig. 24a). *A. lessonii* was always found in cryptic, sheltered places (when it was found at the exposed side). In deep areas, with no solid substrates, *A. radiata* was present, but *A. papillosa* was more common.

*Amphistegina papillosa* Said, 1949

Description.— Small, very flat biconvex *Amphistegina* species.

Affinities.— The test surface is more pustulose on the ventral side than that of *A. radiata*. In living specimens, the septa are not as clearly visible as in *A. radiata*.

Symbiont type.— Diatoms, *Nitzschia frustulum* var. *symbiotica* and other species (Leutenegger et al., 1984; Lee & Anderson, 1991).

Distribution.— In this study *A. papillosa* was the deepest living representative of its genus, occurring on the reef base in all zones, except for the Southern Near Shore Zone (fig. 13). It was found at 6-15 m depth around Lankadea reef, 15-24 m around Samalona reef and 27-33 m (maximum depth of sampling) around Bone Tambung and other reefs in the outer shelf zone. It does not show a preference for slope orientation. *A. papillosa* has a significant preference for sandy substrates (chi square test,  $p < 0.005$ , table 2).

Discussion.— Of the amphisteginids found on the Spermonde Shelf, *A. papillosa* is the deepest living species. It has been reported from down to 120 m depth in the Gulf

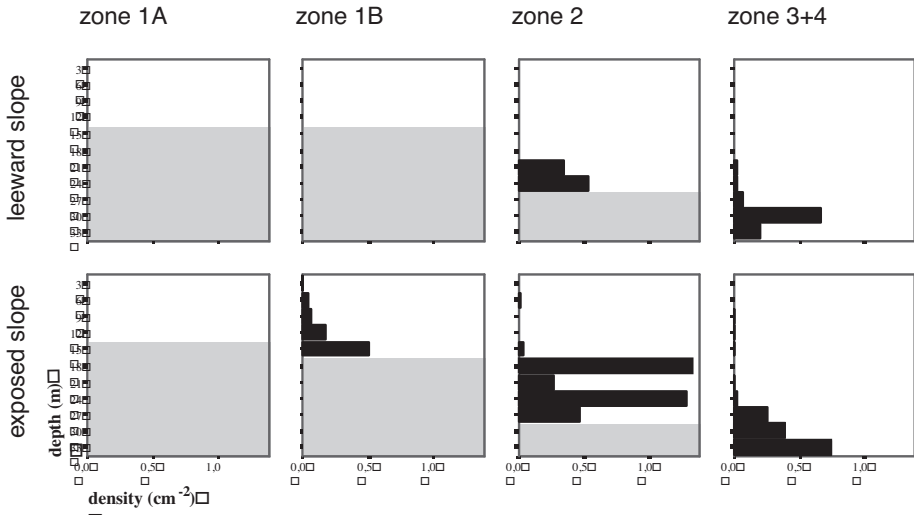


Fig. 13. Bar diagram showing the average density of *Amphistegina papillosa* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

of Eilat (Hansen & Buchardt, 1977), but these authors made no differentiation between dead and living specimens. At Okinawa it has been reported alive from more than 100 m depth (Hohenegger, 1994). No substrate preference has been reported. Though the maximum depth at which *A. papillosa* is found in the Spermonde is much shallower, this species shows a similar distribution pattern as in other regions.

**Family Calcarinidae**

*Neorotalia calcar* (D’Orbigny, 1839)

(fig. 15e, f)

Description.— Trochospirally coiled test, involute on umbilical side. More or less biconvex in side view. Each chamber in last whorl with one short, triangular spine almost in equatorial plane (10-14 in adults). Test surface smooth, showing some pores and no spikes.

Affinities.— This species is most easily misidentified with *Calcarina hispida*, the test of which is entirely covered with small spikes and usually has not as many spines as *N. calcar*.

Symbiont type.— Diatoms, *Nitzschia frustulum* var. *symbiotica* and other species (Hottinger & Leutenegger, 1980; Lee & Anderson, 1991)

Distribution.— *N. calcar* occurs on the reef edge and has no preference for substrate type in the Spermonde Archipelago. It lives in shallow water and is usually restricted to the upper 10 m (fig. 14). *N. calcar* is significantly more abundant on the leeward slope than on the exposed slope (chi square test,  $p < 0.001$ ). On the leeward slope, it may occur in deeper water (down to 30 m, fig. 14).

Discussion.— The occurrence of this species on the Spermonde Shelf is different from that in other regions from where it has been reported. Instead of having its high-

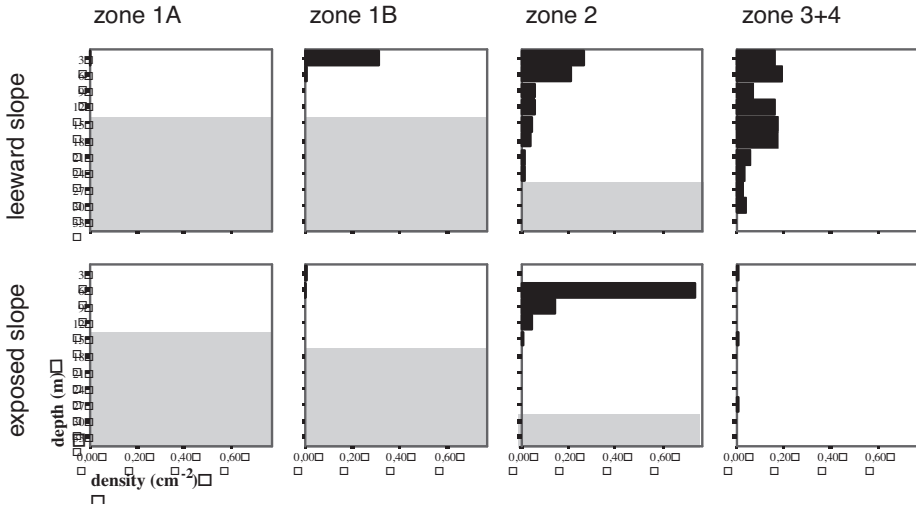


Fig. 14. Bar diagram showing the average density of *Neorotalia calcar* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

est density in the shallowest part of the reef flat, it is more abundant around the reef edge on the leeward side, where the highest densities in zone 1B, 2 and 3+4 are found down to 3, 6 and 18 m (fig. 14), respectively. This species has been found in shallow water on thalli of macroalgae and on firm substrates in the beach region (Hallock, 1984; Hohenegger, 1994; Hohenegger, 1996). Hohenegger et al. (1999) found a significant preference for solid substrates in two transects off Okinawa. Troelstra et al. (1996) found this species in very shallow water as well but with a much higher density on reef flats.

The reef flat of the reefs on the Spermonde Shelf do not show abundant macroalgae growth, due to wave-driven sand movements. This sandy substrate is also not suitable for *N. calcar*. Wave ripples were observed down to about three meter (during fair weather), *N. calcar* becomes more abundant in the areas without wave ripples.

*Calcarina hispida* Brady, 1876  
(fig. 15a, b)

Description.— Test globular, trochospirally coiled. Tuberculate surface in the umbilical area and lateral chambers and spines covered by small spikes. Spines either short and straight or long and bifurcated.

Affinities.— Hohenegger et al. (1999) distinguished two morphotypes. In this study, *C. hispida* f. *defrancii* (long spines) was very rare, and is not considered separately. The short spined form (*C. hispida* f. *spinosa*) of this species resembles *N. calcar*, which has a spine on every chamber and no small spikes, while *C. hispida* has 4-6 spines only.

Symbiont type.— Diatoms, *Nitzschia frustulum* var. *symbiotica* and other species (Lee & Anderson, 1991).

Distribution.— In our study *C. hispida* was the most abundant calcarinid foram. It

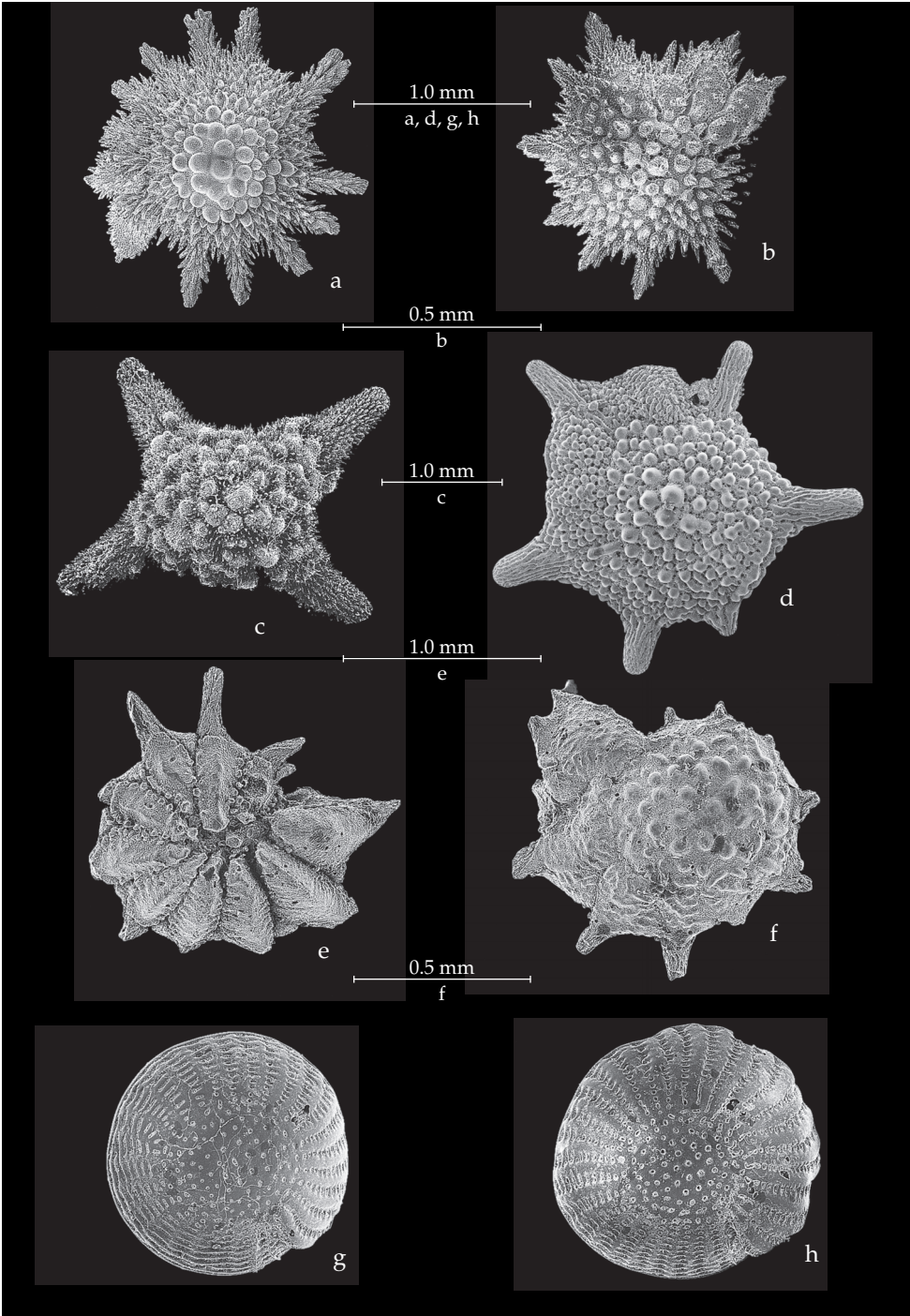


Fig. 15a, b: *Calcarina hispida*. c: *Bacologypsinoides spinosus*. d: *Calcarina gaudichaudii*. e, f: *Neorotalia calcar*. g, h: *Elphidium craticulatum*.

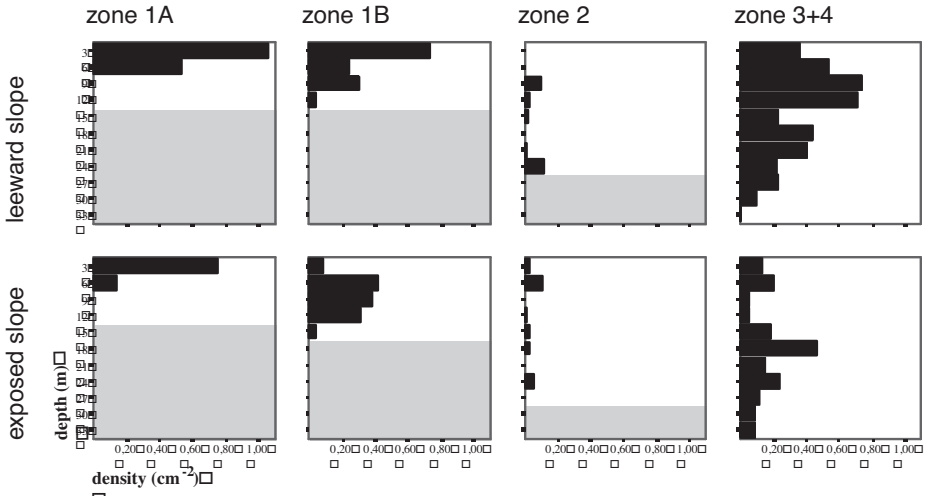


Fig. 16. Bar diagram showing the average density of *Calcarina hispida* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

occurred around reefs in most zones (fig. 16), and was found in 2/3 of the samples. Only *A. lessonii* was found in more samples. *C. hispida* showed no preference for either substrate type or exposed/leeward side of the reefs. In most areas it occurred down to the maximum sampling depth at the reef base while the highest densities occurred at the lower part of the reef slope (fig. 16).

*C. hispida* occurred in high densities in the southern near shore zone, where this was the most abundant species on sandy substrate. Low densities were found on the Midshelf reefs (fig. 16). On reefs in the Northern Near Shore and Outershelf zone, *C. hispida* is abundant at both the leeward and exposed reef slope. On the leeward slope, it occurs on top of barren sediment.

Discussion.— *C. hispida* is reported from 0 to 70 m at Okinawa (Hohenegger, 1994, 1995), where the morphotype *spinosa* is the shallowest one of the two at 0-30 m depth (Hohenegger et al., 1999). At Okinawa it was found to have a preference for firm substrates (Hohenegger et al., 1999). Röttger & Krüger (1990) found this species living on algae covering the sediment in seagrass meadows.

*C. hispida* is the most abundant calcarinid, the occurrence of *C. hispida* around the reefs in zone 1A indicates that it is more tolerant to fluctuations in the environment than the similar *N. calcar*. Hohenegger et al. (1999) explain the higher abundance of calcarinids in their northern transect by the higher availability of nutrients. The high density of *C. hispida* in the Southern Near Shore zone supports this hypothesis.

*Calcarina gaudichaudii* (d'Orbigny, 1839)  
(fig. 15d)

Description.— Test large, flat, and trochospiral with thick chamber walls giving rise to circular contours (Hohenegger, 1999). In our study specimens with only few

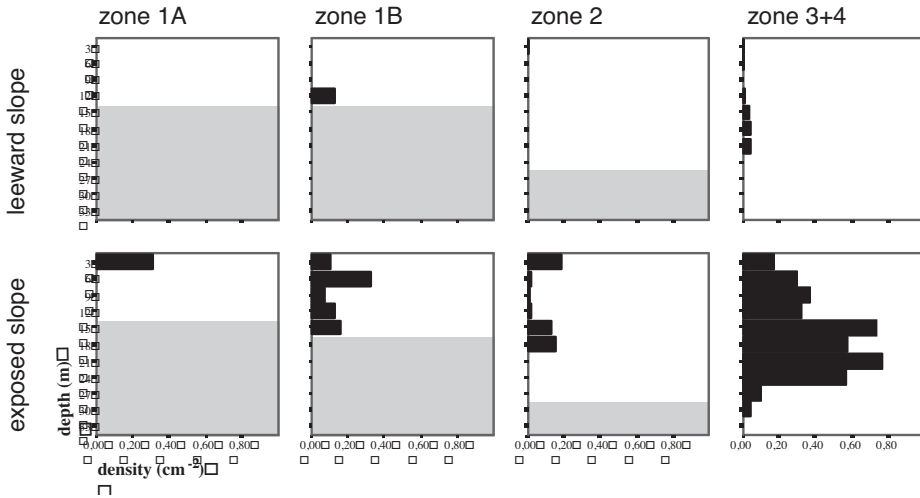


Fig. 17. Bar diagram showing the average density of *Calcarina gaudichaudii* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

spines are more angular with usually only a limited number of long, rounded spines (4-6), showing some parallel striae. Test surface smooth with very small pores. The last chambers often are large with relatively deep sutures, especially at the spiral side.

Affinities.— Easily identified by its spines, large size and smooth, round contours.

Symbiont type.— Diatoms, *Nitzschia frustulum* var. *symbiotica* and other species (Lee & Anderson, 1991).

Distribution.— This species shows a significant preference for both the exposed slopes of the reefs and solid substrates (fig. 24a). Its maximum abundance was at the middle of the slope (9-24 m in the zone 3+4, 3-12 m in zone 2, fig. 17), where it lived below large boulders of rubble or in crevices. The density of this species decreases rapidly as soon as the substrate type at the exposed slope changes from coral rubble into sand. The maximum depth at which it has been recorded is 30 m.

Discussion.— This species is characteristic for high hydrodynamic energy, shallow water (Röttger & Krüger, 1990). Hallock (1984) found this species (as *C. spenglerli*, see Röttger & Krüger, 1990; Röttger et al., 1990) in the upper 5 m (maximum density at 1 m), as did Röttger & Krüger (1990). Hohenegger (1994) and Hohenegger et al. (1999) found it in slightly deeper water, of 0-20 m depth, while their maximum density was in crest pools at 0-10 m depth, where it was associated with algae.

Troelstra et al. (1996) found this species to be most abundant on 'eutrophic' reefs, and less abundant, but conspicuously present on 'oligotrophic' reefs. Re-examining of their samples revealed that they erroneously identified *C. hispida* as *C. gaudichaudii*.

The shift in habitat as observed in *C. gaudichaudii* is similar to *Neorotalia calcar*. Contrary to the latter species, the absence of suitable substrate (macro algae or rubble in quiet areas) in shallow water urges *C. gaudichaudii* to occupy habitats in deeper water. With its robust spines *C. gaudichaudii* can attach strongly to the substrate and is able to withstand higher hydrodynamic energy than *Neorotalia calcar* (Hohenegger, 1994).



*Baculogypsinoides spinosus* Yabe & Hanzawa, 1930  
(fig. 15c)

Description.— Large calcarinid test globular to tetrahedral in outline and covered with large pustules. Its 3 or 4 large, blunt spines covered with short spikes and in some specimens with a few parallel striae on the spines.

Affinities.— Living specimens are greenish grey around the spines and whitish at the centre, compared to an even brownish-green colour in *C. gaudichaudii*.

Symbiont type.— Diatoms, *Nitzschia frustulum* var. *symbiotica* and other species (Lee & Anderson, 1991).

Distribution.— This large calcarinid occurs in a few samples, most of them on the seaward slope of the reefs (fig. 18). It occurs at the upper part of sandy reef bases just below the coral cover on the base of slope, where it lives attached just below the edges of large pieces of coral rubble (e.g. dead mushroom corals) covered by algae (fig. 24b). This pattern is very similar to what Troelstra et al. (1996) found (listed as *Baculogypsina sphaerulata* (Parker & Jones, 1860)).

Discussion.— *B. spinosus* is a relatively deep living calcarinid. It has been reported from up to 80 m with maximum densities at 40-50 m, where it tends to have a preference for solid substrates (Hohenegger, 1994, 1996). This is the same habitat as in which *B. spinosus* was observed in the Spermonde Archipelago, apart from the shallower maximum depth of occurrence.

**Family Rotalidae**

*Elphidium craticulatum* (Fichtel & Moll, 1798)  
(fig. 15g, h)

Description.— Test lenticular, planispiral involute. 22-28 chambers in final whorl are perforate, with rectangular pores parallel to sinuous septa. Umbilical plug perforate.

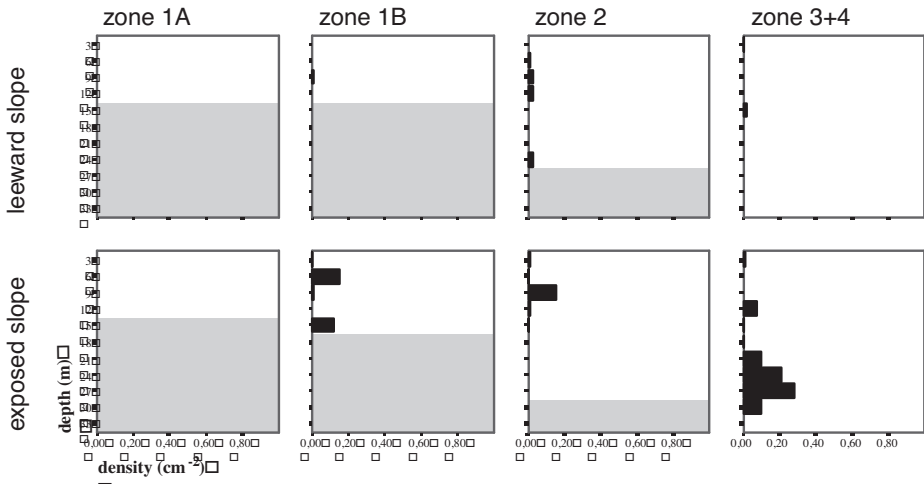


Fig. 18. Bar diagram showing the average density of *Baculogypsinoides spinosus* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

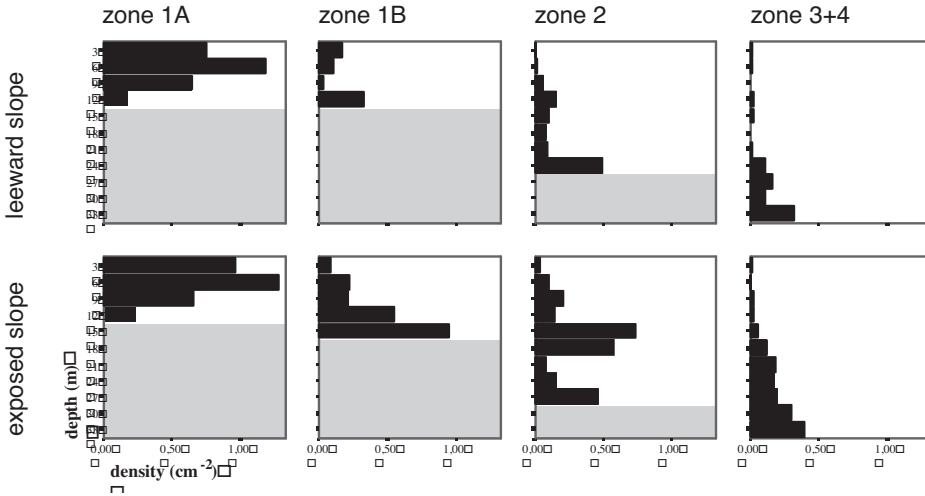


Fig. 19. Bar diagram showing the average density of *Elphidium craticulatum* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

Affinities.— Misidentification impossible.

Symbiont type.— This species does not house symbionts, but shows chloroplast husbandry instead (Reiss & Hottinger, 1984; Lee & Anderson, 1991).

Distribution.— This species occurs all over the shelf. The highest densities were found around near shore reefs (zone 1A) where they co-occurred with *A. radiata* attached to algae on coral rubble and in the deepest samples taken in between the reefs (fig. 24c). *E. craticulatum* can be found at any depth, and seems to occur mostly in conditions at the limits of the range of symbiont bearing foraminifera (fig. 19). This is related to the fewer restrictions of chloroplast husbandry over symbiont housing.

Discussion.— Hollaus & Hottinger (1997) found this species to replace *Amphistegina lessonii* below the thermocline at Crete.

In nutrient-rich water, symbiosis is less advantageous to both the symbiont and the host than in oligotrophic water (Hallock, 1985). In chloroplast husbandry, as shown by *E. craticulatum*, symbionts do not reproduce within the host, but have to be digested continuously (Lopez, 1979). The chloroplasts are left intact for several days and provide the host with energy. This is advantageous in variable environments in which during large parts of the year unfavourable condition for true symbiosis prevail, or in areas within the photic zone, but not warm enough for true symbiosis.

On the Spermonde Shelf, *Elphidium craticulatum* shows the highest densities in the most variable environments, in zone 1A and in the deepest area. In zone 1A large seasonal variation occurs in the nutrient level and the visibility. Seasonal fluctuations have a relatively larger impact at larger depth. Because of the logarithmic decrease in light intensity, the deepest part of the photic zone in the fair weather season the light intensity is too low for species with true symbionts (Renema & Troelstra, in press.). *E. craticulatum* is less sensitive and lives at this depth in zone 1B to 3+4.

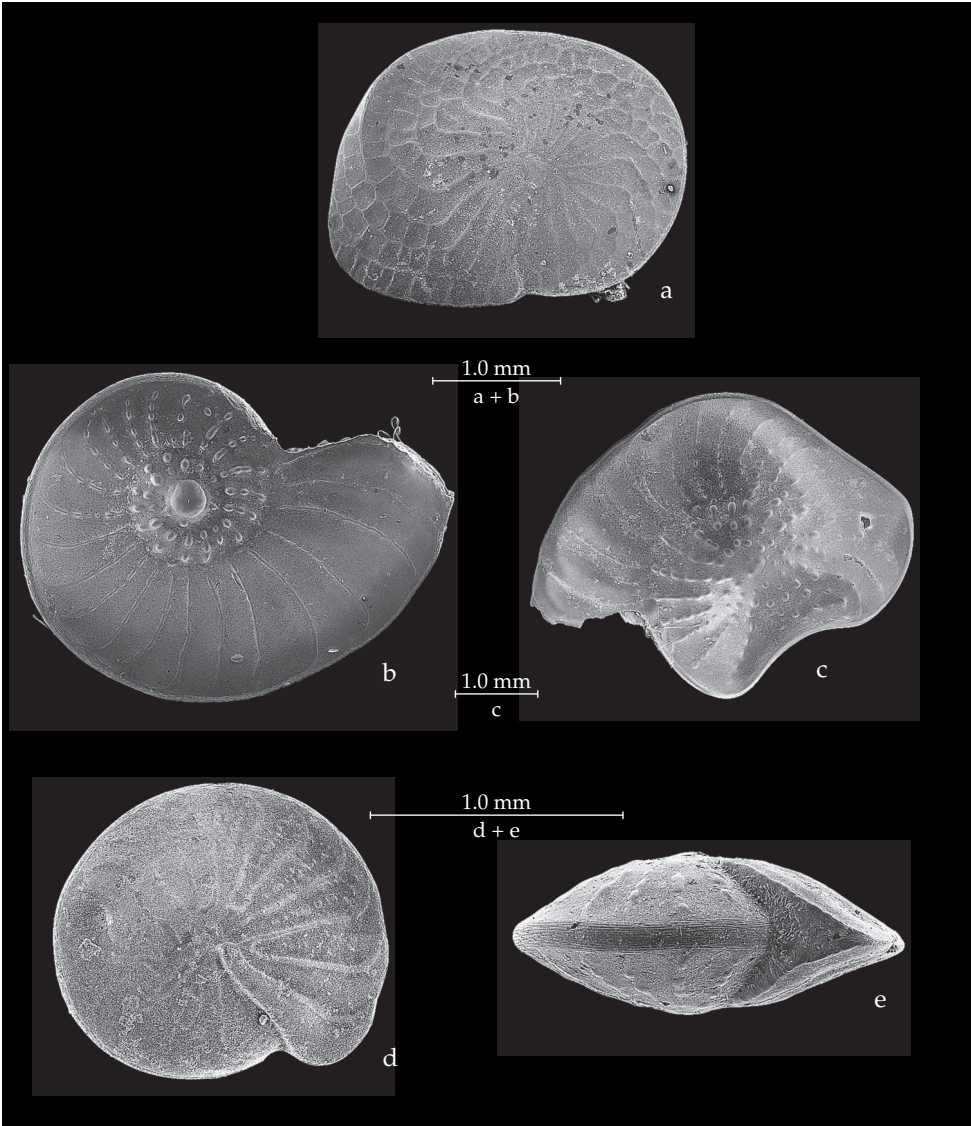


Fig. 20a: *Heterostegina depressa*. b, c: *Operculina ammonioide*. d, e: *Nummulites venosus*.

**Family Nummulitidae**

*Heterostegina depressa* D'Orbigny, 1826

(fig. 20a)

Description.— Shell large, involute, planispirally coiled. Long chambers partitioned in chamberlets and with a marginal cord. Chambers increasingly elongate, but never annular. Small specimens robust; larger specimens with thin and flat outer whorls.

Affinities.— In the present study, this is the only hyaline-walled species showing

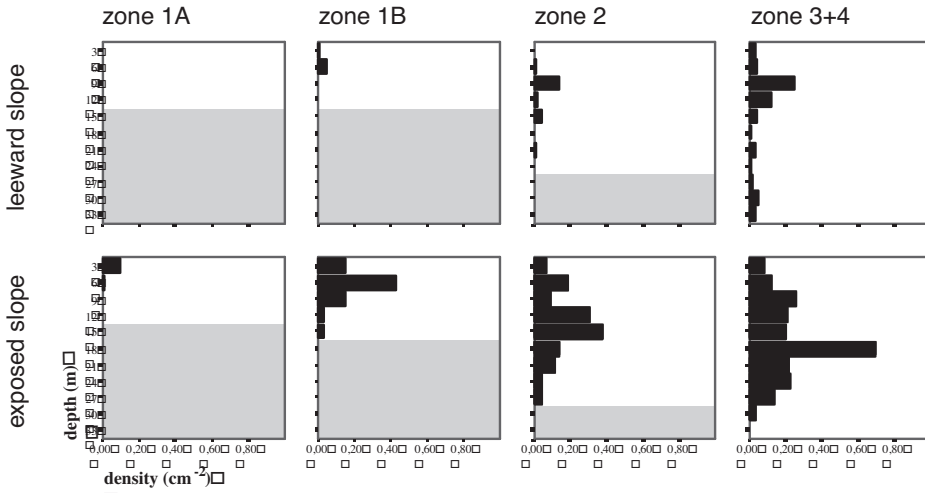


Fig. 21. Bar diagram showing the average density of *Heterostegina depressa* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

chamber partitioning by septules. Others have not been found alive. *H. operculinoides* Hofker is the nearest relative and it has an evolute test with pustules in the centre. *Operculina heterosteginoides* Hofker, only found as an empty shell, is also evolute and its septules do not reach further than half the chamber width.

Symbiont type.— Diatom, *Nitzschia panduriformis* and other species (Leutenegger, 1984).

Distribution.— *H. depressa* is common in the Spermonde Archipelago (fig. 21), with a significant preference for seaward slope sides (chi square test,  $p < 0.05$ , table 2) and for solid substrates (chi square test,  $p < 0.001$ , table 2). The highest densities occur on the exposed slopes, and this species shows a marked increase in depth range going from the Southern Near Shore zone to the Northern Near Shore zone (fig. 21). It is found hidden in sheltered places on coral rubble covered with coralline algae (fig. 24 b). On the sandy leeward sides and on sandy reef bases it occurs in very low densities (fig. 21). Here, very large microspheric specimens were observed, some of which were found attached to echinoids (see picture).

Discussion.— As in the Spermonde Archipelago, *H. depressa* occurs predominantly on solid substrate in all other areas (e.g., Hottinger, 1977; Vénec-Peyré, 1991), and shows a great depth range (0-100 m, (Hallock, 1984), 0-80 m (Hohenegger et al., 1999)). The maximum depth at which *H. depressa* has been found is much shallower though.

*Operculina ammonoides* (Gronovius, 1781)  
(fig. 20b, c)

Description.— Large operculinid, almost round in umbilical view. Coiling semiinvolute to evolute planispiral in the last whorls. Size of the central test region covered with pustules varies with depth (Hohenegger et al. 1999).

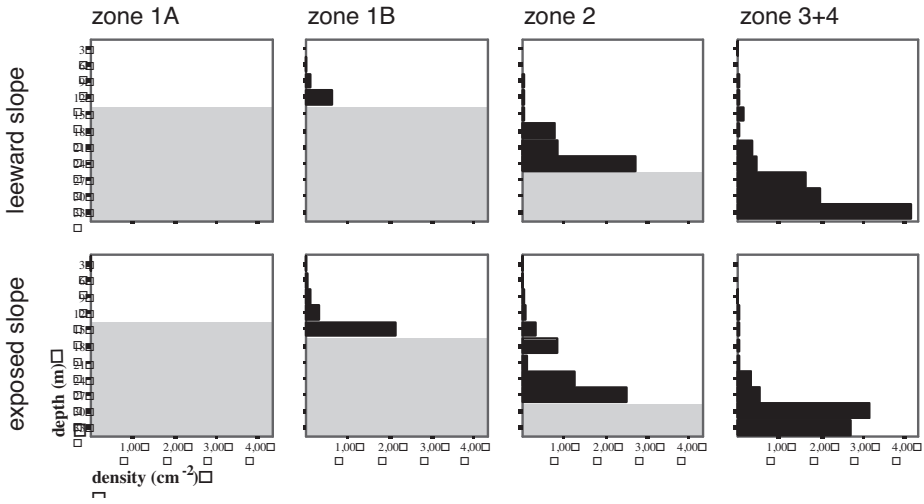


Fig. 22. Bar diagram showing the average density of *Assilina ammonoides* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

Affinities.— No misidentification possible with other species occurring on the Spermonde Shelf. In the West Pacific two other species occur (Hohenegger et al. 1999): 1) *Assilina discoidalis* (d’Orbigny) has involute first whorls, narrow chambers and a large hyaline umbonal plug. 2) *Operculina cf complanata* (Defrance) has a complete evolute test with folded septal flaps (Hohenegger et al., 1999). The expansion rate of the whorls increases going from *A. discoidalis* to *A. ammonoides* to *O. cf complanata*.

Symbiont type.— Diatom, *Nitzschia panduriformis* and other species (Leutenegger, 1984)

Distribution.— At the Spermonde Archipelago, this is the most abundant species, occurring on various sandy substrates, to which it has a significant preference (table 2), especially in patches at reef bases, except those at the Southern Near Shore area (Lae Lae, Baranberingan, fig. 22). It was found dead in grab samples from < 54 m depth E of Langkai, and alive from not deeper than 45 m just west of Kudinkarengkeke. It occurred at slightly shallower depths on sandy leeward reef slopes (fig. 22 + fig. 24e, f). The minimum depth at which it has been found varies from 9 m in zone 1B to 21 m in zone 3+4 (fig. 22).

Discussion.— In previous studies this species has been reported from various habitats, with highest densities usually recorded from sandy substrates varying in depth from 6 m (Troelstra et al., 1996) to 150 m (Hottinger, 1977). More restricted depth ranges were reported from Palau (27-60 m, Hohenegger, 1996, and 20-30 m, Hallock, 1984). According to Hohenegger et al. (1999), this species prefers lower energy environments with medium light intensities, which is confirmed by our observations.

Nummulitids that prefer even lower light intensities do not occur in the Spermonde Archipelago. Empty tests of *Operculina heterosteginoides* have been found, but

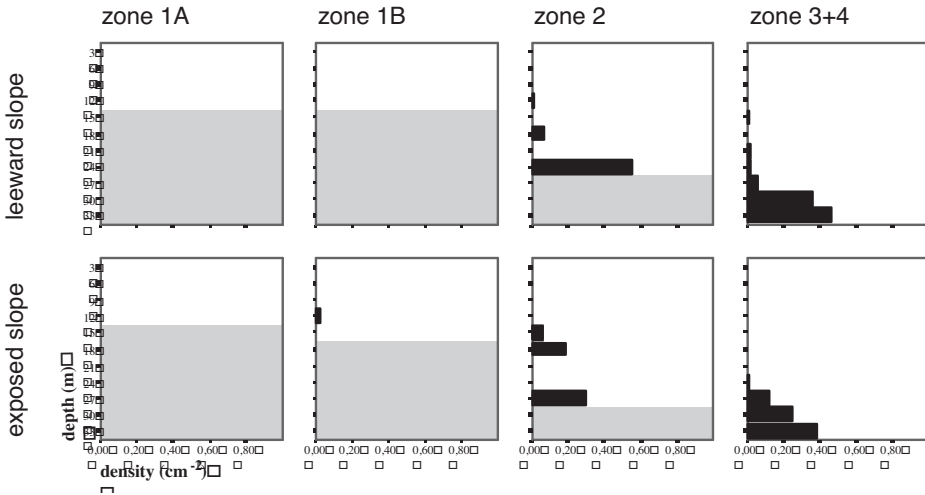


Fig. 23. Bar diagram showing the average density of *Nummulites venosus* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

*Heterostegina operculinoides* and *Cycloclypeus carpenteri* Brady are not present. High seasonal variation in for example depth of the photic zone probably causes this difference.

*Nummulites venosus* (Fichtel & Moll, 1798)  
(fig. 20d, e)

Description.— Large, rather thick planispiral, and involute test with a thick marginal cord. Septa curve backwards at periphery. Outer surface smooth.

Affinities.— In outer appearance this species is similar to *Heterostegina depressa*, from which it differs by the absence of septules in the chambers.

Symbiont type.— Diatom (Leutenegger, 1984).

Distribution.— At the Spermonde Archipelago, *N. venosus* is one of the species showing a preference for soft substrates at the reef base(chi<sup>2</sup> test, p <0.001, table 2). *N. venosus* was collected in low densities at the deepest SCUBA sample depths (fig. 23). It was not found around islands in the Southern Near Shore zone. *N. venosus* was found nearest to the shore around Bone Baku (zone 2). Highest densities were recorded at the reef base around the outer shelf reefs (Bone Tambung, Kudinkarengkeke).

Discussion.— *N. venosus* lives slightly deeper than *Operculina ammonoides* (20-90 m) and has a significant preference for sandy substrates (Hohenegger et al., 1999). At the Spermonde Archipel, its maximum depth is limited by the extent of the photic zone (most probably that of the wet season).

Elsewhere this species is found in the same habitats, but in much deeper water.

**Discussion**

Two important parameters influence the distribution of larger foraminifera over the Spermonde Shelf.

1) The varying influence of terrigenous influx by rivers. Larger foraminifera occur at greater depth in zone 1B than in zone 1A. Both areas are shallower than 20 m, and differ only in the distance to the mainland shore.

In zones 1B, 2 and 3+4 the maximum depth at which foraminifera have been found increases in offshore direction, together with parameters like maximum depth and the maximum depth of coral cover on reef slopes and the transparency of the water (secchi depth).

In zone 1A, only a limited number of species is capable of dealing with the highly variable conditions through the year. On the leeward reef slopes in this zone, these species are *Calcarina hispida*, *Amphistegina lessonii* and *Elphidium craticulatum*. Other species, like *Peneroplis planatus* and *Neorotalia calcar*, found in shallow water on the leeward reef sides in zone 1B to 3+4 were not found in this zone.

On the exposed sides, the shallowest samples were similar to those in the other zones, but *Elphidium craticulatum* occurred in higher densities. The samples at 6-9 m contained *E. craticulatum*, *Amphistegina radiata* and *A. lessonii*. *Heterostegina depressa* was absent.

All species occurring in samples taken at the reef base in the other three zones, were absent from this zone as well.

Hohenegger et al. (2000) reported that several Nummulitidae at the reef slopes around Okinawa showed a similar response to low transparency. Though predicted by models (Hallock, 1987, 1988), it has not yet been demonstrated that species disappear in response to changing environmental parameters.

2) Exposed slope vs leeward slope. Species occurring on reef slopes can be divided distinctly into two groups, with very little overlap. *Calcarina gaudichaudii*, *Baculogypsinooides spinosus*, *Amphisorus hemprichii*, *Heterostegina depressa* and *Amphistegina radiata* occur predominantly on exposed slopes, while *Neorotalia calcar* and *Peneroplis planatus* occur predominantly on leeward slopes. Apart from *A. radiata*, the exposed slope species have all been reported to prefer to live on solid substrates in other areas as well (Hallock, 1984; Hohenegger et al., 1994, 1999).

*Neorotalia calcar* and *Peneroplis planatus* are both shallow water species living attached to algal mats or solid substrate (Hohenegger et al., 1994). Both species live on soft substrates at S. Sulawesi. A habitat like that described by Hohenegger et al. (1994) for *N. calcar* and *P. planatus* is not present in the Spermonde Archipelago at shallow depth. The observations at the Spermonde Shelf show that these two species are plastic in their habitat preferences.

Other species that were found in the same habitat in Okinawa (for example *Baculogypsina spaerulata* and *Calcarina defranciai*) have not been found in the Spermonde Archipelago and do not have the plasticity to live in the conditions on the Spermonde.

Many of the larger foraminifera occurring in the Spermonde Archipelago have been found in other habitats (*Neorotalia calcar*, *Peneroplis planatus*, *Calcarina gaudichaudii*), a narrower range (for example *Alveolinella quoyii* and *Parasorites orbitolitooides*) or a wider range of habitats (*Calcarina hispida*) than previously reported. Differences in local environmental parameters force larger foraminifera to adapt their way of living. Competition between groups can also influence these choices. In the more variable conditions at the Spermonde Archipelago compared to those at Okinawa, species with a short generation time will have an advantage.

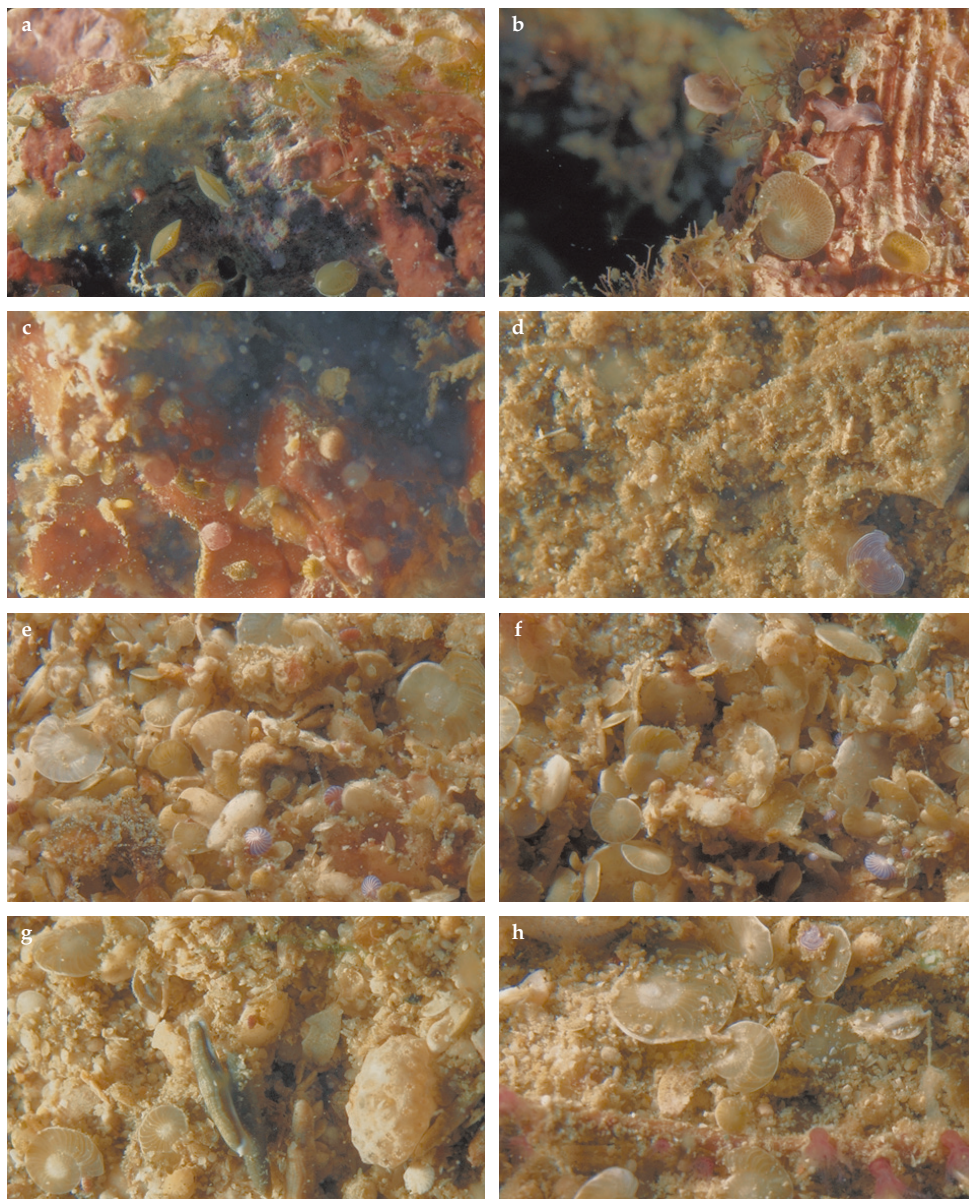


Fig. 24a: *Amphistegina radiata* on coral rubble covered by coralline algae (KKW6). b: *Heterostegina depressa*, *Baculogypsinoidea spinosus* (background *Amphistegina lessonii* and *Calcarina gaudichaudii*) on dead coral fragment covered by (coralline) algae (KKW18). c: *Elphidium craticulatum* on coral rubble covered by red algae (BBW6). d: Soft sediment assemblage with *Operculina ammonoides* and *Dendritina ambigua* (PLW30). e: Soft sediment assemblage with *Dendritina ambigua*, *Alveolinella quoyii*, *Operculina ammonoides* and *Amphistegina papillosa* (SW27). f: Soft sediment assemblage with *Operculina ammonoides* and *Parasorites orbitolitoidea* (SE21). g: Soft sediment assemblage with *Alveolinella quoyii* and *Operculina ammonoides* (SW24). h: *Amphisorus hemprichii* attached to a large boulder of dead coral (LKW6).



Though it is not possible to quantify seasonal variations in the density of foraminifera in the Spermonde Archipelago, the influence of seasonally changing environmental parameters is large. In the samples taken from the reef base, *Elphidium craticulatum* is an important component of the foram fauna. This species shows chlorophyte husbandry and is thus capable of dealing with adverse, dark conditions better than symbiotic species.

### Conclusions

1) Next to already known parameters like substrate type, depth and hydrodynamic energy (Hottinger 1983, 1988; Hohenegger, 1994; Hohenegger et al., 1999), another important parameter for the distribution of larger foraminifera is nutrient concentration. This latter parameter is influenced by the distance to the shore and terrestrial run off by rivers over the shelf area. *Calcarina hispida*, *Amphistegina lessonii*, *A. radiata* and *Elphidium craticulatum* can withstand these conditions better than the other species.

2) In tropical areas away from the equator, the climate is often monsoonal with a dry and a wet monsoon. Seasonal changes in fluvial discharge over the shelf influences nutrient concentration (increasing the concentration of organic particles) and inorganic particle concentration near shore. This seasonal variation also affects the distribution of larger foraminifera over the Spermonde Shelf.

3) The very different set of environmental parameters from other areas where the distribution of living larger foraminifera have been studied, shows that some species are not as critical as others. *Neorotalia calcar*, *Calcarina gaudichaudii* and *Peneroplis planatus* have been recorded at the Spermonde shelf at both different substrates and greater depth than in previous studies.

The absence of habitats forces the species otherwise living in these habitats to occupy other habitats or to be absent.

4) In mesotrophic conditions, *Elphidium craticulatum* is an important faunal component.

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