Larger foraminifera on reefs around Bali (Indonesia)

W. Renema

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Willem Renema, Nationaal Natuurhistorisch Museum, PO Box 9517, NL 2300 RA Leiden (e-mail: Renema@naturalis.nl).

Key words: Formanifera; Bali; Indonesia.
The larger benthic foraminifera fauna from four regions at or near Bali are described. In 132 samples in total 19 species were found. This is a similar to species richness in areas like the Spermonde and Cebu, but the fauna composition differed markedly. For each species the occurrence at Bali and environmental parameters affecting this distribution are discussed.
It is argued that the very low abundance of imperforate species is not due to the absence of their microhabitat, but due to climatic or oceanographic parameters. The most likely is the presence of periodic upwelling, which causes the seawater temperature to drop to low levels seasonally.

Introduction

Larger foraminifera are important components of reef ecosystems, especially for carbonate production (Hottinger, 1977a; Hallock, 1984; 1999). For example, at the Spermonde Shelf (southwest Sulawesi, Indonesia) foraminifera make up 40-80% of the sediment (Renema, 2002). The sands of the southern beaches of Bali (Indonesia) consist for an important part of the skeletons of larger foraminifera (Adisaputra, 1998; Barbin et al., 1987). However, surprisingly little is known of how and where these foraminifera live. In this study the foraminifera on reefs at four sites around Bali have been studied, and their occurrence has been compared with those at two other Indo-West-Pacific reef sites, the Spermonde Archipelago and Cebu (Philippines).

Area

Three sites at the south (east) side of Bali (Sanur, Padang Bai and Tulamben), and Nusa Lembongan were visited (fig. 1A). The Sanur dive localities are along a fringing reef reaching from Nusa Dua to Sanur, interrupted by the entrance to Benoa harbour and a channel just north of Pulau Serangan (fig. 1B). Beginning from the beach, the reef forms a shallow lagoon, in places only 1 m deep at low tide, which extends seaward for more than 0.5 km to the reef edge. The reef slope consists of a gently sloping spur and groove system until 25 m depth, where a coarse-grained sandy bottom with wave ripples is present. The reef slope is exposed to high hydrodynamic energy due to the oceanic swell. Coral (both soft and stony corals) and sponge cover is high, but their colonies form low, massive structures. No loose coral rubble or other 3-D structured habitats suitable for foraminifera are present. The bare substrate is covered by short, filamentous- or larger red algae growing in clumps of up to several centimetres. The channel north of Pulau Serangan offered some sheltered sites, and is slightly deeper (Bal 13 and Bal15). At these sites the microhabitats were more structured, but regularly filled with fine-grained sand.

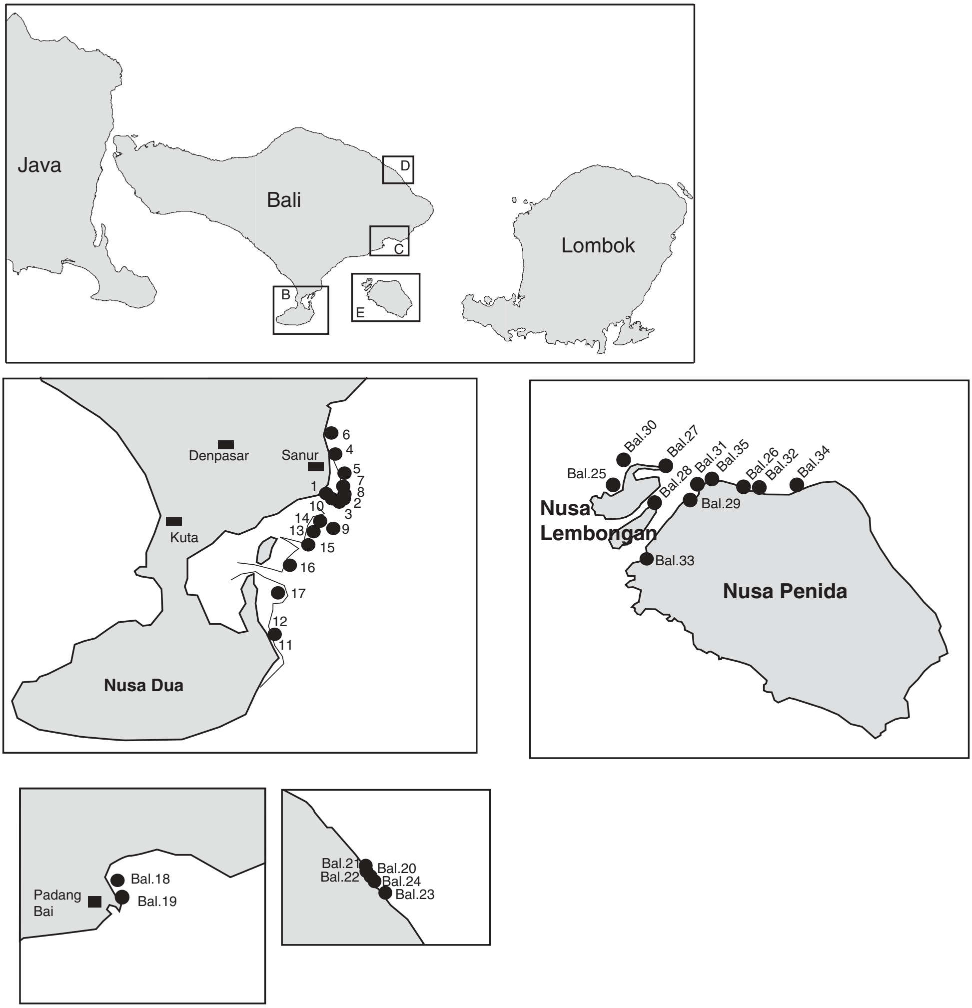

Fig. 1. Location map of the research area. a: overview, b: the Sanur area, c: Padang Bai area, d: Tulamben area, e: Nusa Lembongan/Nusa Penida area.

The two localities visited at Padang Bai were at a sandy reef slope with coral patches of varying size (fig. 1C). This slope is protected from current and swell by a cape. The narrow reef flat is covered by coral rubble, providing a good microhabitat for larger foraminifera. Coral rubble on the reef slope itself is covered by sand.

The Tulamben area consists of a steep slope composed of fine volcanic (black) sand topped by a small area with coral cover (3-9 m depth) and a reef flat with rounded stones (fig. 1D). On the sandy slope coral bommies occur uncommonly. The most important substrate for larger benthic foraminifera on this slope was rounded cobbles covered by algae. Localities Bal20 and Bal21 were located at this sand slope. To the southeast of the sandy slope the coast is dominated by a lava flow, forming a diverse set of reef environments ranging from walls to gentle slopes. Coral cover is rather high, but there are many patches with coral rubble and less commonly sand. In the whole Tulamben area the slope continues to depths of >50 m. Localities Bal22-Bal24 were located at these reefs.

The most complex area visited was Nusa Lembongan/ Nusa Penida (called Lembongan further in the text; fig. 1E). The visited reefs are located along the north coast and the sea strait between the two islands (Selat Toyapakeh). The localities Bal27 and Bal30 were located north of Nusa Lembongan, and exposed to high current velocities and subject to periodic upwelling. Bal29, Bal31, Bal26, Bal32 and Bal34 were located at increasing distance from Selat Toyapakeh, but are, periodically, all subject to relatively cool water. On all sites benthic cover was dense, but did not grow to heights greater than 30 cm. No loose rubble was present at shallow depth. Some rubble was found at > 33m at Bal31, but occurs more shallow further from Selat Toyapakeh (>21 m at Bal34). On the shallower slope the most important substrate is reefrock covered by small algae and clumps of macro-algae.

Bal28 is located in between the Nusa Lembongan and Nusa Celingan in a sea grass field. At this site several species of sea-grasses are present (both *Enhalus* spp. and *Halophilus* spp.) at 1-10 m depth. In between the sea grasses open sandy patches are present.

Methods

During SCUBA diving, samples were taken at least at intervals of 3 m depth, and sometimes in between these depths if suitable sampling sites were present. Samples were coded with Bal followed by the number of the dive site and the depth at which it was taken (for example, Bal05-7.5 stands for a sample taken at station 5 at 7.5 m depth). At some stations several samples were taken from several substrate types at the same depth. Stations Bal01-Bal17 were located along the fringing reef of the Sanur area, Bal18 and Bal19 come from Padang Bai, Bal20-Bal24 from Tulamben and Bal25-Bal34 were taken at Nusa Lembongan.

A sample of all suitable substrate types represents a surface area of 100 cm^2. In some cases a larger surface area was sampled because of the nature of the substrate, but then the surface area was noted. The samples were sun dried. Foraminifera were washed from the substrate and subsequently sieved over a 0.5 mm mesh size. From the residue, specimens living at the time of sampling, recognised by their symbiont colour, were sorted and identified to species level.

The database of 132 samples and densities of 20 taxa was converted using a logarithmical transformation ($y = \log(\text{density}_{\text{species x}} + 1)$). Species that occurred in less than four samples were omitted. With the resulting database, cluster analysis (Sörensens distance measure and Flexible β ($\beta = -0.75$)) and indicator analysis (Dufrêne & Legendre, 1997) were performed. Additionally, a DCA (detrended principal component analysis) was run. All statistical analyses were run using PC-ORD (McCune & Mefford, 1999).

Results

The 132 collected samples yielded in total just over 40 000 living larger benthic foraminifera from 31 sites. In total 19 species of larger benthic foraminifera have been

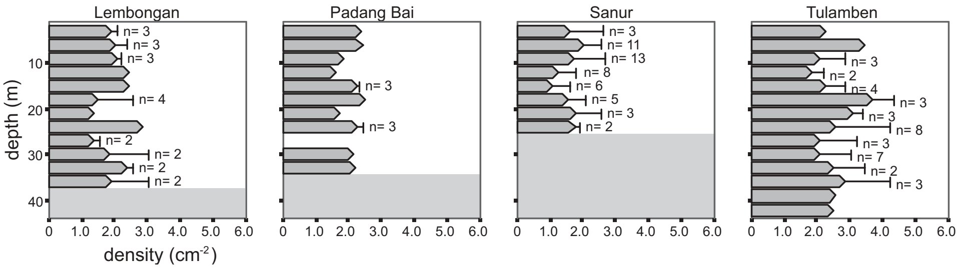

Fig. 2. Average density of larger foraminifera per area. Error bars indicate 95% confidence interval. (number of samples is indicated).

observed. This is comparable to the number of species recorded in similar studies at Cebu and southwest Sulawesi (Renema, 2002; Renema et al., 2001; Renema & Troelstra, 2001). However, the composition of the fauna is quite different. Only five species of imperforate foraminifera were observed, four of which were (very) rare. Only *Sorites orbiculus* was observed commonly, whilst this species was rare at southwest Sulawesi and Cebu (Renema et al. 2001; Renema, 2002).

The two species of *Schlumbergerella* and *Calcarina defrancii* have not been recorded at the other sites. The former are geographically restricted to the Lesser Sunda Islands, but *Calcarina defrancii* is also found in Japan and the Moluccans (Hofker, 1927; Hohenegger, 1994; Hottinger & Leutenegger, 1980).

Up to three larger foraminifera/cm^2 were observed (fig. 2), and no clear trend with depth was present. However, many samples yielded no living larger benthic foraminifera. These localities, all well within the photic zone, also provide relevant information on environmental preferences of larger benthic foraminifera as well. At the sites in front of Kuta Beach (Sanur, Bal01-Bal17, with the exception of Bal15, 16, 11 and 12), the groove and spur continues into a sand bottom at about 20-23 m depth. These sands display large wave ripples and are barren of living larger foraminifera. The reef flat behind the largest breakers at about 3-4 m depth is also almost barren of living larger foraminifera.

At Tulamben, the steep, unstable slopes only yielded larger foraminifera living attached to stones (covered by filamentous algae) that were lying on the sand. Since these were smooth stones without surface rugosities densities were rather low.

Absence of living larger foraminifera shows interesting patterns at the Nusa Lembongan and Nusa Penida area. The sites to the north of Nusa Lembongan (Bal27, Bal30) are characterised by high current velocities, no loose rubble and high low-lying macro-benthos cover. Low temperatures (at the time of sampling 25°C, but temperatures as low as 16°C occur regularly) occur frequently due to up-welling. At these sites no living larger benthic foraminifera were observed.

The sites to the north of Nusa Penida (from east to west: Bal29, 31, 26, 32 and 34) show a similar pattern. No larger foraminifera were seen on the shallow part of the slope, but deeper down the slope low densities were observed. The minimum depth at which larger benthic foraminifera were observed decreased from east to west. The last station at which no larger benthic foraminifera were observed was Bal28, which was in a shallow (0-8 m) sea grass bed in the passage between Nusa Lembongan and Nusa Ceningan.

Peneroplidae

Peneroplis pertusus (Forskål, 1775)

Description.— Planispiral: in one specimen the last chambers are rectilinear. A good discussion of this species is given by Gudmundsson (1994). The specimens in this study are all small and keeled, with a multiple, X-shaped pores on the apertural face.

Affinities.— Due to the size and flat (keeled) appearance, confusion with *P. planatus* is possible. The apertural face shows multiple and complex apertures surrounded by elongated pits and grooves, characters not seen in *P. planatus*.

Occurrence at Bali.— Rare. Five samples, all taken at coral rubble, from Sanur and Nusa Lembongan contained single specimens.

Occurrence elsewhere.— circumtropical (Gudmundsson, 1994).

Peneroplis planatus (Fichtel & Moll, 1798)
(fig. 3)

Description.— Planispiral with last whorls flaring. Test flat with a sharp keel in side view. Gudmunsson (1994) gives a precise description of this species. The Balinese specimens are very similar to that description. The only difference was that in the single row of apertures in the last chamber, the most complex apertures were crescent. Gudmundsson (1994) also found U-, X-, and Y-shaped and even dendritic, apertures.

Affinities.— *Peneroplis planatus* is the only flaring peneroplid in the area.

Occurrence at Bali.— Rare. *Peneroplis planatus* was only recorded in 7 samples from Sanur and Tulamben. They were usually found attached to short, philamentous algae living on coral rubble.

Occurrence elsewhere.— From the Mediterranean to Hawaii and from Japan to New Caledonia (Gudmundsson, 1994) .

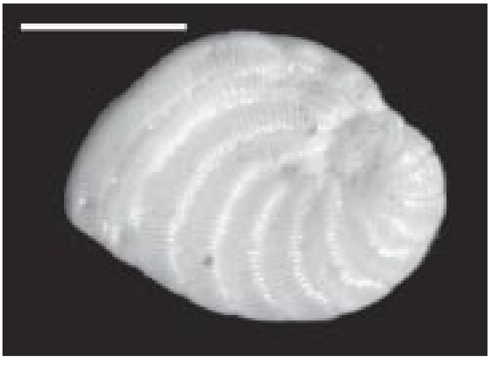

Fig. 3. *Peneroplis planatus* (Fichtel & Moll, 1798) Bal 11-18 scale bar represents 0.5 mm.

Soritidae

Sorites orbiculus (Forskål, 1775)
(figs 4-5)

Description.— Test discoidal. The embrionic apparatus in the macrosphere is formed by a proloculus which

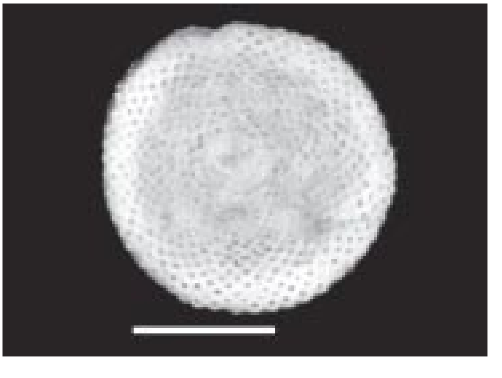

Fig. 4. *Sorites orbiculus* (Forskål, 1775). Bal 32-30 scale bar represents 0.5 mm.

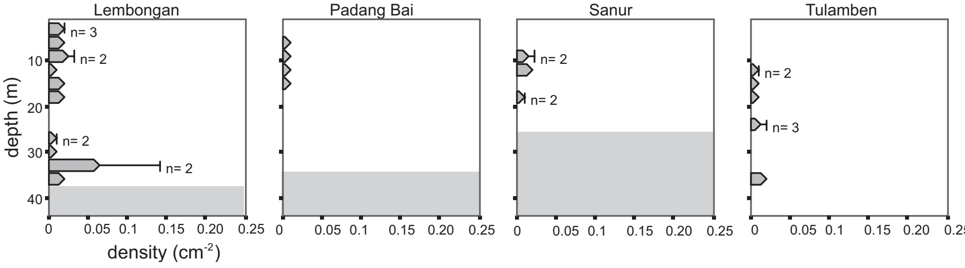

Fig. 5. Average density with depth of *Sorites orbiculus* in the four research areas.

is (almost) completely surrounded by the flexostyle, and followed by 3-7 planispiral chambers and 5-8 flabelliform chambers, followed up to 40 cyclic chambers. The chambers in the cyclic chamber are hexagonal, which makes the sides of the test (seen from above) look serrated. In apertural view there are usually two round, rimmed apertures above each septule.

Affinities.— See *Sorites* sp. and Gudmundsson (1994), Holzmann et al. (2001) and Richardson (2001).

Occurrence at Bali.— Common. *Sorites orbiculus* was found in 27 samples, from all four regions visited, but usually there were not more than 2-3 specimens per sample. Highest numbers were found around Nusa Lembongan. Most specimens were found living epiphytically on thalli of algae, rarely on coral rubble. Depth range was 2-36 m depth.

Occurrence elsewhere.— Circumtropical (Gudmundsson, 1994; Langer & Hottinger, 2000). In southwest Sulawesi and Cebu *Sorites orbiculus* occurred in low numbers as well. In both areas it was rare epiphytically on algae and seagrass.

Parasorites spec.
(fig. 6)

Description.— Test discoidal. Macrosphere has a proloculus completely surrounded by the flexostyle followed by 2-6 planispiral chambers without septula, 11-14 flabelliform with septula, and 8-10 cyclic chambers with chamberlets. Chamberlets rectilinear, about twice as long as high in the cycliclic chambers. The apertural view consists of one row of small, round apertures placed above the septula.

Affinities.— The specimens resemble *S. orbiculus* var. *marginalis* in having a single row of apertures, but the shape of the initial chambers resembles that of the genus *Parasorites*. The test is not of a


Fig. 6. *Parasorites* spec. Bal 23-30. Scale bar represents 0.5 mm.

similar whitish porcelaneous carbonate as in other species of *Parasorites* (see Gudmundsson, 1994), and compared to specimens from southwest Sulawesi). The Balinese specimens do not have green symbionts (chlorophytes), but brownish ones as reflected by their colour when alive.

Occurrence at Bali.— Rare. *Parasorites* sp. was found in several samples from the Tulamben and one from the Sanur area, but always in low numbers.

Occurrence elsewhere.— not known until taxonomy is resolved.

Marginopora cf. *vertebralis* Quoy & Gaimard in Blainville (1930)

Description.— One macrospheric specimen was found at Tulamben. Discoidal. The test embryonic apparatus consists of a proloculus and a fortex that is almost completely surrounded by the vorhof (terminology as in Gudmundsson, 1994). The embryon is followed by about 40 cyclic chambers with square chamberlets, that are about twice as high as long. The apertural view consists of a row of marginal apertures at each side of the test with irregularly placed, round to ovate median apertures (up to five next to each other).

Affinities.— Although the taxonomy of soritids is not yet resolved, the combination of the structure of the embrionic apparatus and the presence of multiple rows of marginal apertures is only seen in *Marginopora vertebralis*. The Bali specimen differs in being thinner and smaller than specimens from other localities.

Occurrence at Bali.— Only one specimen was found at 25 m depth on coral rubble at the Tulamben drop-off.

Occurrence elsewhere.— In comparative studies at the Spermonde Archipelago and Cebu this species was not observed.

Amphisteginidae
Amphistegina lessonii (Orbigny, 1826)
(figs 7a-b, 8)

Description.— Test planoconvex to biconvex. Involute. Sutures simple, bent backward at the periphery. Alar prolongations complicate the suture pattern in large specimens. On the umbilical side, the umbilical area is formed by an umbilical plug, which is more pronounced in planoconvex specimens. The apertural area is covered with papillae, which are usually arranged in lines. The last chamber is covered by papillae at the part nearest to the aperture. The spiral side is formed by stellate arranged gently curved septa. Most often with only a small umbilical plug.

Affinities.— Can only be confused with *Amphistegina lobifera*; see that species for diagnostic characters. The other *Amphistegina* species at Bali, *A. radiata,* has stellate septa at either site.

Occurrence at Bali.— The most abundant species, found in all except one sample. Highest numbers were found at 6-33 m depth. In shallower samples *A. lobifera* replaces *A. lessonii*.

Occurrence elsewhere.— From Red Sea (Hottinger et al., 1993) to Hawaii (1984) and north to Japan (Hohenegger, 1994; Hohenegger et al., 1999). *Amphistegina lessonii* is the most abundant larger foraminifera in the IWP. No substrate preference is found at Bali, but in southwest Sulawesi it was observed in higher frequencies at soft sub-

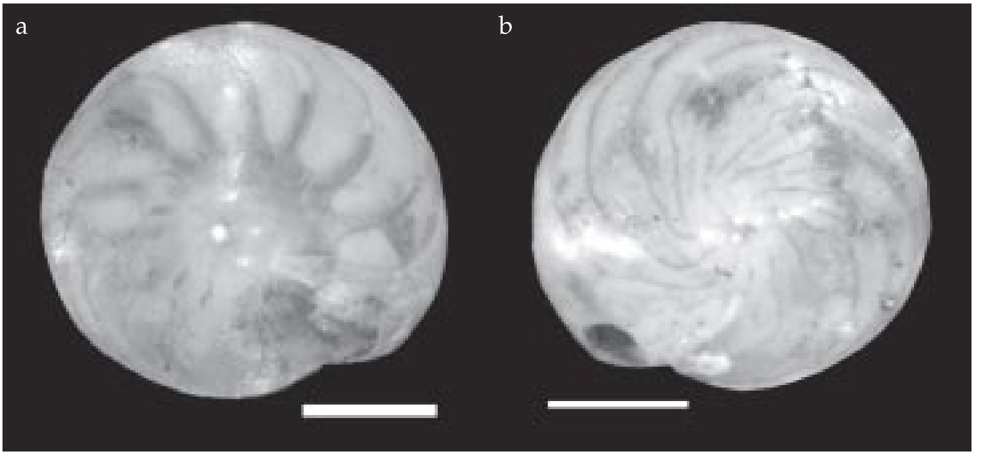

Fig. 7. *Amphistegina lessonii* (Orbigny, 1826) Bal 18-23 a: umbilical side, b: spiral side. scale bars represent 0.5 mm.

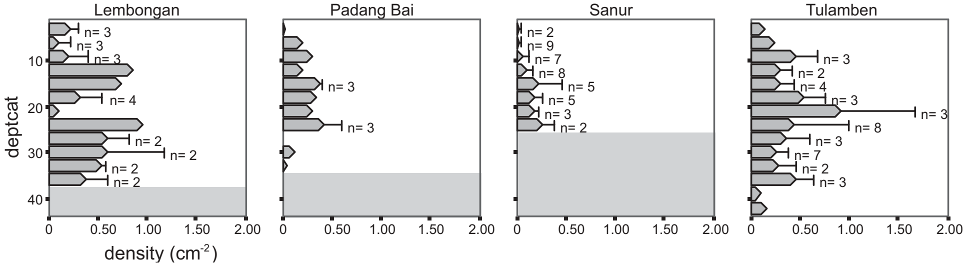

Fig. 8. Average density with depth of *Amphistegina lessonii* in the four research areas.

strate, while *A. radiata* was more abundant at coral rubble (Renema, 2002; Renema et al., 2001; Renema & Troelstra, 2001).

Amphistegina lobifera Larsen, 1976
(figs 9a-b, 10)

Description.— Test biconvex to (most often) planoconvex. Involute. Test papillate on the apertural face. Many parallel ridges cover the distal part of the last chamber on the umbilical site. The sutures on the umbilical side are highly lobate, which obscures the overall shape of the septa. The spiral site has a well-developed umbilical plug. The septa are finely lobate which, also on this side, blurs the overall shape of the septa.

Affinities.— Very similar to *A. lessonii*, especially in smaller specimens when the lobate shape of the septa is not yet developed. In general appearance, *A. lobifera* is more robust and has a better-developed umbilical plug on the spiral site. However, variation is large in both species and some overlap exists. The parallel ridges on the umbilical side of the last chambers have never been found in *A. lessonii*, but are very difficult to see using light microscopy only.

Occurrence at Bali.— Abundant in samples taken at < 20 m depth, occasionally

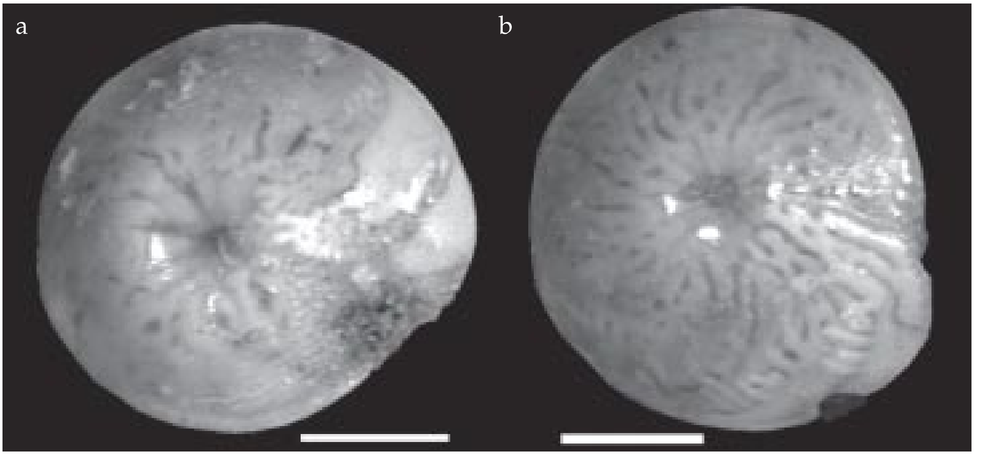

Fig. 9. *Amphistegina lobifera* Larsen, 1976. Bal 16-11. a: umbilical side, b: spiral side. scale bars represent 0.5 mm.

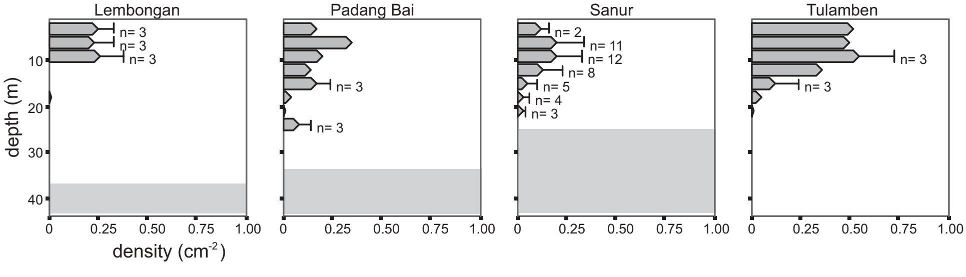

Fig. 10. Average density with depth of *Amphistegina lobifera* in the four research areas.

deeper. In these samples, equally abundant in all four regions.

Occurrence elsewhere.— From Red Sea (Hottinger et al., 1993) to Hawaii (Hallock, 1984) and North to Japan (Hohenegger, 1994; Hohenegger et al., 1999). The habitat preference of *A. lobifera* is comparable at all sites. It occurs in the shallowest samples, with a slight preference for solid substrate.

Amphistegina radiata (Fichtel & Moll, 1798)
(figs 11a-b, 12)

Description.— Test biconvex. Involute. Sutures simple, straight with a sharp angle near the periphery. Between the sutures there are short, often broken, intersepta, which may give the test a papillate appearance. On the umbilical site there is never more than one interseptum between two septa, on the spiral site there are regularly two intersepta between two adjacent septa.

Affinities.— At Bali there are no similar species to *A. radiata*. However, the rather similar and easily confused *A. papillosa* Said occurs elsewhere in the Indo-Pacific. Especially deeper living specimens of *A. radiata* with intersepta that produce a papillate appearance of the test can be confused with *A. papillosa*. *Amphistegina*

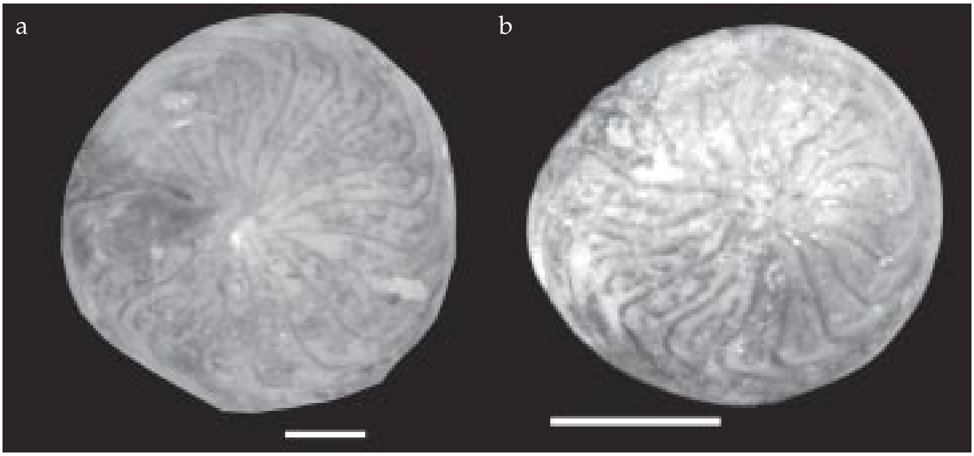

Fig. 11. *Amphistegina radiata* (Fichtel & Moll, 1798). a: umbilical side, Bal32-30 b: spiral side, Bal18-17. Scale bars represent 0.5 mm.

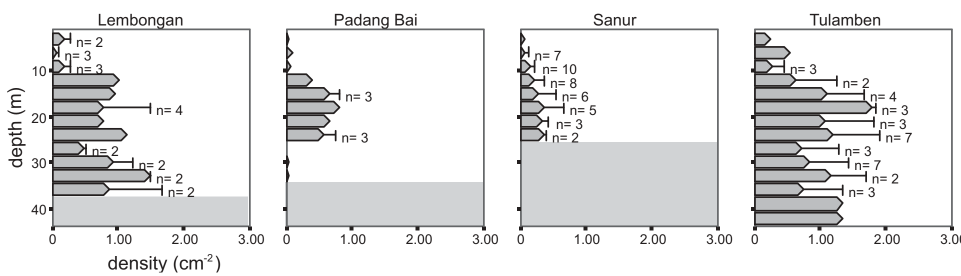

Fig. 12. Average density with depth of *Amphistegina radiata* in the four research areas.

papillosa is a smaller and flatter species, usually with two or more intersepta in between two adjacent septa on the spiral side. The aperture in *A. radiata* is lid-like, surrounded by many papillae (though mainly in the peripheral region of the test), whilst in *A. papillosa* the aperture is rounded and surrounded by a single row of papillae.

Occurrence at Bali.— Abundant, found in most samples. The highest numbers were found in samples >10 m depth. *Amphistegina radiata* prefers solid substrates, and highest densities occur on well structured coral rubble, where they occur in cryptic places.

Occurrence elsewhere.— Geographic distribution is not clear. Hottinger et al. (1993) reported *A.* aff. *radiata* from the Red Sea. This species is morphologically and ecologically different from *A. radiata* in the Indo-Pacific region. The westernmost specimens that I have seen of *A. radiata* originate from the Seychelles and its range extends to the east to New Caledonia (Hottinger et al., 1993). The ecological preferences of *A. radiata* found in this study, compare well with those found elsewhere (Hohenegger, 1994; Hohenegger et al., 1999; Renema, 2002; Renema et al., 2001; Renema & Troelstra, 2001)

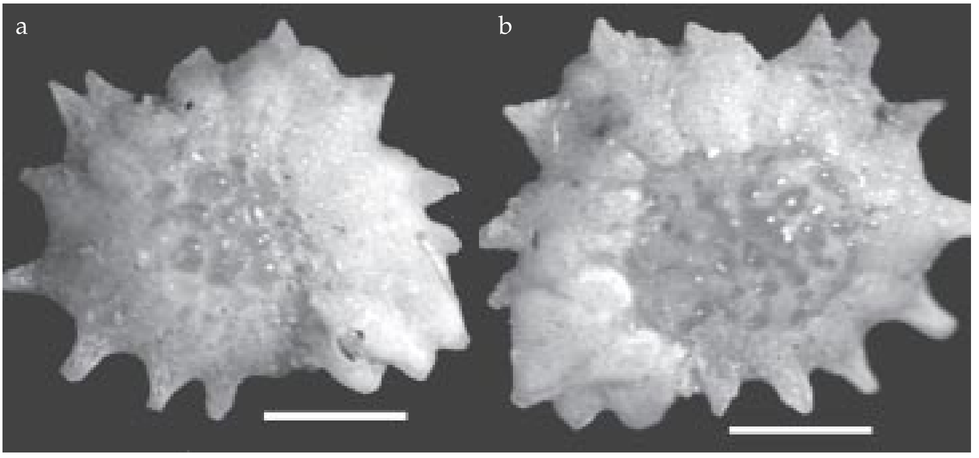

Fig. 13. *Neorotalia calcar* (d'Orbigny, 1839). Bal11-18. a: umbilical side, b: spiral side. Scale bars represent 0.5 mm.

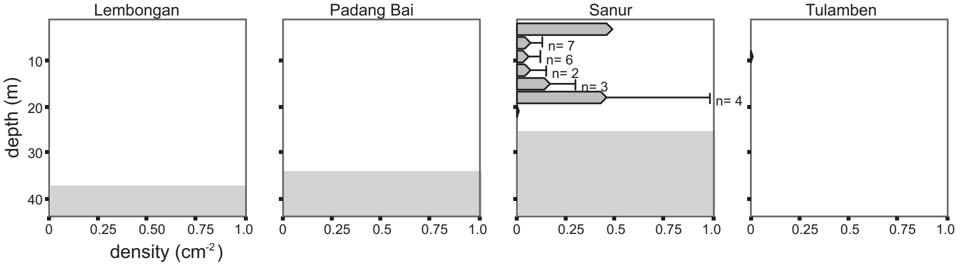

Fig. 14. Average density with depth of *Neorotalia calcar* in the four research areas.

Calcarinidae
Neorotalia calcar (Orbigny, 1839)
(figs 13a-b, 14)

Description.— Trochospiral with chambers inflated on the spiral side. The chambers are radially elongated and peripherally pointed, with spinose projections giving the test its typical stellate outline (Hottinger et al., 1991). The amount of elongation and the length of the stellate projections is variable, and usually longest in the chambers adjacent to the last chamber. The dorsal side shows a central area with large pustules surrounded by pores. The chamber walls of the last whorl are slightly sunken and in some specimens the chambers appear shouldered. On the umbilical side all chambers are shouldered and have a deep suture, around which some small pustules are lined. In the umbilical area several pustules are either small and numerous or large and few and arranged in a spire.

Affinities.— In the samples taken at Sanur a species of *Pararotalia* is present with which *N. calcar* can be confused. In *Pararotalia* the sutures on the umbilical side are even deeper and not lined by pillars, the chambers are not shouldered and not elongated. In some specimens of *Pararotalia* a slight onset of elongation is present.

Occurrence at Bali.— Abundant at Sanur, but not found elsewhere. In Sanur it was found at 3-18 m depth, with the highest densities at 10-18 m. It was found predominantly epiphytic at algae in relatively high-energy systems.

Occurrence elsewhere.— From the Central Atlantic to the Marshall Islands, but not recorded in the Mediterranean (Langer & Hottinger, 2000). Abundant in southwest Sulawesi and Cebu, where the highest densities were reached at the reef flat (Cebu; Renema, 2002), or the upper reef slope (southwest Sulawesi, Renema et al. 2001; Renema & Troelstra, 2001). *Neorotalia calcar* seems to prefer to live epiphytic, but can also live on soft substrates as is seen in southwest Sulawesi.

Calcarina mayori Cushman, 1924
(figs 15-16)

Description.— Medium-sized *Calcarina* with few (usually ≤6) long, sharp radial spines. Sutures, apart from the late formed chambers, are hardly distinguishable due to surface ornamentation. Test covered by large pustules and short spikes, providing a hispid appearance. The test is covered by openings of the intraseptal canal system. The last chambers are covered by short spikes. The spines show parallel laminae, which are blurred by spikes.

Affinities.— Has been confused with *C. spengleri* and *C. gaudichaudii*, for a discussion see Renema & Hohenegger, submitted a, b).

Occurrence at Bali.— Rather rare, but found in all four regions, usually at depths ranging 12-36 m and on hard substrates. Field observations show a preference for rubble overgrown by algae, of which the area in between may or may not be filled with sand.

Occurrence elsewhere.— Indo-Pacific, from west Indonesia to New Caledonia (Lobegeier, 2002). It was found in

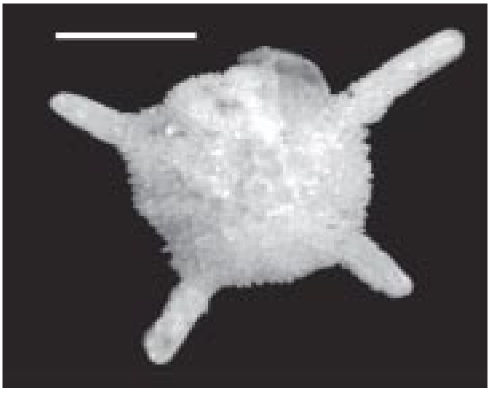

Fig. 15. *Calcarina mayori* Cushman, 1924. Bal18-23. Umbilical side. Scale bar represents 0.5 mm.

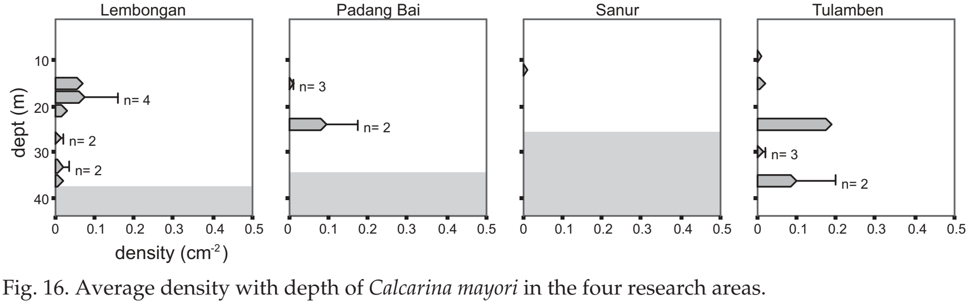

Fig. 16. Average density with depth of *Calcarina mayori* in the four research areas.

similar habitats at Cebu and the Spermonde (Renema, 2002; Renema et al., 2001; Renema & Troelstra, 2001).

Calcarina spengleri (Gmelin, 1791)
(figs 17a-d, 18)

Description.— Large trochospiral test with ≤ 7 short, blunt spines. Sutures, apart from the last formed chambers, are hardly distinguishable due to surface sculpture.

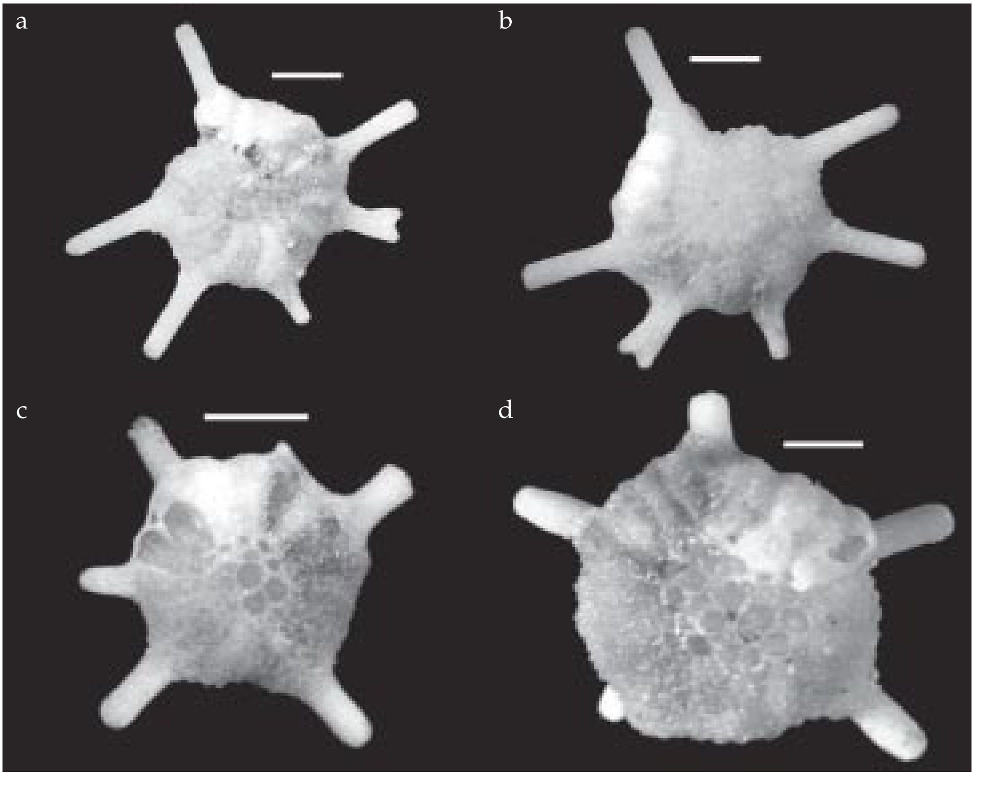

Fig. 17. *Calcarina spengleri* (Gmelin, 1791). a: umbilical side, Bal 23-27, b: spiral side , Bal 23-27, same specimen as fig. 17a, c: umbilical side, Bal23-27, d: umbilical side Bal 13-21. Scale bars represent 0.5 mm.

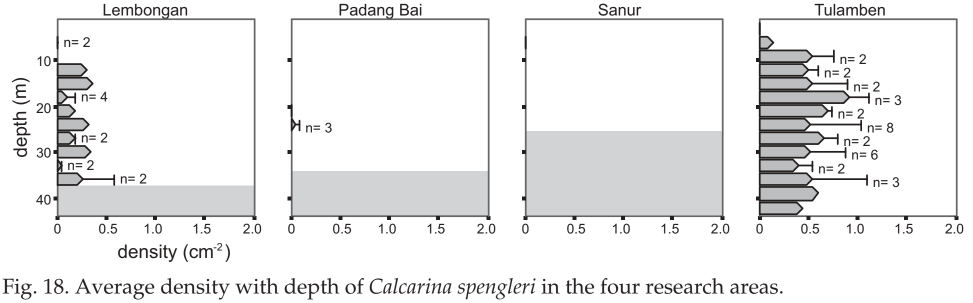

Fig. 18. Average density with depth of *Calcarina spengleri* in the four research areas.

Test covered by large, smooth pustules, which are largest in the central area of the test. The entire test is covered by openings of the intraseptal canal system in which small spikes are present. On the last formed chambers no pustules are present, ornamentation on the ventral side of these chambers consisting of alternately placed ridges (zipper-like structure) with many small pores between them.

The spines are canaliculate throughout and do not have a massive central part in cross-section. The spines show parallel lamellae that decrease in length and radial openings of the canal system. The spikes in the openings at the central test appear as thin parallel ridges on these lamellae.

Affinities.— Due to large intra-specific variation and some erroneous interpretations, a revision of the calcarinidae is needed to redefine species limits in this group. This is especially true for *Calcarina spengleri* (Renema & Hohenegger, submitted a, b). Several authors have interpreted small spinose specimens as juvenile forms of *Calcarina spengleri*, instead of separate species (*C. hispida* or *C. mayori*), further increasing the systematic confusion in this group.

Occurrence at Bali.— *Calcarina spengleri* is abundant at Tulamben and Nusa Lembongan, but at both Sanur and Padang Bai only single specimens were found. At Tulamben *C. spengleri* occurred from 6-42 m at the drop off, living attached to algae and coral rubble. It was hardly found at the volcanic sand slopes around the shipwreck. At Lembongan it was found from 10-36 m depth at the reef slope north of Nusa Penida.

Occurrence elsewhere.— Abundant on reef slopes in east Indonesia, the Philip-

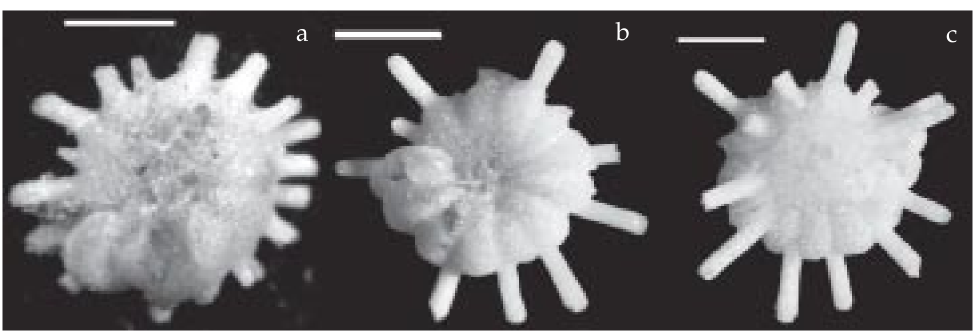

Fig. 19. *Calcarina defrancii* Orbigny 1839. a: umbilical side Bal 13-12, b: umbilical side Bal 18-23-2, c: spiral side Bal 18-23-2. Scale bars represent 0.5 mm.

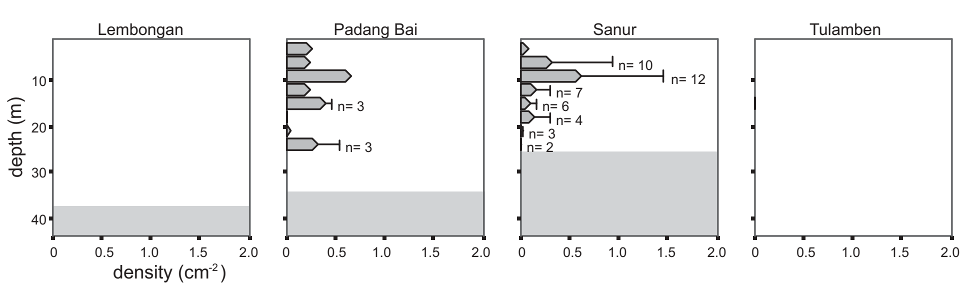

Fig. 20. Average density with depth of *Calcarina defrancii* in the four research areas.

pines, Palau and North to the Ryukyu Islands (Japan) (Renema & Hohenegger, submitted a). *Calcarina spengleri* seems prefers similar habitats in all studied areas.

Calcarina defrancii Orbigny, 1839
(figs 19a-c, 20)

Description.— Relatively small *Calcarina* with the chamber sutures clearly visible at the ventral side of the shell, with few but large pustules in the central region. The dorsal side is entirely covered by small pustules. Short, rarely bifurcating radial spines at most of the chambers in the last whorl. The openings of the intraseptal canal systems with well-developed ridges in them. Spine structure as in *C. spengleri.*

Affinities.— A very typical species, which is probably closely related to, but clearly distinguishable from, *C. spengleri*.

Occurrence at Bali.— Found at Sanur and Padang Bai, where it occurred from 3-23 m depth, with a maximum at 10 m depth. In Padang Bai it occurred deeper than at Sanur. It lived epiphytically on red algae.

Occurrence elsewhere.— *Calcarina defrancii* has a very patchy distribution in the West Pacific and Indonesian region. It was not found at SW Sulawesi and Cebu (Renema et al., 2001; Renema, 2002).

Baculogypsinoides spinosus
Yabe & Hanzawa, 1930
(figs 21-22)

Description.— Test globular with up to four large, massive and fully canaliculate spines that give the test a triangular to tetrahedral appearance. The spines are arranged in one plane, or at low angles with this plane. Many large pustules alternate with irregular inflated chambers with highly porous chamber walls. The complete test surface including the spines is hispid.

Affinities.— unmistakeable.

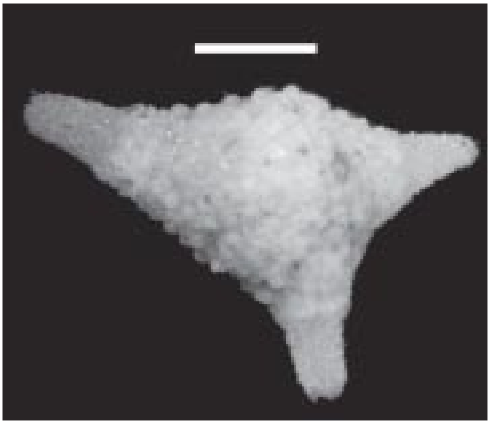

Fig. 21. *Baculogypsinoides spinosus* Yabe & Hanzawa, 1930. Bal 33-36. Scale bar represents 0.5 mm.

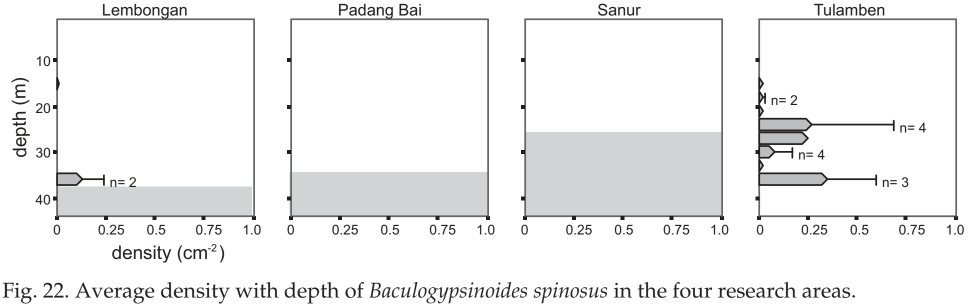

Fig. 22. Average density with depth of *Baculogypsinoides spinosus* in the four research areas.

Occurrence at Bali.— On deep reef slopes (high numbers at >23 m) at Tulamben and Nusa Lembongan at coral rubble.

Occurrence elsewhere.— east part of the Indo-West Pacific. At southwest Sulawesi and Cebu it was found on coral rubble on the deeper part of slopes with high coral cover (Renema, 2002; Renema et al., 2001; Renema & Troelstra, 2001).

Schlumbergerella floresiana
(Schlumberger, 1896)
(figs 23-24)

Description.— Test large, globular with short, usually four, thin spines arranged tetrahedrally that lack an internal canal system. The test is formed by trochospiral initial whorls followed by radiating piles of chamberlets, alternated with columns that show as large bosses on the external surface. Pores cover the chamber walls.

Fig. 23. *Sclumbergerella floresiana* (Schlumberger, 1896). Bal 13-12. Scale bar represents 0.5 mm.

Affinities.— *Schlumbergerella* is the only calcarinid genus with chamberlets that lacks a canal system in the core of their spines. The following species, *S. neotetraedra*, has been regarded as a variety of *S. floresiana* by some authors (Hanzawa, 1952; Hottinger & Leutenegger, 1980). Hofker (1927, 1970) gave a very detailed description of both species. In the Balinese specimens I find both types with hardly any intermediates and a clearly different distribution pattern, and I will treat them as separate species. A re-evaluation of all characters is needed to show whether *S. neotetraedra* is a valid species or merely a variety of *S. floresiana*.

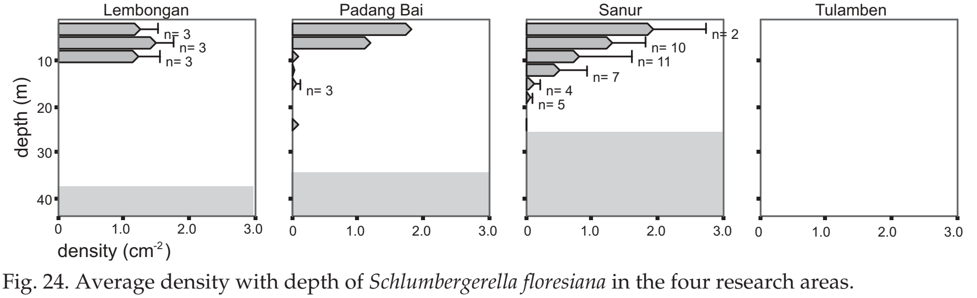

Fig. 24. Average density with depth of *Schlumbergerella floresiana* in the four research areas.

Occurrence at Bali.— *Schlumbergerella* occurs in high densities at <15 m in Sanur, <12 m in Lembongan and <= 6 m in Padang Bai. In Lembongan *S. floresiana* is only found at the very narrow reef tops, while it is absent at the reef slope (exposed to much cooler water).

Occurrence elsewhere.—Only found on the Lesser Sunda Islands and Java.

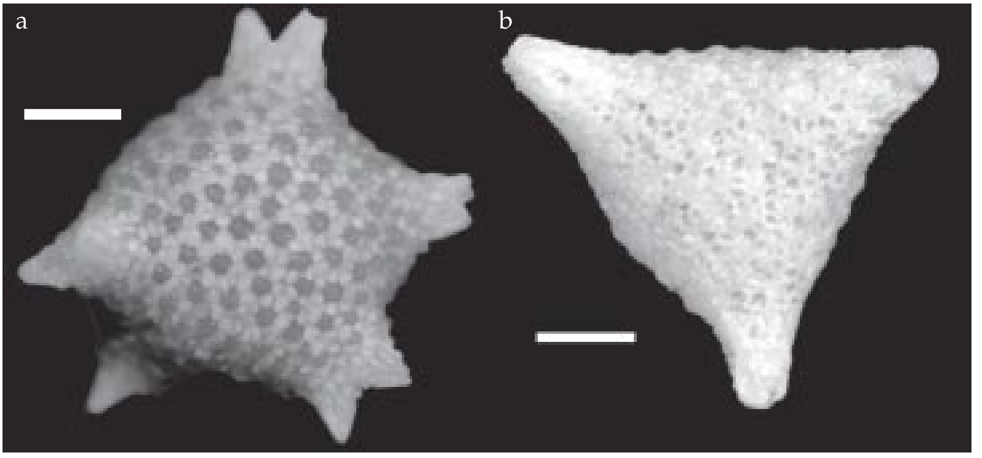

Fig. 25. *Schlumbergerella neotetraedra* (Tobler, 1918). A: Bal14-10, b: Bal 23-03. Scale bars represent 0.5 mm.

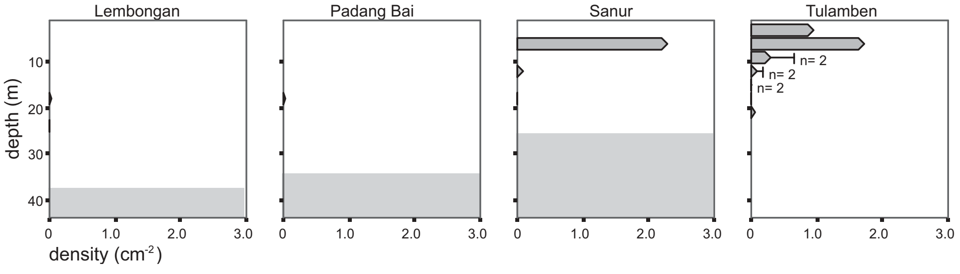

Fig. 26. Average density with depth of *Schlumbergerella neotetraedra* in the four research areas.

Schlumbergerella neotetredra (Tobler, 1918)
(figs 25-26)

Description.— Like *S. floresiana* but tetragonal instead of globular. Sides usually concave, the distal parts of the test usually with several small spines. For a discussion of differences in the internal structure see Hofker (1927; 1970).

Affinities.— See *S. floresiana*

Occurrence at Bali.— Occurs at 0-12 (21) m at the reef slope of Tulamben. It was found together with *S. floresiana* in a sample twice. In Bal03 at 6 m depth *S. neotetraedra* was found in high number, whilst at all other depths at the same side (including 5 and 7 m) *S. floresiana* was very abundant. *Schlumbergerella* was especially abundant on rubble covered by red coralline algae (fig. 36a-b) and to a lesser extent in algal mats.

Occurrence elsewhere.— Hofker (1970) found this species living at reefs south of Java, especially Jakarta Bay and argued that *S. Schlumbergerella neotetraedra* was restricted to Java.However, the species was described from fossils found at Sumbawa (Tobler, 1918), in the east part of the Lesser Sunda islands.

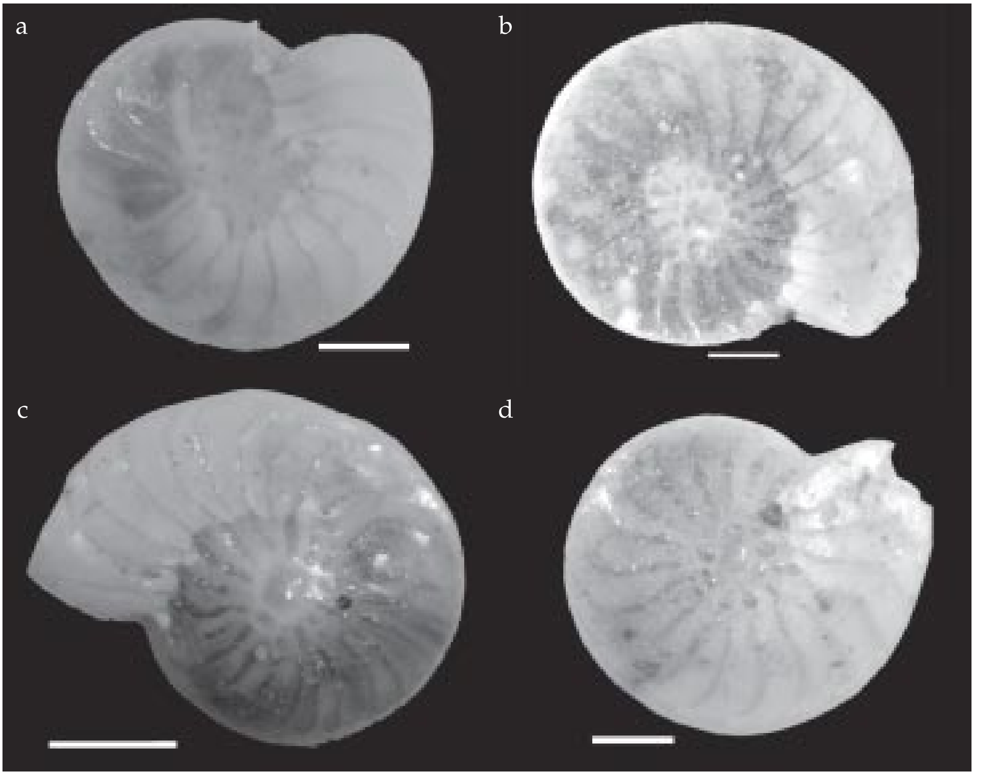

Fig. 27a-d. *Operculina ammonoides* (Gronovius, 1781) Bal 17-24. Scale bars represent 0.5 mm.

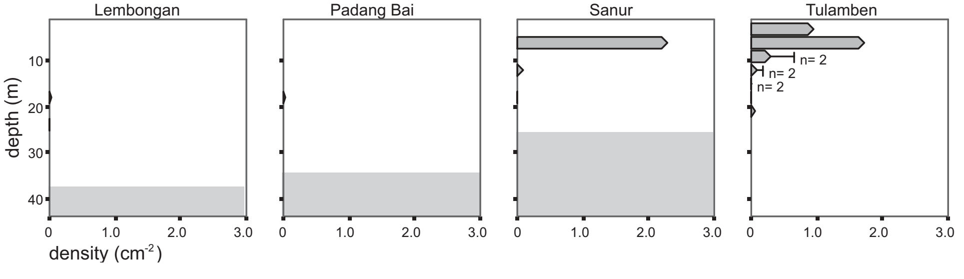

Fig. 28. Average density with depth of *Operculina ammonoides* in the four research areas.

Nummulitidae
Operculina ammonoides (Gronovius, 1781)
(figs 27a-d, 28)

Description.— Planispiral, flat, almost completely evolute to involutely coiled with a marginal cord. Septa straight, curved backwards at periphery, in the first 1.5-2 whorls with septal pustules. A highly variable species in which two distinct morphotypes can be found (Hohenegger et al., 1999; 2000; Hottinger, 1977a; Pecheux, 1995). The semi-involute type has a less rapidly expanding whorl rate; elevated septal traces and is relatively thicker than the semi-evolute type.

Affinities.— For a more complete discussion of species of Nummulitidae see Hohenegger et al. (2000), and Hottinger (1977b).

Occurrence at Bali.— The semi-involute morphotype is found in low numbers on reef slopes living on coral rubble on a sandy substrate. The semi-evolute type is found in much higher densities (up to 1.5 cm^{-2}) on coarse-grained sand at the deeper parts of the slope at Sanur and Padang Bai.

Occurrence elsewhere.— Indo West Pacific from the Red Sea to Hawaii and from south Japan to southwest New Caledonia (Langer & Hottinger, 2000). At the Spermonde Archipelago the semi-evolute type was the most abundant larger foraminifera at coarse sand substrates at the reef base (Renema et al. 2001), whilst at Cebu only the semi-involute type was found at coral rubble (Renema, 2002).

Operculina complanata (Defrance, 1822)
(fig. 29)

Description.— Planispiral, evolute with rapidly expanding whorls. Test flat, surface entirely covered by pustules. In the later whorls *O. complanata* has a folded septal flap.

Affinities.— Similar to the semi-evolute type of *O. ammonoides*, but even more rapidly expanding, see Hohenegger et al. (2000).

Occurrence at Bali.— In total eight specimens in five samples from Tulamben, Padang Bai and Sanur.

Occurrence elsewhere.— Recorded in the Indo West Pacific from east Indonesia (e.g. southwest Sulawesi, Komodo (Renema, 2002; Renema et al., 2001; Renema & Troelstra, 2001) and Japan (e.g. Hohenegger et al., 2000). *Operculina complanata* prefers sandy substrates and low light intensities (Hohenegger et al., 2000). At the Spermonde Archipelago it occurred at sandy substrates, slightly deeper than *O. ammonoides*.

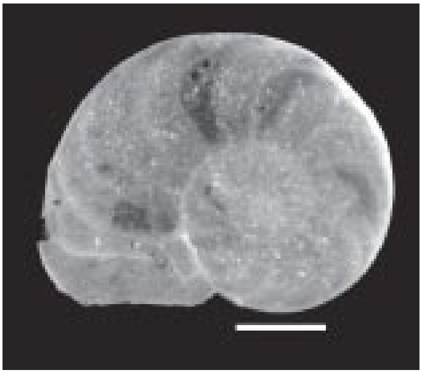

Fig. 29. *Operculina complanata* (Defrance, 1822). Bal 23-42. Scale bar represents 0.5 mm.

Heterostegina depressa Orbigny, 1826
(figs 30a-b, 31)

Description.— Planispiral, involute with rapidly expanding whorls. In large specimens the later whorls are flattened. Chambers divided into chamberlets.

Affinities.— The only involute extant nummulitid with chambers completely divided into chamberlets.

Occurrence at Bali.— One of the most common species, recorded in 118 out of 132 samples. Highest numbers on reef slopes with coral rubble (usually covered by coralline algae, fig. 36a) or structured reefrock. High densities were found living at algal mats as well (fig. 36c). Less commonly living epiphytic on thalli of macro-algae or sea-grass. Very large microspheric specimens were uncommonly found at greater depth at Tulamben (>28 m) (fig. 36d).

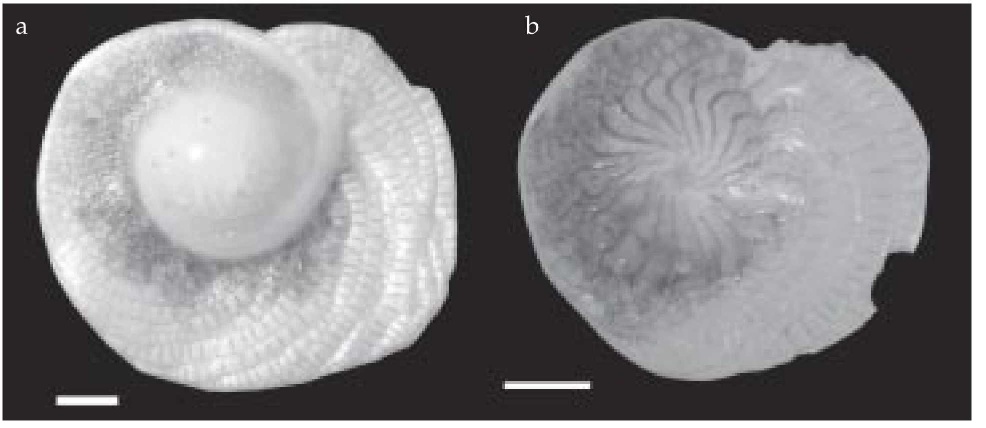

Fig. 30. *Heterostegina depressa* Orbigny, 1826. Bal 32-30 a: Microspheric specimen, b: macrospheric specimen. Scale bars represent 0.5 mm.

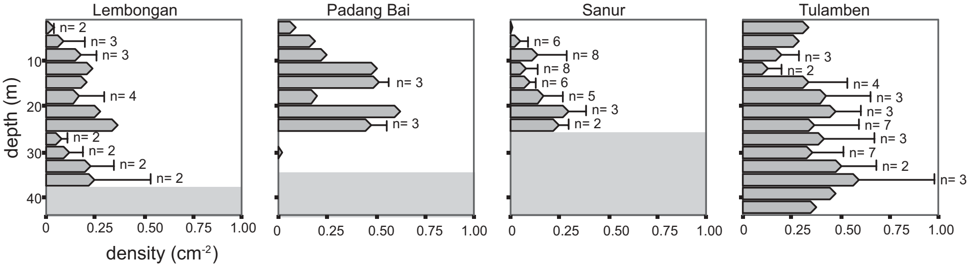

Fig. 31. Average density with depth of *Heterostegina depressa* in the four research areas.

Occurrence elsewhere.— Circumtropical (Langer & Hottinger, 2000). In the Indo West Pacific *H. depressa* is one of the most common species, together with *Amphistegina lessonii* and *A. radiata*. Generally, it occurs in lower numbers than *Amphistegina*. *Heterostegina depressa* occurs in a wide range of microhabitats. The highest numbers are consistently recorded on hard substrates on the reef slope, but rare specimens occur at larger depth on sandy substrate as well. As in Bali, highest numbers are recorded on rubble covered by coralline algae, or in algal mats (Hallock, 1984; Hohenegger, 1994; Hohenegger et al., 1999; 2000; Renema, 2002; Renema et al., 2001; Renema & Troelstra, 2001).

Heterostegina operculinoides Hofker, 1927
(fig. 32)

Description.— Completely evolute test with chambers divided into chamberlets. Septal and septula traces elevated on the test surface, often obscured by coarse granulation.

Affinities.— Most closely related to *H. depressa*, from which it is easily distinguished by its completely evolute test. For a more detailed discussion see Hohenegger et al. (2000).

Fig. 32. *Heterostegina operculinoides* Hofker, 1927. Bal 15-22-1. Scale bar represents 0.5 mm.

Occurrence at Bali.— Very rare, four specimens found in three samples from Padang Bai, Sanur and Tulamben.

Occurrence elsewhere.— From Red Sea (Hottinger et al., 1993) to the western margin of the Pacific Ocean. *Heterostegina operculinoides* prefers sandy substrates and low light intensities in calm water (Hohenegger et al., 2000). Hohenegger et al. (2000) found it at comparable depth to *O.* cf. *complanata*. The optimum in distribution of these species was about 40 m deeper than the optimum in *Operculina ammonoides*.

Assemblages

Cluster analysis resulted in the recognition of six clusters of samples, each characterised by a combination of species (fig. 33). Only one of these clusters was observed in all four areas, and two have been found in only one of the four areas, indicating the large differences among the sites visited.

Indicator value-analysis resulted in a hierarchical relationship between the six clusters. The first division is based on the abundant species. *Amphistegina lessonii* and *A. lobifera* are more abundant in the first group, whilst *A. radiata* and *Heterostegina depressa* occur in highest abun-

Table 1 Characteristic species of cluster A-F (species with highest indicator value (IV), which is at least twice as high as the IV in any of the other clusters), and average depth and standard deviation at which the cluster was observed in the complete database and for each area separately. The number in brackets is the number of samples that were allocated to this assemblage.

	A	B	C	D	E	F
Species with high IV	*Schlumbergerella floressiana* *Amphistegina lobifera*	*Calcarina spengleri* *Baculogypsinoides spinous*	*Operculina ammonoides* *Elphidium craticulatum*	*Calcarina defrancii*	*Neorotalia calcar*	*Calcarina spengleri* *Schlumbergerella neotetraedra*
Depth	7.2 ± 2.6 m (33)	25.6 ± 7.9 m (41)	21.4 ± 6.2 m (23)	13.8 ± 4.4 m (11)	12.4 ± 5.1 m (14)	7.6 ± 3.6 m (5)
Tulamben	(0)	26.5 ± 8.0 m (15)	22.6 ± 7.5 m (10)	(0)	(0)	7.6 ± 3.6 m (5)
Nusa Lembongan	6.2.9 ± 2.4 m (9)	24.2 ± 8.0 m (15)	30 m (1)	(0)	(0)	(0)
Sanur	7.9 ± 2.6 m (22)	(0)	19.0 ± 5.0 m (8)	12.8 ± 4.3 m (5)	12.4 ± 5.1 m (14)	(0)
Padang Bai	4.5 ± 2.1 m (2)	(0)	20.8 ± 2.9 m (4)	14.7 ± 4.7 m (6)	(0)	(0)

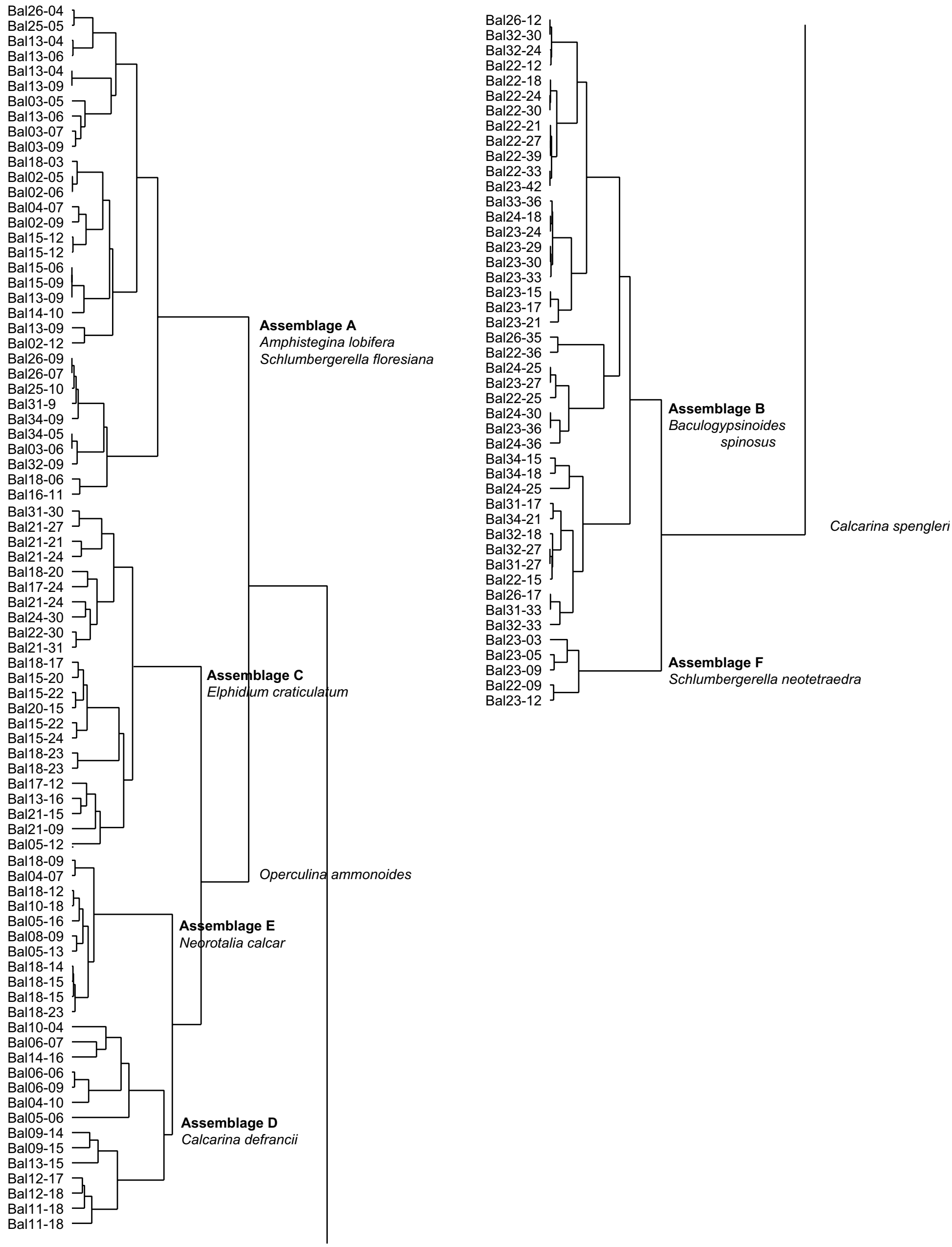

Fig. 33. Cluster diagram (Sörensens distance measure, flexible β, β = -0.75) with the indicator species for 6 assemblages indicated.

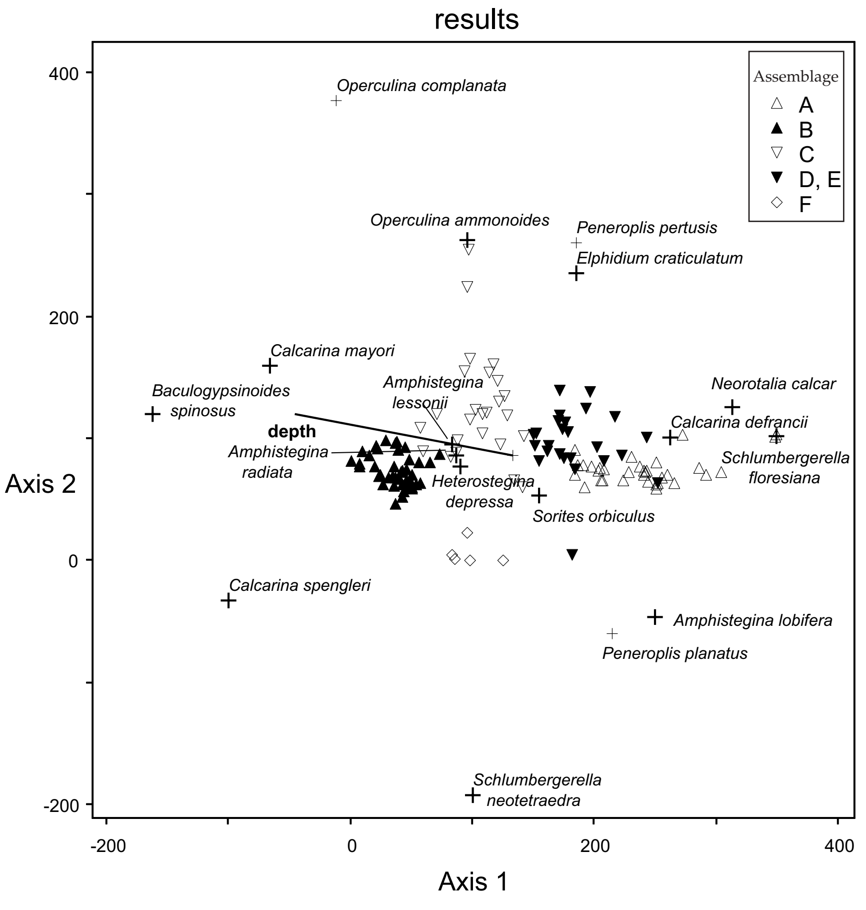

Fig. 34. Results of a decorona analysis performed with 132 samples and 19 species. Crosses indicate species, **fat** crosses indicate frequently occurring species, whilst thin crosses indicate rare species. Cluster names as in fig. 35.

dance in the second group. *Calcarina spengleri* is almost restricted to and occurs in most samples placed in the second group, and is thus by far the best indicator.

The first group can be divided into a cluster characterised by *Schlumbergerella floresiana* (cluster A) and a group of three clusters characterised respectively by *Operculina ammonoides* (in combination with *Elphidium*; cluster C), *Calcarina defrancii* (cluster D) and *Neorotalia calcar* (cluster E).

The second group can be divided into two clusters, one characterised by *Baculogypsinoides spinosus* (cluster B) and the other by *Schlumbergerella neotetraedra* (cluster F). The latter cluster appears at the same place in the dendrogram when *S. neotetraedra* is treated as being conspecific with *S. floresiana*, with the difference that the indicator values are lower.

The results of the Decorona-analysis confirm those from the cluster analysis to a large extend (fig. 34). The clusters are separated in two-dimensional space, and the species with the highest indicator values plot in similar parts to the clusters. The assem-

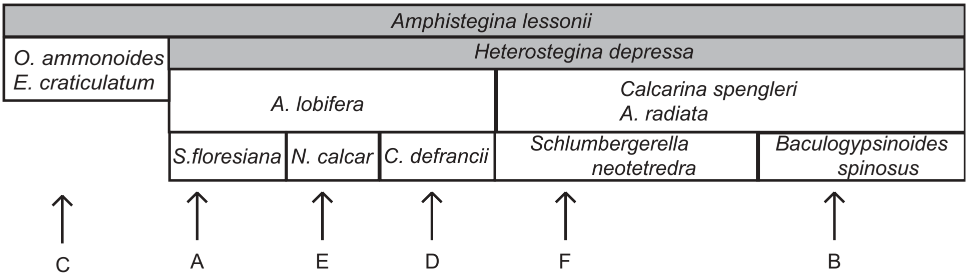

Fig. 35. Block diagram that shows the relation between clusters and assemblage composition. The clusters as defined in fig. 33 are indicated by arrows. Reading in the direction of the arrow the characteristic species are indicated. The species indicated in grey also occur in most of the samples in the cluster, but are of low indicative value because of their abundance.

blages can be separated as two deepwater and four shallow water assemblages (table 1).

The first axis explains 66% of the variation in the data set, with a mere 12% for the second axis. The third axis does not need to be taken into consideration, as it explains only 0.8%. The r^2 of the first axis with depth is 0.62. The first axis is not correlated ($r^2 < 0.2$ in all cases) with summary variables like sample size, number of species and Shannon's index.

Discussion

Faunal composition

Three of the abundant species (*Calcarina defrancii*, *Schlumbergerella floresiana* and *S. neotetraedra*) have only been recorded at Bali, and not at the other sites at which directly comparable work has been done. Of these the *Schlumbergerella* species are, biogeographically, restricted to the lesser Sunda islands, and have ecological similar species outside this area (*Baculogypsina sphaerulata*), which was not observed at Cebu or the Spermonde.

All imperforate larger benthic foraminifera were rare compared to the other areas, apart from *Sorites orbiculus*. The latter species was found in 32 samples (25%), but always in low density. Of the other five species of imperforate foraminifera only 22 specimens have been found in total, with a maximum of seven samples in which a species was found (*Peneroplis planatus*).

Absence of species can be caused by a number of factors, which can be summarised in intrinsic physiological and external physical parameters of the environment.

The large, unstructured reefrock microhabitat, which is especially abundant at Sanur and Lembongan, serve as good substratum for *Amphisorus* sp. at Cebu and the Spermonde, whilst at Bali these are covered by filamentous algae. These might exclude *Amphisorus* spp., but form a good substrate for *Peneroplis* spp (e.g. Hohenegger, 1994; Hohenegger et al. 1999). The most abundant foraminifera found in this habitat, however, are the lamellar perforate *Calcarina defrancii*, *Amphistegina* spp. and *Neorotalia calcar.* Another suitable substrate for *Amphisorus hemprichii* are larger pieces of coral rubble, which are available at the shallow reef slope of Tulamben. In conclusion, apart from *Alveolinella quoyii* and *Parasorites* spp., the substrate type at which the imperforates occur elsewhere is present, so the absence of these species should be explained otherwise.

The sites visited at Bali are all subject to large temperature variations, at both seasonal but sometimes also daily scale. Currents running through the Bali-Lombok straight cause these temperature variations. Observations around Komodo, to the east of Bali, show that *Amphisorus* sp. occurs there only at places not subject to upwelling and temperature variations.

Due to orientation of calcite crystals, transparency of the test wall is lower in imperforate foraminifera (Haynes, 1981; Hallock, 1999). Thus, at a similar light intensity and test wall thickness, less light reaches the symbionts. In high-energy environments the test wall of imperforates could become to thick in order to prevent breakage unless other mechanisms to increase shell strength are developed. For example, the imperforate *Amphisorus* spp. and *Marginopora* spp. live in high-energy environments, but cement their tests strongly to the substrate in order to prevent breakage. Additionally, lamellar perforate foraminifera are capable of test strengthening by secreting successive layers of calcite over previously formed chambers, and by forming ridges, spines, bosses and lateral chamberlets, all test characters that are not seen in imperforate foraminifera.

Possible explanations for this difference in faunal composition could be the tolerance to periodical low seawater temperatures. However, the most abundant imperforate foraminifera at Cebu and southwest Sulawesi and lacking from the sites visited during this study, *Amphisorus* sp. has been reported from Shark Bay (Western Australia) from a wide range of temperatures (14-38°C) (Davies, 1970; as *Marginopora vertebralis*). Distribution patterns around Komodo suggest that *Amphisorus* only occurs at places with high temperatures all year round (pers. obs, 2002). There are several ways in which low temperatures could affect imperforates more than lamellar perforates.

1. Perforates house diatoms as symbionts, whilst imperforate foraminifera house several other groups (chlorophytes, rhodophytes and dinoflagellates) but no diatoms (Lee & Anderson, 1991).
2. Peneroplidae, Archiasinae and *Parasorites* all require one specific species of symbiont, whilst dinoflagellate and diatom bearing foraminifera have been reported to house several species of symbionts, each with their own tolerance to environmental parameters (e.g. Lee et al. 1980a,b; Lee and Lawrence, 1990; Lee and Anderson, 1991 and references therein). Relying on different species of symbiont might increase the survival chances in more variable environments. However, the soritid *Amphisorus* sp. also accepts a range of diatoms as symbiont, but has not been found.
3. Symbiont-bearing imperforate foraminifera are most common in shallower habitats and tend to have a more restricted depth range than larger rotaliids (Hallock, 1987; 1988; 1999). The test composition and structure differs from that in lamellar perforate foraminifera (Haynes, 1981; Hallock, 1999), as well as the calcification mechanism (ter Kuile, 1991). The high-magnesium calcite in imperforate tests is more easily precipitated in high alkaline environments (Hallock, 1999). Also, imperforates use carbonate directly from the seawater and not out of a pool (ter Kuile, 1991). Temperature limits of the advantage of both metabolic pathways are not known to me. Above can lead to two speculations that should be tested by laboratorium studies:

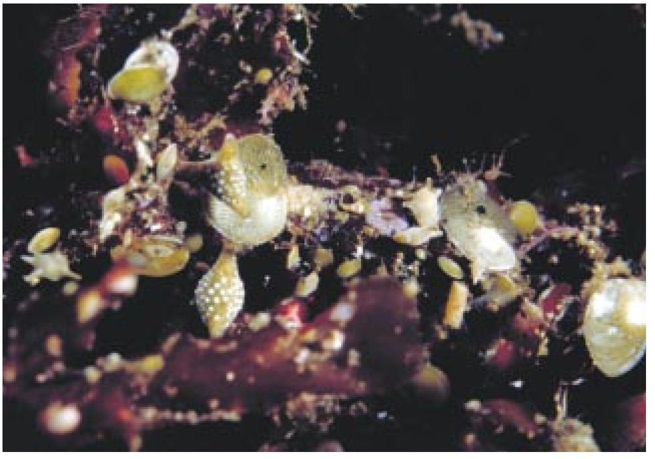

Fig. 36a. *Heterostegina depressa*, *Calcarina spengleri*, *Schlumbergerella neotetraedra* and *Amphistegina radiata* at red coralline covering coral rubble. Bal 24 8m depth, photo B.W. Hoeksema

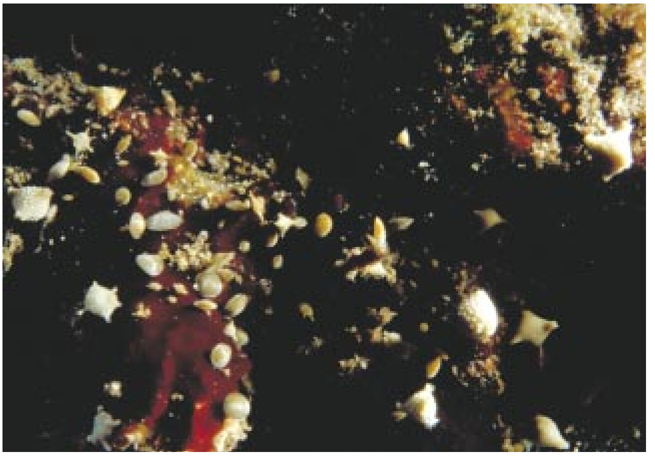

Fig. 36b. *Amphistegina lessonii*, *Schlumbergerella neotetraedra*, and *Calcarina spengleri* at red coralline algae. Bal 23 12m depth, photo B.W. Hoeksema.

Fig. 36c. Large microspheric specimen of *Heterostegina depressa* in an algal mat. Note the less conspicuous presence of many smaller specimens among the algae (*Calcarina sengleri*, *Amphistegina* spp., more *Heterostegina depressa*). Bal 24 30m depth, photo B.W. Hoeksema.

a. The water composition of the Bali region is more alkaline, which renders it more difficult to secrete a high magnesium test.
b. The metabolic pathway in imperforates is more sensitive to low temperatures, or temperature change.

Some other species have been recorded at different habitats than in former studies. For example *Operculina complanata* was found at coral rubble, although always in very low number.

Assemblages

The assemblages found at Bali show the wide variety in ecological parameters around the island. Only the assemblage characterised by *Operculina ammonoides* and *Elphidium craticulatum* is found at four areas. All samples were collected from depths ranging 15-30 m on coral rubble of which the open spaces were filled by sand, or which was completely covered by sand. On average, the deepest occurring cluster is that of *C. spengleri-B. spinosus*. This is characteristic for well-structured rubble with cryptic spaces at depths >25 m (fig. 36c). In shallower water the *C. spengleri-Schlumbergerella neotetraedra*-cluster is found at solid substrates, often covered by algae (fig. 36a-b). Equivalent assemblages to these clusters were found at the Spermonde Archipelago (Renema & Troelstra, 2001) and Cebu (Renema, 2002), although *S. neotetraedra* was absent.

At Sanur and Padang Bali hydrodynamic energy is very high due to the direct exposure to oceanic swell from the Indian Ocean. At both areas the spur and groove system is characterised by abundant algae cover and the absence of coral rubble. Here the *Schlumbergerella floresiana-Amphistegina lobifera* cluster is found at sites dominated by macro-algae, whilst the *Neorotalia calcar* cluster is found on sites dominated by short, filamentous algae.

Due to the hierarchical structure in the cluster diagram, the cluster composition can better be represented as in fig. 35. The characterising species for an assemblage are the species indicated above the arrow. *Amphistegina lessonii* occurs in all clusters and ads (in this respect) nothing to environmental interpretation. Thus, cluster A is characterised by the co-occurrence of *A. lobifera* and *Schlumbergerella floresiana*, whilst cluster E is characterised by the co-occurrence of *A. lobifera* and *Neorotalia calcar*.

In conclusion, the assemblage structure is comparable to that in other areas, especially in the well-structured rubble part. Where sediment, or epiphytic substrates are involved, the relationships among environmental parameters and assemblage composition are more complex and will require further research to define.

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