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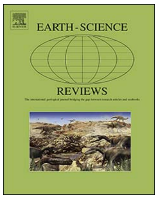

Terrestrial influence as a key driver of spatial variability in large benthic foraminiferal assemblage composition in the Central Indo-Pacific

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A B S T R A C T

Large benthic foraminifera (LBF) are important components of tropical shallow-marine ecosystems, in which they are abundant on both coral reefs and in the inter-reef areas. These protists are, similar to reef-building corals, photosymbiotic, restricted to warm (> 14 °C) seawater temperatures, and to benthic habitats within the photic zone. Because of their abundance, similarities to corals, short life-spans, and sensitivity to water quality, LBF are widely applied in environmental assessments of reef habitats.

I review data on alive LBF assemblages within their environmental context. To be able to do so, I review the occurrences of individual species of the, in most environments, most abundant Central Indo-Pacific LBF, the Amphisteginidae, Calcarinidae, and Nummulitidae. In doing so I highlight the large uncertainties with respect to ecophenotypic and genetic variation among populations. In each of these families there appears to be substantial cryptic diversity, and thorough investigation using new morphological techniques results in higher diversity than previously known.

Field observations of LBF show that nutrient availability, hydrodynamic energy, light intensity and spectrum, substrate type (sand, rubble, rubble with sand, algae, sea grass), and temperature are important environmental parameters for the occurrence of individual species. Many of these parameters are interrelated and are in some way influenced by water depth at least in part because occurrences have been related to conditions in the overlying watercolumn, and not to the microhabitat within the benthic boundary layer where the LBF live. In addition, I argue that differences in tolerance to terrestrial influence among species plays a large role in the occurrences of LBF, not only on the predominantly hard substratum reefs, but also in the predominantly sandy substratum inter-reef areas. Hence, there are distinct assemblages on reefs surrounded by deep, oceanic water, compared to terrestrially influenced reefs.

Furthermore, assemblage composition is not only determined by water-quality parameters, but also by ecological dynamics of the benthic habitat on coral reefs, including shifts away from high coral cover. Abrupt changes resulting in permanent or temporal changes in the benthic habitat of coral reefs result in changes in the LBF assemblage. Especially calcarinids become more abundant with increased algal cover.

Assemblage composition of benthic foraminifera, especially the weighted contribution of LBF to the total benthic foraminifera assemblage (the FoRAM Index), has been used to provide an assessment of water quality. Here I show that, in the Central Indo-Pacific, several species of LBF can occur abundantly in nearshore settings experiencing high terrestrial run-off. For a more consistent application of this method, the sampling and processing protocols (e.g., depth, sieve fractions included) should be standardised. Furthermore, differences in regional species pools require regional calibrations of the method, or finding alternative ways of simple assessments of reef quality using LBF.

1. Introduction

Large benthic Foraminifera (LBF) are an important component of tropical shallow-marine ecosystems, including coral reefs (e.g., Hottinger, 1983; Hallock, 1984, 2001; Renema and Troelstra, 2001; Hohenegger, 2006 and many others) and inter-reef (mixed) carbonate shelfs within the photic zone (e.g., Tudhope and Scoffin, 1988; James et al., 1999; Renema, 2006b). LBF are comparatively large, unicellular protists with a carbonate test that, similar to zooxanthellate corals, depend on photosymbiotic algae (Röttger, 1976; Kremer et al., 1980; Lee and Anderson, 1991). Although they harbour a wider range of symbionts than corals, this symbiotic relationship imposes similar

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environmental requirements to these protists. LBF house diatoms, dinoflagellates, rhodophytes, and chlorophytes as photosymbionts, and cyanobacteria are present in many hosts as well (see review of Lee, 2006). Because of their abundance and fossil record, LBF have been studied by biologists and paleontologists alike. These studies range from local to regional distribution patterns and paleoclimate (e.g., Hottinger, 1983; Hallock, 1984; Adams et al., 1990; Hohenegger, 1994; Langer and Hottinger, 2000; Renema et al., 2008; Weinmann et al., 2013a, 2013b), fundamental research on symbiosis, calcification and growth (e.g., Muller, 1978; Leutenegger, 1984; ter Kuile and Erez, 1991; Nobes et al., 2008; Uthicke and Altenrath, 2010; Walker et al., 2011), to LBF as environmental indicators (e.g., Hallock et al., 2003; Hallock, 2012; Uthicke and Nobes, 2008; Uthicke et al., 2010), and to their importance for the sediment budget on reefs (e.g., Hallock, 1981a; Hohenegger, 2006; Fujita and Fujimura, 2008; Langer, 2008; Doo et al., 2017). Historically, LBF have been used for the stratigraphy of tropical shallow-marine environments, mostly because in these environments they were one of the few stratigraphic markers that were available (e.g., Adams, 1984; Serra-Kiel et al., 1998; Lunt and Allan, 2004). Additionally, because of their size they can be recognized in the field and do not need elaborate processing to provide a rough idea about the age of the rocks. In stratigraphical studies geographical variation was deemphasized. Intra-test variability of geochemical proxies, either using stable isotopes (e.g., Purton and Brasier, 1997; Saraswati et al., 2004), or trace elements (e.g., Segev and Erez, 2006; Evans et al., 2013) allows reconstructions of paleoenvironment, including seasonality. To be able to interpret these measurements, a good understanding of the biology and calcification of LBF is needed (e.g., Raitzsch et al., 2010; Evans et al., 2015).

Currently there is an upsurge of the use of LBF because of their sensitivity to environmental conditions (e.g., Ziegler and Uthicke, 2011; Fujita et al., 2011; Prazeres et al., 2016b; Schmidt et al., 2014), and (paleo)biogeography (Renema et al., 2008; Weinmann et al., 2013a, 2013b) as well as environmental assessments, in both recent sediments (e.g., Fujita et al., 2014a; Pisapia et al., 2017; Muruganantham et al., 2017) and sediment cores (Uthicke et al., 2012; Reymond et al., 2013b; Narayan et al., 2015).

Large benthic foraminifera are sensitive to variations in the ambient environment (Hallock et al., 2003; Hallock, 2012 and subsequent publications). They respond to water quality (Uthicke and Nobes, 2008; Schueth and Frank, 2008), increased sediment stress (Renema, 2010), and benthic habitat structure (Renema, 2010). They follow different response trajectories to environmental change than corals and other carbonate producers (e.g., Uthicke et al., 2010; Tager et al., 2010; Reymond et al., 2011). Their shorter life-spans, greater sensitivity to photic stress, and lower sensitivity to temperature compared to long-living, sessile corals is probably underpinning this difference (Hallock et al., 2003, 2006; Uthicke et al., 2010). This more rapid response contributes to their potential use for monitoring water quality in coral-reef ecosystems (Hallock et al., 2003, 2006; Hallock, 2012).

The ecology of LBF has not been studied as extensively as that of zooxanthellate corals in laboratory conditions. Important exceptions include laboratory experiments on *Amphistegina* spp. (Muller, 1974; Lee et al., 1980; Hallock, 1981b; Hallock et al., 1986) and *Heterostegina depressa* (Röttger and Berger, 1972; Röttger, 1976) that focused largely on responses to light and documenting physiological dependence on algal endosymbionts. More recently, a second wave of studies using experimental approaches focused primarily on the effects of anthropogenic environmental change, such as ocean warming, acidification, pollution, eutrophication, as well as their cumulative effects, on LBF using both in situ (Uthicke and Altenrath, 2010) and laboratory experimental approaches (e.g., Ziegler and Uthicke, 2011; Nobes et al., 2008; Reymond et al., 2013b; van Dam et al., 2012; Schmidt et al., 2011, 2014; Walker et al., 2011). However, this has been, to a large extent, restricted to a small number of taxa (*Amphistegina* spp., *Heterostegina depressa*, and *Marginopora* spp.).

LBF play an important role in the sediment budget of (sub)tropical carbonate shelves and coral reefs, while in zooxanthellate corals, carbonate production is concentrated in coral reefs (Langer, 2008; Tudhope and Scoffin, 1988). In inter-reef environments, LBF can contribute up to 70% of the sediment (e.g., Tudhope and Scoffin, 1988; Renema, 2006b). Measured over an onshore-offshore transect in the central Great Barrier Reef, LBF were estimated to be the second most important carbonate producer, behind calcareous algae, but ahead of zooxanthellate corals (Tudhope and Scoffin, 1988). Note that most of this production was observed in the (deeper) inter-reef habitats. In reef sediments this contribution is typically limited to on average 5%, exceptionally to 25% (Hewins and Perry, 2006; Perry et al., 2011). However, carbonate production by LBF is critical to the maintenance of reef cays on atolls in the Pacific Ocean, in which the sand is dominated by LBF (Perry et al., 2011; Yamano et al., 2000), especially the calcarinids *Baculogypsina sphaerulata* and *Calcarina gaudichaudii*, and *Amphistegina lobifera* (Hallock, 1981a; Woodroffe and Morrison, 2001; Fujita et al., 2009; Dawson et al., 2014). These sediments are sourced primarily from the reef flat and preferentially transported towards the islands (Perry et al., 2011; Hohenegger, 2006; Fellowes et al., 2016). Furthermore, LBF play a critical role in maintaining white sand beaches on tropical islands, such as Bali and in southern Japan (Hohenegger, 2006), and are as such important for maintaining some of the largest turtle rookeries (Dawson et al., 2014). This is further demonstrated by the expansion of *Amphistegina* in the Mediterranean Sea that resulted in beaches being transformed from dark volcanic to white carbonate sands in Cyprus and southern Turkey (Koukousioura et al., 2011; Langer et al., 2012).

Most of the sediment production by LBF is by diatom-bearing nummulitids, calcarinids, and amphisteginids; dinoflagellate-bearing foraminifera contribute less. This is reflected both in lower sediment production rates per m^2 (e.g., Fujita et al., 2009; Doo et al., 2012, 2017), and in the limited surface area inhabited by dinoflagellate-bearing LBF (Tudhope and Scoffin, 1988; Renema and Troelstra, 2001; Renema, 2006b).

In this paper I review the ecology of extant LBF from the Central Indo-Pacific, comprising the tropical waters of the western Pacific Ocean, the eastern Indian Ocean, and the connecting seas. I will focus on geographical variability in assemblage composition by reviewing 1) the most important environmental parameters determining LBF distribution; 2) adaptations of LBF to accommodate (variations in) the environmental parameters; 3) habitat fractionation along nearshore-offshore gradient, 4) variation in assemblage composition; and 5) recognition and environmental tolerances of individual species of lamellar perforate LBF. All occurrences referred to in the manuscript concern live specimens. Appendix 1 shows the region of interest, and the most important study areas and data sources.

2. Environmental parameters shaping the LBF habitat

Large benthic foraminifera are confined to tropical to warm temperate shallow-marine seas, with a sea surface temperature (SST) during the coldest month of > 14–16 °C (Langer and Hottinger, 2000; Weinmann et al., 2013b), and benthic habitats within the photic zone. The lower tolerance limit to SST has been inferred from niche-modelling using extant occurrences (Langer and Hottinger, 2000; Weinmann et al., 2013b). This has demonstrated that each taxon has a different lower tolerance limit, ranging from > 14 °C in *Amphistegina* spp. to > 24 °C SST in *Operculina heterosteginoides* (Langer and Hottinger, 2000). However, *O. heterosteginoides* is a species of the lower photic zone, whereas *Amphistegina* spp. includes multiple taxa, including at least one, *A. lobifera*, that lives on the reef flat where water can be warmer than the seawater surrounding the reef due to restricted flow during low tide. In the tropics, temperatures at the lower limit of the photic zone (140 m) usually are > 20 °C and probably not limiting to the occurrence of LBF (Hohenegger, 2004; Renema, 2006b), apart from areas with upwelling or exposure to internal waves (Pomar et al., 2012). The bathymetric temperature gradient is steeper at higher latitudes than in the tropics, which, in combination with reduced light in the winter months, might restrict the lower depth limit of LBF at higher latitudes. Hollaus and Hottinger (1997) found that the occurrence of *A. lessonii* around Crete was truncated at 16–18 °C or 40–50 m water depth. Koba (1977) found that the distribution of *Cycloclypeus carpenteri*, one of the deeper-living LBF, could be described by the > 20° isotherm at 100 m depth in Japan. In these studies no upper SST limit on the distribution of species was found (Langer and Hottinger, 2000; Weinmann et al., 2013a, 2013b).

Experimental studies on three reef-flat species found net oxygen production between seawater temperatures of ∼20–35 °C, with minimal differences among species (Fujita et al., 2014b), which is in agreement with the lower temperature limits found by niche-modelling. Furthermore, experimental studies show that the immediate response to shock, and chronic exposures of LBF to high temperatures, reduced the photosynthetic efficiency resulting in decreased fitness, growth and reproduction (Reymond et al., 2013a; Schmidt et al., 2014; Titelboim et al., 2016; Prazeres et al., 2016b), which can lead to substantial loss of photosymbionts (bleaching) (Talge and Hallock, 1995; Williams and Hallock, 2004; Schmidt et al., 2011) and increased mortality (Uthicke et al., 2012). Maximum photosynthetic yield of the photosymbiont system in *Calcarina gaudichaudii*, *Baculogypsina sphaerulata*, and *Amphisorus kudikajimaensis*, three reef flat species from Japan, peaked around the mean summer seawater temperature (Fujita et al., 2014b), indicating their capacity to adapt to ambient temperature conditions. Finally, Stuhr et al. (2017) found no reduction in photosymbiont activity in *A. gibbosa*, the western Atlantic sister species of A. *lessonii* and *A. lobifera*, in response to single and episodic temperature stress events, whereas chronic stress resulted in extensive bleaching. Thus, most LBF populations appear to be well-adapted to the temperature dynamics in their ambient environment.

Remaining questions include how sensitive they are to chronic temperature stress and to variability over longer than experimental time-scales. The occurrence of *Pararotalia calcariformata* in a chronical thermally polluted site implies that the photosymbiotic system can adapt to elevated temperatures (Titelboim et al., 2016). However, such data are only available for few species, and these show substantial differences in the upper tolerance limit between *Amphistegina lobifera* (32 °C) and *Pararotalia calcariformata* (36 °C) (Titelboim et al., 2016).

In most studies on the distribution of LBF, depth is the primary environmental parameter that is directly measured (e.g., Hottinger, 1977a; Hallock, 1984; Hollaus and Hottinger, 1997; Hohenegger, 1994; Renema and Troelstra, 2001). In a bathymetric gradient along a slope, species are arranged following their light requirements, hydrodynamic energy, and substrate type (e.g., Hallock, 1987; Hohenegger, 1994; Renema, 2006a). However, depth only affects LBF indirectly (Fig. 1). Light (intensity and wave length), substrate type, hydrodynamic energy, and seasonal variation in environmental parameters exert direct controls on LBF distribution, and are all related to water depth.

Light intensity decreases with depth dependent on the transparency of the water column. In diverse photosymbiotic organisms the limit of effective photosymbioisis is at ∼1% surface photosynthetical active radiation (PAR; Huston, 1985; Kahng et al., 2010; Pomar et al., 2017), and this level is also inferred to be the lower tolerance limit for LBF (Hohenegger et al., 2000; Hohenegger, 2004). Despite a much larger tolerance to light intensity inferred from the depth distribution of LBF (Hohenegger et al., 2000; Hohenegger, 2006), light saturation was observed at much lower light levels of 1–10% surface PAR for species with diatom symbionts in experimental set-ups (Nobes et al., 2008; Uthicke and Nobes, 2008; Walker et al., 2011), even though these were performed with species living on the upper-reef slope.

Light attenuation is influenced by nutrient availability and terrestrial influx (Fig. 1). In areas with high terrestrial influx, transparency will be lower because of the higher concentration of both inorganic and organic particles. Nutrients increase the abundance of planktonic organisms, thus decreasing transparency. Light intensity decreases both by absorption by water molecules and scattering by particles. The nature of the particles, e.g., organic, clay minerals, carbonate, determine the amount of scattering and the spectral attenuation of light (Morel and Prieur, 1977).

Light attenuation in clear ocean water is entirely dominated by absorption, and blue light travels deepest (Morel and Prieur, 1977; Doron et al., 2007). However, in estuarine conditions, scattering is more important and green to yellow light reaches deeper parts of the photic zone (Morel and Prieur, 1977; Cunningham et al., 2013; Fig. 2). Photosymbiotic foraminifera respond to both light intensity (Röttger and Berger, 1972; Hallock et al., 1986) and the light spectrum (Richardson et al., 1983; Kirk, 2011). The response to light is strongly related to the symbiont type. Chlorophytic symbionts typically are unable to grow in very low light environments and they reach maximum photosynthesis rates in higher light intensities (Richardson et al., 1983; Walker et al., 2011; Waters and Hallock, 2017). Species with dinoflagellate symbionts also have higher photosynthetic rates than diatom-bearing species (Fujita and Fujimura, 2008). The diatom-bearing *Amphistegina* spp. and *Heterostegina depressa*, all living on the reef slope, survive in very low light intensities (1–2% surface PAR), and can tolerate relatively high light intensities for limited periods of time, but they cannot increase their rate of photosynthesis to take advantage of the increase in radiant energy (Richardson et al., 1983; Walker et al., 2011; Nobes et al., 2008). Exposure to high light intensity in reef slope, diatom-bearing species can cause reduced growth rates (Nobes et al., 2008) and bleaching (Talge and Hallock, 2003; Williams and Hallock, 2004; Schmidt et al., 2011). However, in the reef flat diatom-bearing species *Calcarina gaudichaudii* and *Baculogypsina sphaerulata*, which are naturally exposed to high light intensity and often live on the sediment surface, no photoinhibition was observed at light intensities equal to or even higher than surface PAR (Fujita and Fujimura, 2008). Thus, despite the occurrence of reef slope, diatom-bearing species in light intensities of 60–80% surface PAR (Hohenegger, 2004), they likely need much lower intensities. Indeed, most such LBF species are found in cryptic micro-habitats below coral rubble and in interstitial space between rubble (Renema, 2006a, 2008). In natural conditions, LBF can modify their position in the substratum, especially in rubble with open interstitial spaces (pers. obs.). Possibly this is also the case for inter-reef soft substrate dwellers, but no comparable data are available for these species.

Hydrodynamic energy both directly and indirectly affects the occurrence of LBF (Fig. 1). In areas with continuous battering of high waves or strong currents, LBF are swept away or broken into pieces. In soft sediments, waves disturb the sediment too frequently, so that foraminifera are buried and thus no longer profit from their symbionts. On reef slopes with coral growth, waves break down coral colonies, creating open patches with coral rubble, which serves as a protective substrate for foraminifera. Some species are more affected by wave (or current) energy. For example, the robust *Nummulites venosus* occurs on sandy substrate below the fair weather wave base in Japan, while the paper-thin and friable *Cycloclypeus carpenteri* only occurs below the storm wave base on the same slopes (Hohenegger et al., 2000).

Within species the diameter/thickness ratio (D/T) tends to increase with depth (e.g., Larsen and Drooger, 1977; Hallock, 1979) as the result of decreased hydrodynamic energy (Hallock et al., 1986). More sheltered conditions in nearshore areas results in a lower D/T at the same depth compared to offshore settings (Renema, 2005).

Substrate type is an important, but complex, environmental parameter influencing the local distribution of LBF (e.g., Hottinger, 1977a; Hallock, 1984; Hohenegger, 1994; Renema and Troelstra, 2001; Renema, 2006a). The most important substrate types include sand, rubble, and algae (or sometimes seagrasses), but gradation between these categories occurs (Renema, 2006a, 2008). In areas with low sedimentation rates compared to reef accretion rate, rubble accumulates

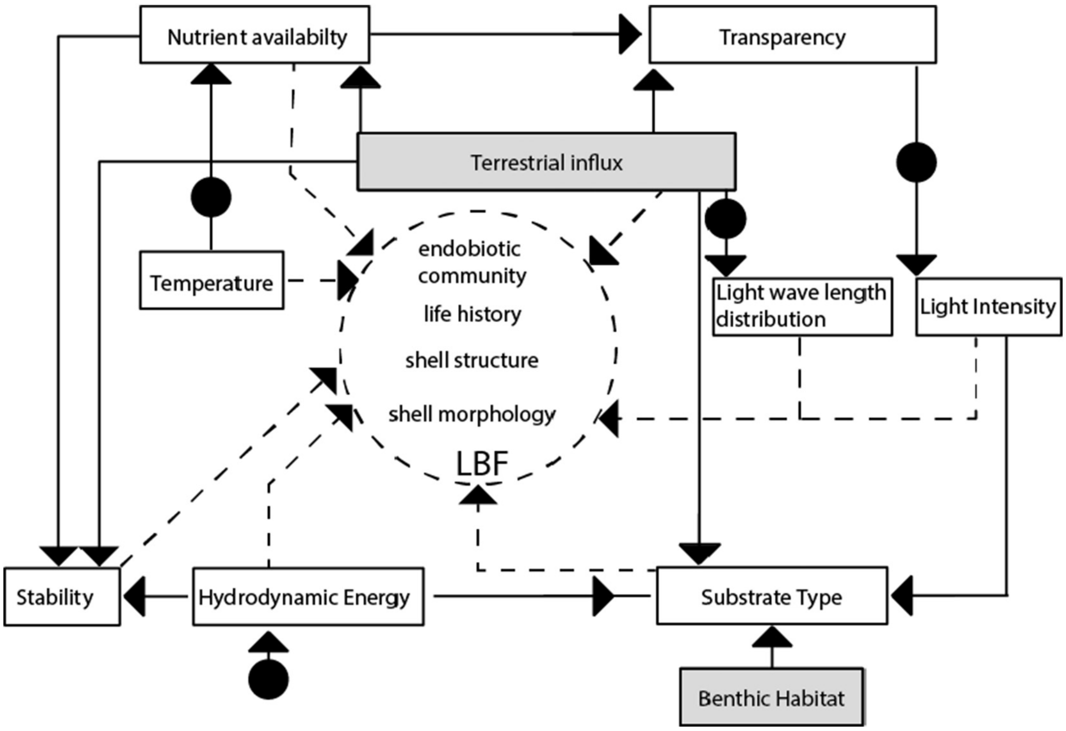

Fig. 1. Schematic representation of abiotic environmental parameters influencing the distribution of LBF and traits of the LBF to accommodate these. Note the key role of terrestrial influence affecting the LBF holobiont both directly and indirectly. Solid arrows: environmental interactions; dashed arrows: environment-LBF interactions. Black circles are at the most important places where depth is interacting with environmental parameters.

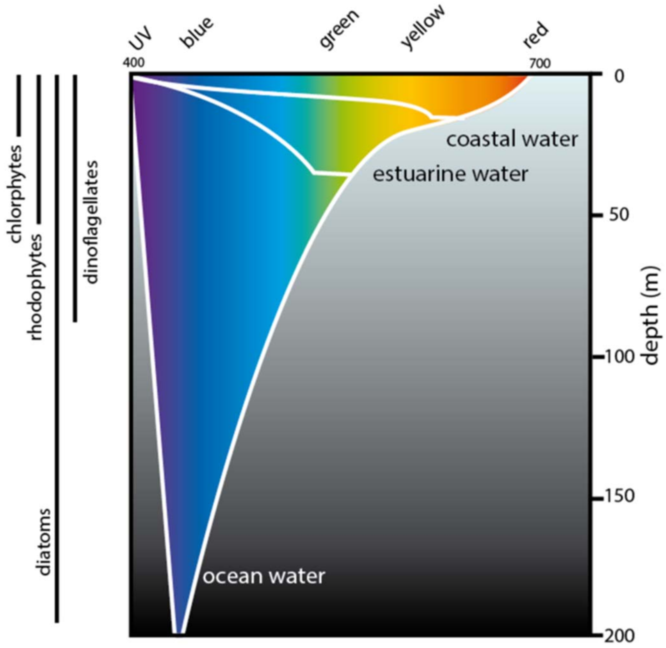

Fig. 2. Difference in light penetration between oceanic conditions dominated by absorption, and coastal and estuarine conditions which are dominated by refraction. Modified from Cunningham et al. (2013).

in patches between corals. The interstitial space is filled with water, leaving a large surface of substrate for LBF. Remineralization of organic biomass, diffusion–advection with the overlying watermass, and the use of nutrients affect nutrient concentrations in the interstitial water (Hatcher, 1990). The part of the rubble patch directly exposed to seawater experiences more exposure to light, wave and current energy. Light intensity and hydrodynamic energy decrease with depth in the rubble. Although little studied, dissolved and particulate nutrients change in concentration and composition from near the rubble–water interface to deep inside the rubble (see e.g., D'Elia and Wiebe, 1990). Along this gradient LBF species change. *Amphisorus* spp. is limited to the rubble–water interface, and *C. spengleri*, *H. depressa*, and especially *A. radiata* are found as deep as 10–15 cm within the rubble. The occurrence of monospecific *Amphisorus* assemblages, attached to the substratum in the breaker zone of the reef crest can be interpreted as a reduction in the subdivision of vertical space (tiering) within the substrate (Renema, 2006a). The amount of tiering is reduced and the nutrient dynamics change when the interstitial space is filled with sediment. In these conditions *A. radiata*, *C. spengleri*, and *H. depressa* occur in lower density, and *Neorotalia gaimardi* and *Calcarina defrancei* are more abundant.

The abiotic conditions discussed above are measured at a local to regional scale. Temperature, light, and nutrients are typically measured in the water column, not in the micro-habitat of the LBF. Processes in the benthic boundary layer affect the micro-environment where the LBF occur. Shashar et al. (1996) recognized three types of boundary layers over coral reefs, the benthic boundary layer, the momentum boundary layer, and the inner boundary layer. The momentum boundary layer is closely associated with the morphology of individual colonies and likely to be the least important to LBF (possibly with an exception of the strongly wrinkled tests of some *Marginopora vertebralis* and fossil saddle shaped taxa). The benthic boundary layer controls the interaction of the reef with open seawater and reflects the impact of the overall community on material exchange (Shashar et al., 1996; Jokiel, 2011). Within environments that are important for LBF, different dynamics in the benthic boundary layer can be observed between coral reefs, seagrass meadows, and sandy substrates where the benthic boundary layer is thinnest. The inner boundary layer, in which flow is slow around the substrate-seawater interface between the corals, is where most reef-associated LBF are found. In cavities and crevices (such as the interstitial space between coral rubble) dissolved organic carbon is removed, whereas particulate organic matter is enhanced, resulting in a micro-environment that is quite different from the ambient conditions on the reef (de Goeij and van Duyl, 2007; de Goeij et al., 2013). In seagrass meadows some LBF occur higher in the benthic boundary layer by attaching to the seagrass leafs, but usually highest densities are at the base of seagrasses or even at the root structures (Reich et al., 2015).

The diffusion boundary layer is related to diffusion-limited processes directly surrounding the organism and has a spatial scale of a few mm or less. Köhler-Rink and Kühl (2000) measured the diffusion boundary layer around LBF tests, which was typically < 0.5 mm thick and the thickness decreased with flow around the test. The physical-chemical microenvironment around LBF tests is largely controlled by irradiance and water flow (Köhler-Rink and Kühl, 2000). Both respiration rates of the foraminiferal-algal association and the photosynthesis rates of the endosymbionts increased under flow conditions.

All the evidence presented above highlights the importance of the benthic boundary layer which modifies, among others, the nutrient availability, hydrodynamic energy, and light intensity in the microhabitat of LBF.

3. Adaptations of LBF to accommodate (variability in) environmental parameters

Large benthic foraminifera are a polyphyletic group with a wide variety in shell structure and morphology. In extant LBF, divisions based on symbiont type and wall structure are most frequently used. There are two types of wall structure, lamellar perforate and imperforate. In lamellar perforate tests, gas-exchange is enhanced by small pores in the outer test wall. Symbionts are positioned below the inner pore mouth to fully profit from these pores (Hottinger, 2000). Furthermore, the calcite crystal axes are arranged in parallel sheets enhancing transparency of the test wall. In imperforate foraminifera, to the contrary, there are no pores and the calcite crystals are randomly oriented resulting in an opaque test. Transparency of the test can be modulated by groves, pits or otherwise thinned chamber walls in soritids (Hottinger, 2000). Imperforate LBF are typically restricted to shallower depth than perforate ones (Hottinger, 2000).

Four main types of eukaryotic endosymbionts have been found in foraminifera. Each type is observed in a limited set of taxa which usually houses only a single type of symbiont (Lee and Anderson, 1991). The lamellar perforate nummulitids, amphisteginids and calcarinids and the imperforate porcelaneous alveolinids house diatoms. Within the imperforate LBF there is a wider diversity of symbionts. Peneroplids house rhodophytic algae, most soritids have dinoflagellate symbionts, and *Parasorites* and *Laevipeneroplis* house chlorophytes. Since each symbiont type uses its own range of the light spectrum, the foraminiferal hosts are restricted in their depth distribution (Fig. 2). Chlorophyte-bearing LBF (using orange light) are restricted to the shallowest habitats, dinoflagellate-bearing taxa have an intermediate depth limit, whereas diatom-bearing species can live in the deepest settings (e.g., Hottinger, 1983; Hohenegger, 1994; Renema and Troelstra, 2001).

Although most specimens from which the symbionts were identified harboured only one species at a time, in many foraminiferal species several symbiont species have been identified (Lee and Anderson, 1991), thus expanding the environmental tolerance of a species beyond that of a single symbiont species. These early results were based on isolating symbionts, culturing them, and identifying them based on morphological characteristics of the test. Since then molecular techniques have become available to identify symbionts in LBF (Pawlowski et al., 2001a, 2001b; Holzmann et al., 2006). These studies found that the eukaryotic endosymbionts in the archaiasinids (Pawlowski et al., 2001a), soritids (Pawlowski et al., 2001b), nummulitids (Holzmann et al., 2006), and amphisteginids (Barnes, 2016) were monophyletic.

The dinoflagellate-bearing soritids have recently received a lot of attention as a potential source for restocking zooxanthellate in corals following large-scale bleaching events (Pawlowski et al., 2001a; Pochon et al., 2001, 2007; Garcia-Cuetos et al., 2005; Fay et al., 2009). A large diversity of *Symbiodinium* clades has been discovered, of which several were unique to foraminifera (e.g., Pochon and Pawlowski, 2006). Whereas a strong specificity was suggested in some studies on dinoflagelate host-symbiont relationships (Pawlowski et al., 2001a; Pochon et al., 2001; Garcia-Cuetos et al., 2005), recent studies suggest a high degree of flexibility in foraminifera-symbiont partnerships (Pochon et al., 2007; Fay et al., 2009; Momigliano and Uthicke, 2013). Differences in *Symbiodinium*-clade composition was observed among and within populations of *Marginopora vertebralis* (Momigliano and Uthicke, 2013), and in some cases multiple clades were observed simultaneously in a single test (Fay et al., 2009; Momigliano and Uthicke, 2013). Each *Symbiodinium*-type has its own set of environmental tolerances and has specific biogeographic and ecological distributions (Garcia-Cuetos et al., 2005; Pochon et al., 2007). Within *Amphisorus* test, a differentiation in symbiont type from center to margin was observed, possibly in response to a heterogeneous internal environment and function (Fay et al., 2009). Such detailed studies have not been done in taxa housing other than *Symbiodinium*-symbionts. However, symbiotic chlorophyte- and diatom- LBF relationships do not seem to be strictly specific, as different foraminiferal species can share the same symbiont type (Pawlowski et al., 2001b; Holzmann et al., 2006).

Like other reef-associated organisms, LBF host a high diversity of endobiotic prokaryotes (Bourne et al., 2013), many of which are of vital importance to the host (Lesser et al., 2004; de Goeij et al., 2013). Even though this was noted long ago (Lee et al., 1985), our understanding of the importance of host-associated microbes in LBF is still in its infancy (e.g., Bourne et al., 2013; Webster et al., 2013, 2016; Prazeres et al., 2017), and has mostly been explored in relation to ocean warming and ocean acidification (e.g., Webster et al., 2013). Recent in-situ and experimental analyses of the prokaryotic microbial community in LBF tests demonstrated changes in response to elevated temperatures and decreased pH, with a significant shift involving both the loss of taxa and the appearance of new ones (Webster et al., 2016). This finding was interpreted as LBF being more sensitive to such changes compared to other taxa that were investigated (including corals and sea-urchins) in the same study (Webster et al., 2016). However, without understanding the roles performed by these endobiotic microbes, this can also be interpreted as having a high potential to accommodate environmental change by adjusting the endobiotic community (Prazeres et al., 2017). This all indicates that there might be a much more complex symbiont-host relationship than previously suspected, which can affect the environmental tolerance of LBF taxa, and their capacity to accommodate environmental change.

Both within and between species, test shape varies in response to environmental parameters. Test shape is a compromise between hydrodynamic resistance and light and metabolic requirements (Haynes, 1965; Hallock et al., 1986, 1991). In shallow water, irradiation levels are high and the light intensity reaching the symbiont has to be reduced. This can either be done by moving the symbionts towards less irradiated places within the test, by thickening of the test wall, or by moving to a more shaded location. On the other hand, in deep water, light intensity reaches very low levels and the host has to find a way to concentrate the light on the symbionts. This is done by flattening of the shell and the production of interseptal piles. These interseptal piles increase the strength of the shell (allowing even further thinning) and serve as lenses to concentrate the available light on the symbionts (Hottinger, 2000). These very thin shells are prone to breakage and can only live under very calm conditions, while more robust shells can occur in areas with higher hydrodynamic energy, where the foraminiferal test should not break, not be swept away, nor buried by sediment. Breakage is prevented by a more robust test, while removal is guarded against by developing ways to increase the potential to stick to the surface. This can either be by developing a protoplasmic sheath (*Heterostegina depressa*), pseudoplasm plugs at the end of spines (calcarinids) or changes in morphology of the apertural faces (amphisteginids). Some flat species, especially soritids, attach physically to the substrate (Hottinger, 2000).

4. Habitat fractionation along the nearshore-offshore gradient

Similar to coral reefs, LBF are associated with high light and oligotrophic conditions in which the photosymbionts efficiently recycle the few available nutrients (Hallock, 1981b). Using a mathematical model, Hallock (1981b) argued that housing symbionts is most profitable in conditions where organic matter is concentrated in particles. The host collects and digests the particulate organic matter, and the symbiont feeds on the dissolved waste product of the host. Excess energy (photosynthate) produced by the symbiont is in turn used by the host (Hallock, 1981b). In warm waters, the metabolic rate of LBF is higher than in cool water. This is expressed as the Q_{10} or the rate of change as a consequence of a 10 °C increase in temperature. No estimates of Q_{10} are available for benthic foraminifera, but in photosymbiotic planktonic foraminfera the Q_{10} of respiration was estimated at 3.18 ± 0.27 and for net photosynthesis at 2.69 ± 0.36 (Lombard et al., 2009). Because of the increased metabolic rate, apparent nutrient availability is lower at higher temperatures with the same nutrient concentrations in the ambient environment (Hallock, 1981b). Hence, sufficiently oligotrophic conditions are more likely to occur in warm tropical, rather than in cooler subtropical seas (Hallock, 1981b).

However, the abundant occurrence of LBF close to river mouths and populated shorelines shows that LBF are not limited to low nutrient conditions (e.g., Renema and Troelstra, 2001; Renema, 2006a, 2008; Schueth and Frank, 2008; Nobes et al., 2008). Experiments have shown that although mixotrophs can be highly efficient in oligotrophic conditions, where up to 90% of their energy can be supplied by the symbionts, in more nutritious conditions they are less dependent on their symbionts for growth (ter Kuile and Erez, 1991).

Discussing the relationship between nutrients and LBF distribution, Hallock (1987, 1988) presented a model in which the community structure of LBF is described as a function of nutrient flux, directly influencing euphotic zone depth. Light penetration into the water column is limited by turbidity, which is a function of plankton density and fluvial influx of dissolved organic matter and suspended sediments. Besides suspension by water turbulence, increasing nutrient supply promotes an increase in densities of planktonic organisms and a decrease in transparency. Furthermore, in eutrophic environments, variability, on both diurnal, seasonal and interannual time scales, is higher than in oligotrophic conditions (Hallock, 1987). Hallock's model predicts that species that are highly specialized to low levels of light availability can respond to some loss of water transparency by compressing their depth ranges, i.e., an increased fractionation of the depth gradient into niches (hereafter referred to as bathymetric habitat fractionation). However, if water transparency is reduced too much, the deepest-living species will disappear, especially when less specialized species are available (Fig. 3; Hallock, 1987). This model was found to fit well with the distribution of LBF along nearshore-offshore gradients in Indonesia (Renema and Troelstra, 2001; Renema, 2006b), West Australia (James et al., 1999) and the Great Barrier Reef (Renema et al., 2013). Renema and Troelstra (2001) hypothesized that reduced habitat fractionation was related to seasonal variations in transparency, and thus light reaching the benthic environment, to which deep-living species are more sensitive than shallow-living foraminifera. This sensitivity might be, in part, due to reduced cryptic behavior of deep-living species. Whereas upper reef-slope species can position themselves in cryptic microhabitat deep between the coral rubble (Renema, 2006a), deep-living species occur mostly on top of the substrate. During periods of lower light intensity the former can reposition towards more illuminated places, whereas the latter have nowhere to go.

To further evaluate this model for reef-associated taxa, I calculated the tolerance of each species by dividing the depth range of a species by the maximum depth of live coral cover. Hence, when the environmental tolerance is equal to 1, species occur over the entire depth gradient, and lower values indicate increased habitat fractionation along the depth gradient. At all localities the maximum depth of coral cover was noted after sampling the entire depth range in intervals of not > 3 m (for sampling procedure see Renema and Troelstra, 2001; Renema, 2006a, 2006b, 2008). In the Spermonde Archipelago and Kepulauan Seribu, transparency of the water was measured using a secchi disc (Renema and Troelstra, 2001; Renema, 2008). It was found that, although secchi depth varies between seasons, there is a linear relationship between depth of maximum coral cover and secchi depth (Renema and Troelstra, 2001) in both areas. For the Derawan archipelago, secchi measurements are not available, thus for standardization between the regions, I used the maximum depth of live coral cover. This ratio was calculated for each site, and averaged per subzone. Increasing distance along the nearshore-offshore gradients results in (1) an increase in species richness; (2) an increase in maximum depth of occurrence; and (3) increased habitat fractionation (Fig. 3; Renema and Troelstra, 2001, Renema, 2006b, 2008), all of which are consistent with the Hallock (1987) model.

When evaluating the distribution of LBF species along nearshore-offshore gradients with respect to bathymetric habitat fractionation, distinct patterns in both reef (Fig. 4) and inter-reef (Fig. 5) associated taxa were observed. This is expressed in distinct assemblages on the reef flat of oceanic reefs, with characteristic species such as *Calcarina gaudichaudii*, *Baculogypsina sphaerulata*, *Laevipeneroplis malayensis*, and *Marginopora vertebralis*. On nearshore and mid-shelf reefs especially *Neorotalia gaimardi* and *C. hispida* are dominant in algal-dominated settings, whereas on reef flats with higher coral cover and lower abundance of algae, *Amphistegina lobifera* and *Sorites orbiculus* (when seagrass is present) are the most abundant taxa (Renema, 2010).

Apart from the shallowest part of the reef, reef-slope assemblages also show an increased fractionation along the depth gradient from nearshore to offshore conditions (Figs. 4, 6). In the nearshore area the

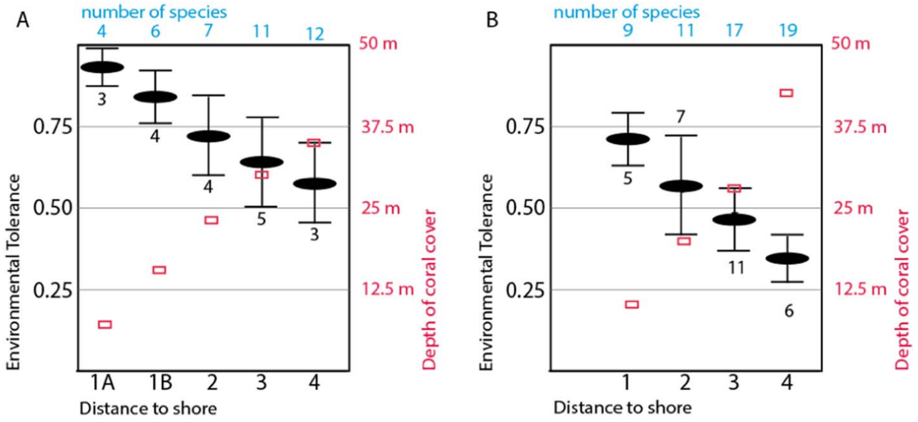

Fig. 3. Environmental tolerance, species richness and depth of coral cover in reef-slope assemblages in the Spermonde (A) and Derawan Archipelagos. Error bars includes 2 SE, number of islands is indicated below the error bar.
Details on the zonation can be found in Renema and Troelstra (2001) for the Spermonde Archipelago, and Renema (2006a) for the Derawan Archipelago.

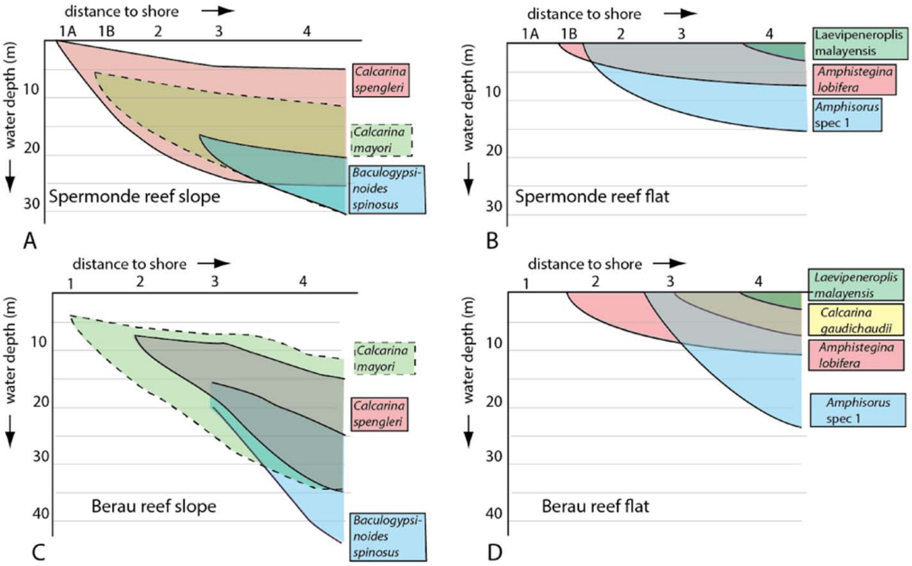

Fig. 4. Depth range of some characteristic species of the reef slope (A,C) and reef flat (B,D) as a function of distance to shore in the Spermonde Archipelago (A, B) and Berau Shelf (C,D). Distance to shore is in reef zones. A,B: 1A: nearshore, 1B inner shelf, 2 mid-shelf, 3 outer shelf, 4 barrier. C,D: 1 nearshore, 2 mid-shelf/inside barrier, 3 barrier, 4 oceanic. Data from Renema and Troelstra (2001; A, B), Renema (2006a; C,D).

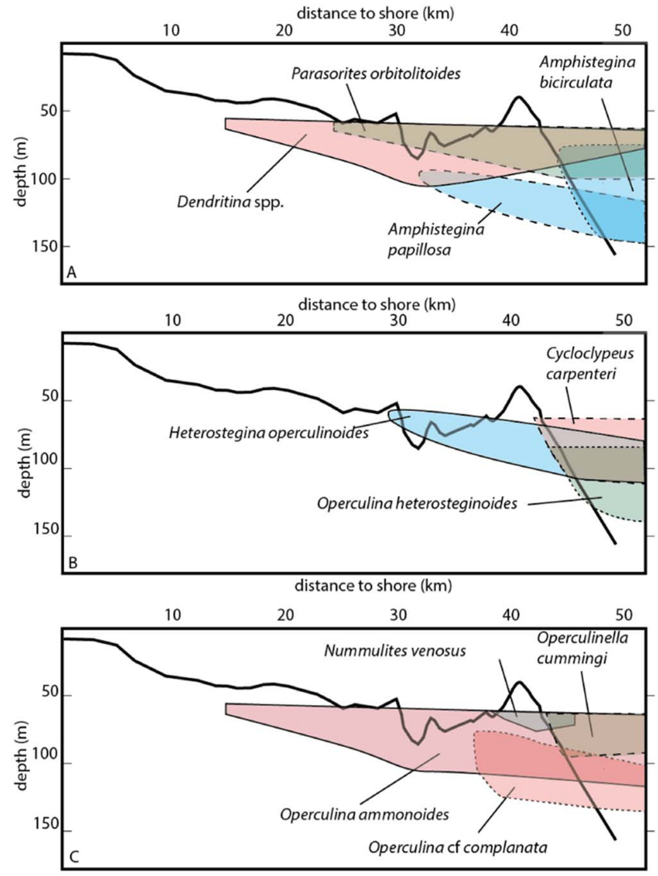

Fig. 5. Depth range of some characteristic species from the inter-reef area in the Derawan Archipelago plotted on an across-shelf depth profile. Note the sometimes comparable depth range, but widely varying tolerance to terrestrial influence between species pairs (e.g., *Amphistegina bicirculata* vs *A. papillosa* and *Heterostegina operculinoides* vs *Operculina heterosteginoides*).
Data from Renema (2006a, 2006b).

assemblage is dominated by generalist taxa, whereas distinct upper and lower reef-slope assemblages can be recognized further offshore. This pattern is consistent between the three Indonesian areas shown here, but noteworthy differences occur between areas. The pattern is most clearly present in the Spermonde Archipelago. Both in the Kepulauan Seribu and Berau Shelf, differences occur within the calcarinids (Renema, 2010). *Baculogypsinoides spinosus* is relatively rare, and only found in the deepest samples in the Spermonde Archipelago, whereas in the two other areas it is much more abundant, and can be a major part of the assemblage (> 20%) from 15 m water depth. Furthermore, the dominant *Calcarina* species in the Spermonde reef-slope assemblages was *C. spengleri*, with rare *C. mayori*. In both other areas *C. spengleri* was much less abundant, whereas *C. mayori* occurred in higher abundance. This is accompanied by an increase in algal cover in the latter two reef systems (Renema, 2010).

Comparable data are rare from other regions. This is, in part, due to differences in methods between foram workers, such as the size fraction used (ranging from everything > 0.063 mm to > 0.5 mm), or only identifying taxa up to genus level. Secondly, there are large differences in the species pool. For example, calcarinids occur in high abundance (up to 50% of the assemblage) in the Coral Triangle, and comprise four genera and at least 12 species. Here they show distinct differences in habitat, both with respect to water quality, substrate type and bathymetry (Renema, 2010). Further east in the Pacific Ocean, the number of genera quickly reduces to two (Weinmann et al., 2013a), and the number of species to at most four to five. In New Caledonia only a single species was observed (Debenay, 1988) and calcarinids are absent from Moorea (Vénec-Peyré, 1991; Fajemila et al., 2015).

Although from the Great Barrier Reef there is no single study describing nearshore to offshore gradients in LBF assemblage composition, several separate studies have described the assemblage composition in areas that can be compared and interpreted in this context. For example, *Baculogypsina sphaerulata* and *Calcarina capricornia* occur on the reef flat and uppermost reef-slope of mid- and outer-shelf reefs (Lobegeier, 2002; Jell et al., 1965; Yamano et al., 2000) and are not found in the inner-shelf and nearshore reefs (e.g., Uthicke and Nobes, 2008; Reymond et al., 2013b). *Marginopora vertebralis* is found further offshore in higher energy settings, exemplifying the nearshore to offshore addition of species to the LBF assemblage. Even less information on the distribution of LBF from the Great Barrier Reef is available for the inter-reef area. Again, available observations fit within the framework observed in Indonesia. In inter-reef environments close to the shore no LBF were observed, whereas the first assemblage containing LBF is found in the inner part of the mid-shelf zone, and includes *Amphistegina*, *Operculina*, and the rhodophyte-bearing *Peneroplis* (reported as *Dendritina*, but apertural face shows multiple apertures rather than a single dendritine aperture) (Horton et al., 2007). Along the outer shelf, assemblages are arranged by depth, with *Operculina* dominating the shallower parts and *Cycloclypeus* and *Heterostegina* in the outer reef area

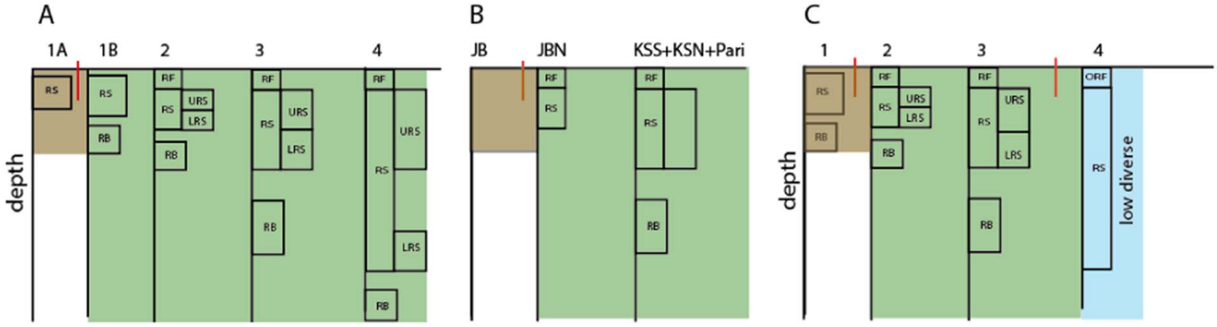

Fig. 6. Assemblage structure on the reef slope in a nearshore-offshore transect in the Spermonde (A) and Derawan (C) Archipelagos and the Kepulauan Seribu (B). The red lines indicate major faunal breaks, in brown the nearshore zone, in green mid- to outer-shelf and in blue-water reefs. Characteristic species of the assemblages: RS (reef slope): *Amphistegina lessonii*, *A. radiata*, *Heterostegina depressa*, *Calcarina spengleri* and *C. mayori*; URS (upper reef-slope): RS species and *Amphistegina lobifera*; *Amphisorus* sp., LRS (lower reef-slope): RS species and *Baculogypsinoides spinosus*; RF (reef flat): *Amphistegina lobifera*, *Neorotalia gaimardi*, *C. defrancei* (in Fig. B only), *Sorites orbiculus*; ORF (oceanic reef flat): *Calcarina gaudichaudii*, *Laevipeneroplis malayensis*; *Amphisorus* sp., *Marginopora vertebralis*. RB (Reef Base) (see Fig. 5).
Data from Renema and Troelstra (2001; A), Renema (2006a; C) and Renema (2008; B).

(Renema et al., 2013).

Although species numbers are reduced, analogues nearshore-offshore trends can be deduced for multiple other areas, i.e. Palau (Hallock, 1984; Hohenegger, 1996), the West Australian shelf (James et al., 1999), Oáhu (Hawaii; Hallock, 1984) and the Maldives (Parker and Gischler, 2011). The combined evidence strongly suggests that the nearshore-offshore gradient not only affects the depth range over which LBF occur, but also the assemblage composition. On the reef flat, reef slope, and inter-reef, differential tolerance to sediment, nutrients, and wave exposure determine the assemblage composition. In most areas, distinct nearshore (*Elphidium*, *Neorotalia gaimardi*), mid-shelf (*Heterostegina*, *Amphistegina*, *Calcarina*), and offshore (*Baculogypsina sphaerulata*, *Calcarina gaudichaudii*, *C. capricornia*, *Amphisorus*, *Marginopora*) assemblages can be recognized.

5. The importance of terrestrial influence on LBF assemblages

Location on the reef (reef flat, reef slope, reef base, and inter-reef) is the most important parameter determining the LBF assemblages composition (e.g., Hottinger, 1977a; Reiss and Hottinger, 1984; Hallock, 1984; Hohenegger, 1994; Renema and Troelstra, 2001; Narayan and Pandolfi, 2010), underpinned by differences in substrate and depth preferences among species (Hohenegger, 1994; Renema, 2006a, 2008). The reef base and inter-reef are dominated by taxa living on sand, while reef-slope and reef-flat assemblages are dominated by species preferring solid and epiphytic substrates.

5.1. Inter-reef habitats

The inter-reef is defined as the part of the sea floor that is within the photic zone and below the storm wave base. Around reefs it starts below the reef slope, the steep area covered by live coral cover or coral rubble. In barrier reef systems, the inter-reef area often has a larger surface area than the combined coral reefs. For example, in the Great Barrier Reef < 10% of the total shelf area is covered by coral reefs (Furnas et al., 2005). Towards the northern and southern margins of the tropics this area can be truncated by the bathymetrical temperature gradient (Koba, 1977; Hollaus and Hottinger, 1997), resulting in temperatures that are too low in the lower part of the photic zone. Surprisingly few data are available for the recent distribution and environmental tolerances of LBF in these environments, even though LBF are an important component of the sediments in these areas (Tudhope and Scoffin, 1988; Renema, 2006b).

Rimmed or unrimmed mixed carbonate-silisiclastic shelfs are characterized by a gradient from shallow coastal areas with a large terrestrial influence, especially near river mouths, to deep areas with no or very limited terrestrial influence (Renema and Troelstra, 2001; Langer and Lipps, 2003; Narayan and Pandolfi, 2010; Fajemila et al., 2015). In coastal areas *Dendritina*, *Peneroplis* and *Parasorites* can be important elements (Renema and Troelstra, 2001; Horton et al., 2007), and these are gradually replaced by nummulitids and amphisteginids in clearer water (Renema and Troelstra, 2001; Renema, 2006b). The rhodophyte bearing *Dendritina* is restricted to these settings, possibly due to the different optical behavior of light (Fig. 2). *Operculina ammonoides* is the next species to appear. When the accumulation rate of LBF tests (mostly by *O. ammonoides*) exceeds clastic sedimentation rates, a shift from fine muddy sediment to coarse carbonate sand facilitates colonization by additional taxa such as *A. papillosa*, *Operculina* cf. *complanata*, and *Heterostegina operculinoides* (Fig. 5; Renema, 2006b). On the oceanic side of the shelf system, this assemblage is more diverse (Hohenegger et al., 1999; Renema, 2006b; Renema et al., 2013) and produces so much carbonate that LBF determine the grain size of the shelf sediments (Renema, 2006b). In deeper parts of the shelf that are below the photic zone, grain sizes are much smaller than in the shallower areas (Renema, 2006b). Especially in coastal seas in seasonal climates, a twilight zone can develop, which is within the photic zone during the dry season, but during the wet season, the water is too turbid for light to reach the seafloor. Benthic environments within this twilight zone are characterized by the large abundance of species characterized by chloroplast husbandry (Renema and Troelstra, 2001).

When there are homogeneous slopes, individual species distribution can be fitted to the depth profile and each species has its specific depth distribution (Hohenegger, 1994; Hohenegger et al., 2000). In more heterogeneous slopes, e.g., with terrace development and different sedimentary facies types, this trend can be attenuated and distinct shallow and deep assemblages can be recognized (Renema, 2006b; Renema et al., 2013). In all cases *Heterostegina operculinoides* and *Cycloclypeus carpenteri* belong to the deepest-living LBF, and their occurrence indicates a very deep habitat, usually > 50 m deep (Renema, 2006b; Renema et al., 2013).

A very different assemblage that is so far only recorded from the Coral Sea, is an inter-reef assemblage dominated by porcellaneous species, most notably large and flat *Marginopora* spp., *Alveolinella quoyi*, and *Parasorites* sp. Locally this is accompanied by *Operculina* spp. and *Amphistegina* spp. This assemblage is found in 15–40 m water depth.

Next to the commonly used variation in the depth distribution consistent with attenuating light availability, the tolerance to terrestrially derived sediments is an equally important parameter to understand the occurrence of inter-reef LBF (Fig. 5). For example, *Heterostegina operculinoides* is more tolerant to terrestrially derived sediments than *Operculina heterosteginoides*, even though both species have a comparable range in light tolerance.

5.2. Reef slope

The reef slope is the most homogeneous and least diverse habitat. The most characteristic species include *Calcarina mayori*, *C. spengleri*, *Heterostegina depressa*, *Amphistegina lessonii* and *A. radiata* (Hohenegger, 1994; Renema and Troelstra, 2001), but not all of these species occur over the entire Central Indo-Pacific. In offshore areas with limited algal growth, the reef slope can be differentiated into lower reef-slope, with *Baculogypsinoides spinosus* and an upper reef-slope with *Amphisorus* sp. (Renema and Troelstra, 2001). However, when algal growth is more abundant, *B. spinosus* can occur in much shallower conditions obscuring this depth zonation (Renema, 2006a, 2008). This can either be related to terrestrial influx (e.g., Renema, 2008) or upwelling along the shelf edge (e.g., Renema, 2006a). However, on the reef slope there is a distinction between areas with limited amounts of interstitial space between the coral rubble, usually due to transport of carbonate sediment from the overlying reef flat. In these conditions *N. gaimardi* and *C. mayori* are more abundant than *C. spengleri* and *Amphistegina radiata* (Renema, 2006a). A second habitat type is characterized by abundant macro-algae, where *Calcarina defrancei*, *C. mayori* and *Baculogypsinoides spinosus* are more abundant. A final distinct reef-slope fauna is found on reef walls with vertical to overhanging slopes. These usually receive relatively little light compared to gentle reef-slopes in the same area, experience (intermittently) fast currents and have very little habitat suitable to LBF. On sand on ledges, in crevices, and in small caves, typically low-diversity LBF assemblages are found, consisting of the most eurytopic taxa, such as *Heterostegina depressa* and *Amphistegina lessonii* (Renema, 2006a).

In reef-slope assemblages, species richness is highest in the western Pacific Ocean. In this area also the differentiation along the depth gradient is strongest, especially because of the presence of diverse calcarinids (Renema, 2010). LBF diversity declines to the east in the Pacific Ocean and west in the Indian Ocean, and the reef-slope assemblages are less differentiated by depth (Hohenegger, 1994; Reymond et al., 2013b).

5.3. Reef flat

On the reef flat, LBF can occur in very high densities. Especially calcarinids can occur in densities of up to 10 cm^{-2} (Hallock, 1981a; Lobegeier, 2002; Fujita et al., 2009; Doo et al., 2012), and high carbonate sand production rates (Perry et al., 2011; Yamano et al., 2000; Woodroffe and Morrison, 2001; Fujita et al., 2009; Dawson et al., 2014; Fellowes et al., 2016) result in coral cays constituting of LBF-dominated sands (Perry et al., 2011). Whereas in the inter-reef the strongest faunal difference is found between the terrestrially influenced coastal area and the rest of the shelf, in the reef flat the dominant discontinuity in assemblage composition is found between terrestrially influenced and oceanic reefs, further offshore (Fig. 6). In most of Indonesia, oceanic reefs are situated outside the carbonate shelves, but in the Great Barrier Reef this assemblage is abundant in the mid-shelf reefs. In oceanic reefs *Baculogypsina sphaerulata*, *Calcarina gaudichaudii* and *C. hispida* (in the North Pacific Ocean) and *Calcarina capricornia* (in the Coral Sea) are the most abundant LBF, but *Amphistegina lobifera* and various species of *Peneroplis*, *Parasorites*, and *Sorites* occur, sometimes in high abundance, in this habitat as well. At the reef crest in high-energy environments, *Marginopora* and *Amphisorus* can be found as well.

In terrestrially influenced reefs, the reef flat is either dominated by *Amphistegina lobifera* or various *Calcarina* species (Renema, 2010). The *Amphistegina* dominated assemblage is associated with low algal abundance, and moderate coral cover, whereas the calcarinids abound in algal dominated environments (Renema, 2010). In the Kepulauan Seribu *Neorotalia gaimardi* is the LBF species occurring closest to Java in monospecific mass accumulations on algae (Renema, 2008). The latter calcarinid dominated assemblage was not found on the reef flat or reef crest of coastal reefs in the GBR (Reymond et al., 2013b). Carbonate sand production rates are lower, and the LBF contribute a smaller fraction to the sand of the coral cays (Madden et al., 2013).

In conclusion, terrestrial influence is a key driver of LBF assemblage composition that was previously underappreciated. In both soft sediment and reefal conditions, assemblages differ markedly in turbid (further referred to as brown water) compared to oceanic (further referred to as blue water) environments, even though the major changes may occur at different sites along the nearshore-offshore gradient (Fig. 6). Sediment production in both the inter-reef and reef-flat assemblages is highest in blue-water conditions, far from terrestrial influence.

6. Identification and environmental tolerances of individual species of laminar perforate LBF

Generally speaking, LBF are thought to be wide ranging species, and frequently the same names are used for specimens from across the entire Indo-Pacific (Langer and Hottinger, 2000). Improved methods to describe morphological variation, such as scanning electron microscopy and high-resolution computed tomography, have contributed to an improved understanding of ecophenotypical, ontogenetical, and phylogenetical variation among species (e.g., Hottinger, 2001; Lee et al., 2004; Görög et al., 2012). In many groups of foraminifera, morphology-based species hide a large amount of genetic diversity (Morard et al., 2016). This added layer of cryptic diversity, however, does not mean that all morphotaxa constitute a collection of much narrower ranging cryptic species (Pawlowski and Holzmann, 2008). Morphological variation that was originally attributed to ecophenotypic variation is now increasingly thought to have a phylogenetic component as well (Holzmann et al., 2001; Holzmann and Hohenegger, 2003; Lee et al., 2004). The geographic ranges of some benthic foraminiferal clades defined by molecular phylogenetical techniques cover entire ocean basins, demonstrating that not all species include a wide variety of cryptic diversity (Pawlowski and Holzmann, 2008). Within the genus *Calcarina*, more species than the commonly used four (Renema and Hohenegger, 2005) have been recognized in Indonesia (e.g., Renema, 2008, 2010). So far, relatively few studies on molecular phylogeny of LBF have been performed, and only for the family Soritidae phylogenetic trees with extensive geographic coverage are available. These show distinct clades of species and the presence of multiple distinct clades in each of the three genera, *Marginopora*, *Amphisorus* and *Sorites* (Holzmann et al., 2001; Lee et al., 2004; Garcia-Cuetos et al., 2005). So far, only in *Amphisorus* multiple species are recognized based on morphological characters (*A. hemprichii*, *A. kudikajimaensis* and *A. sauronensis*; Gudmundsson, 1994; Lee et al., 2004).

All-in-all the paradigm of relatively few, wide ranging taxa is slowly shifting towards higher species diversity with more restricted geographic ranges. Examples are found in the genera *Calcarina*, *Amphisorus* and *Operculina*. Variable interpretation of species names hampers comparisons between regions, especially when no specimens have been illustrated. Here I focus on the lamellar perforate species. I do this because in the Central Indo-Pacific they dominate LBF assemblages, occur in the widest range of habitats, and their taxonomy and recognition is less in a flux. This group includes the Amphisteginidae, Calcarinidae, and Nummulitidae. Authorities to the taxon names are provided in Appendix 2.

6.1. Family Amphistegindae

There is only one extant genus in this family, the genus *Amphistegina*.

6.1.1. Genus Amphistegina

The genus *Amphistegina* is characterized by a low trochospiral, lenticular and unequally biconvex test, that can be bi-involute or partially evolute on the spiral side. Chambers are strongly arched at the periphery (Loeblich Jr and Tappan, 1987). Species can be grouped into two easily separated morpho-groups, each containing at least three species. The *A. lessonii*-group is asymmetrical in axial view, with widely spaced curved septa, whereas the *A. radiata*-group is almost symmetrical, with narrowly-spaced, straight septa, that abruptly bend backwards near the periphery.

Amphistegina is one of the most widespread and ubiquitous LBF genera. In most reef areas it is represented in the vast majority of samples, frequently in high numbers. Larsen (1976) studied the distribution of the genus in the Red Sea, and described *A. papillosa*, whereas Debenay (1985) redescribed *A. quoyi* both are deep-living species within the *A. radiata*-group.

Despite their abundance, uncertainty exists concerning species boundaries and the number of species. Grouping of taxa within regions usually is straightforward, at least in part due to correlation with environmental (especially substrate) conditions. However, minor but sometimes consistent small differences exist between regions. Furthermore, also within morphospecies, distinct genetic differences between *A. lobifera* populations from the Red Sea and the Great Barrier Reef have been observed (Schmidt et al., 2016). It is likely that there is more hidden diversity within this genus: for example, Debenay (2012) reported a so far undescribed morphospecies from New Caledonia.

For detailed description of the taxonomy and morphological features of *Amphistegina* see Larsen (1976), Debenay (1985, 2012) and Hottinger et al. (1993).

6.1.1.1. Amphistegina lessonii (Fig. 7)

6.1.1.1.1. Recognition. Planoconvex to umbilconvex convex in outline. Chamber involute, arranged in a low trochospire. Dorsal chamber sutures sharply bent backwards in a falciform arch, sutures of the alar prolongations radial to sigmoidal, alternating with single, short sinusoidal or straight hemiseptular sutures of variable length (dorsally). Umbo small, transparent. Peripheral outline angular. Apertural area is pustulose over a smaller area than in *A. lobifera*.

6.1.1.1.2. Geographic range. Amphistegina lessonii is one of the widest ranging species in the Indo-Pacific and ranges from the Red Sea to Mozambique (Langer et al., 2013; reported as *Amphistegina* spp., but, their Fig. 8, specimen 20 can be identified as *A. lessonii*), and from Rottnest Island (West-Australia; pers. obs.) to southern Kyushu (Japan) (Sugihara et al., 2006) to Lord Howe Island (Todd, 1976) and east to at least the Pitcairn Islands (Whittaker and Hodgkinson, 1995).

6.1.1.1.3. Habitat. This species is one of the most ubiquitous and abundant species: it occurs in nearly all samples taken on reef slopes down to ~60 m water depth all over the Central-Indo Pacific (e.g., Hohenegger, 1994; Renema and Troelstra, 2001; Fajemila et al., 2015). It occurs both on sandy and coral rubble substrate and can live attached to rubble of which the interstitial space is filled with sediment (Hohenegger, 1994; Renema, 2006a, 2008). Hohenegger et al. (1999) distinguished an umbiconvex-form that was more abundant on soft substrates, and a biconvex-form that was more abundant on hard (rubble) substrates. The test-shape is influenced by the hydrodynamic energy, with specimens in lower hydrodynamic energy being flatter than specimens in higher hydrodynamic energy (Hallock et al., 1986; ter Kuile and Erez, 1991).

6.1.1.2. Amphistegina lobifera (Fig. 8)

6.1.1.2.1. Recognition. Lenticular to subglobose, planoconvex to subconvex in outline. *Amphistegina lobifera* is very similar to *A. lessonii*, from which it is distinguished by its lobate sutures of the alar prolongations (dorsally) and the chamber sutures (ventrally). Smaller specimens are sometimes difficult to recognize (Hohenegger et al., 1999). Peripheral outline rounded to subacute. Apertural area is pustulose over a larger area than *A. lessonii*.

6.1.1.2.2. Geographic range. The geographical range of *A. lobifera* is comparable to that of *A. lessonii*. The geographic range of *Amphistegina lessonii* and *A. lobifera* has expanded rapidly during the final decades of the 20th century, and it occurs now in large parts of the eastern Mediterranean (Caruso and Cosentino, 2014; Triantaphyllou et al., 2009; Meriç et al., 2016), and is likely to expand further as the result of climate change (Weinmann et al., 2013a, 2013b). It is included in the list of 100 worst invasive species in the Mediterranean Sea (Streftaris and Zenetos, 2006) and is generally regarded as a Lessepsian immigrant, but recently occurrences predating the closure of the Suez canal have been discovered (Meriç et al., 2016). *Amphistegina lobifera* is by far the most abundant of the two species in the Mediterranean, and can alter the benthic environment by its dominance and large carbonate production resulting in (1) a loss of benthic biodiversity, (2) alterations of foraminiferal community structures, and (3) shifts in abundances of functional groups of foraminifera (Mouanga and Langer, 2014; Langer and Mouanga, 2016).

6.1.1.2.3. Habitat. Amphistegina lobifera is the shallowest-living representative of the genus *Amphistegina* at nearly all localities (e.g., Hohenegger, 1994; Renema, 2006a; Prazeres et al., 2016a). It is rare at > 10 m water depth and replaced by *A. lessonii* in deeper samples. The depth distribution does not vary much between regions, nor with distance from shore (Renema and Troelstra, 2001; Renema, 2006a). Highest densities occur on the upper reef-slope, reef flat and shallow back-reef areas, but is rare on reef rock and macro-algal and to a lesser degree turf algal substrate (Hohenegger, 1994; Renema, 2010). It is usually found attached to the underside of coral rubble, and is thus less abundant at places with high sedimentation rates filling the interstitial space between rubble (Renema, 2006a). This species is replaced by calcarinids when coral cover on the reef flat is lost and replaced by macro-algae (Renema, 2010).

6.1.1.3. Amphistegina bicirculata (Fig. 9)

6.1.1.3.1. Recognition. Amphistegina of the *A. lessonii group*. Flat, lenticular test, often with a sharp periphery. It is the most symmetrical (in cross section) member of the *A. lessonii*-group, and can be biconvex, dorsoconvex or ventroconvex (Hottinger et al., 1993). On the apertural

Fig. 7. *Amphistegina lessonii*. Spermonde Archipelago (SW Sulawesi, Indonesia). Scale bar 200 μm.

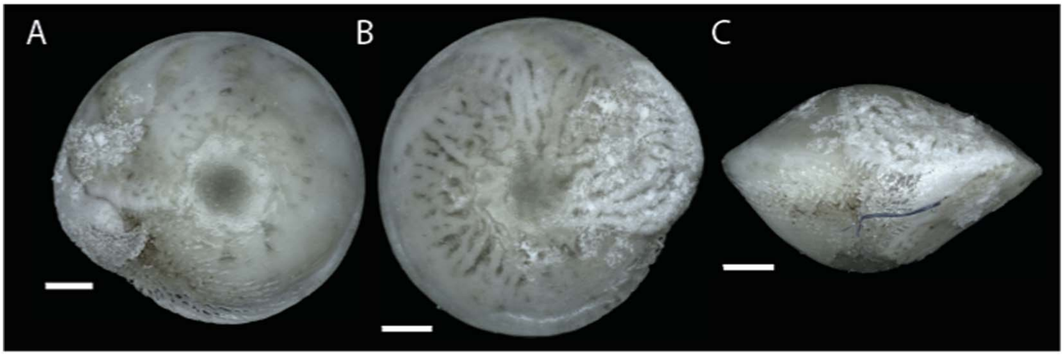

Fig. 8. *Amphistegina lobifera*. Spermonde Archipelago (SW Sulawesi, Indonesia). Scale bar 200 μm.

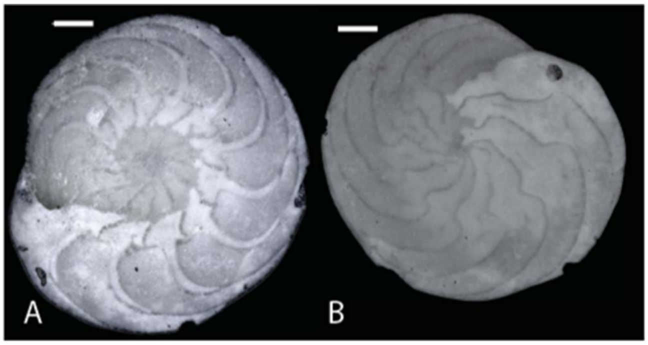

Fig. 9. *Amphistegina bicirculata* Hydrographer's Passage (Queensland, Australia). Scale bar 200 μm.

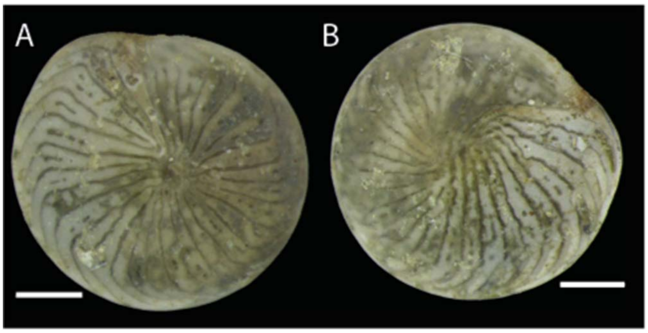

Fig. 10. *Amphistegina radiata* Spermonde Archipelago. Scale bar 500 μm.

side coiling is slightly evolute. Dorsal chamber sutures bend backwards in a falciform arch in the peripheral part of the chamber, but bend forward in the proximal part. There often is a single, incomplete hemiseptulum (Hottinger et al., 1993). Regional variation includes chamber size, which for example is much larger (fewer chamber per whorl) in the Great Barrier Reef (Fig. 9; Renema et al., 2013) and New Caledonia (Debenay, 2012) than in Kalimantan (Renema, 2006b).

6.1.1.3.2. Geographic range. Widely distributed along the western border of the Pacific Ocean to the Red Sea. Because of its deep habitat, the exact range is poorly known. It was described from the Red Sea, and subsequently has been reported from the Maldives (Parker and Gischler, 2011), southern Japan (Hohenegger, 1994), Indonesia (Renema, 2006b), Palau (Hallock, 1984), the Great Barrier Reef (Renema et al., 2013) to the lagoon of New Caledonia (Debenay, 1988), and as far east as Tahiti (Fujita and Omori, 2015) and Hawaii (Hallock, 1984).

6.1.1.3.3. Habitat. Together with *A. papillosa*, *A. bicirculata* is the deepest occurring species of *Amphistegina*. It lives from 40 to 130 m water depth in the clearest waters around Japan (Hohenegger, 1994), and in 40–100 m water depth offshore East Kalimantan (Renema, 2006b). It was not found in more terrestrially influenced areas such as the Java Sea and SW Sulawesi. In the Great Barrier Reef, living specimens were found from 53 to 129 m water depth (Renema et al., 2013). Compared to *A. papillosa* this species has a preference for firm substrates (Hohenegger, 2004), but in East Kalimantan and the Great Barrier Reef, it occurs predominantly on coarse sand (Renema, 2006b; Renema et al., 2013).

6.1.1.4. Amphistegina radiata (Fig. 10)

6.1.1.4.1. Recognition. Biconvex, almost planispiral, almost symmetrical in the plane of coiling. Peripheral margin angular. Surface smooth. Chamber sutures straight to falciform, deflecting almost 90 degrees (in opposite direction of coiling) over the peripheral 2/3–3/4 of the spiral wall. A single not raised, opaque, radial, sometimes interrupted hemiseptulum can be present between the sutures (Hottinger, Halicz, and Reiss, 1993). Chambers very narrow. Aperture very small and peripherally placed. Narrow umbo on either side of the test. Deeper-living specimens are flatter and get more pillars. Largest species of the *A. radiata* group with a diameter that can exceed 2.5 mm.

6.1.1.4.2. Geographic range. Amphistegina radiata is widely distributed in the Indo-Pacific, and its occurrence is confirmed from the Seychelles in the west to at least New Caledonia in the east (Debenay, 1988), and from southern Japan in the north (Hohenegger, 1994) to Moreton Bay (south Queensland) in the south (Narayan and Pandolfi, 2010).

6.1.1.4.3. Habitat. This species is abundant on the reef slope (Hottinger, 1983; Hallock, 1984; Hohenegger, 1994; Hohenegger et al., 1999; Renema and Troelstra, 2001; Renema, 2006a), and rare on the reef crest and reef moat. It was found from 10 to 90 m water depth in Okinawa, but was most abundant at 20 m water depth (Hohenegger et al., 1999; it cannot be excluded that the deepest specimens refer to *A. quoyi* as illustrated (as *A. radiata*) in Hohenegger, 1994), but in considerably shallower water in the Indonesian reef systems (Renema and Troelstra, 2001; Renema, 2006a) and the Great Barrier Reef (Prazeres et al., 2016a, 2016b). *Amphistegina radiata* is most abundant on firm substrates (Reiss and Hottinger, 1984; Hohenegger, 1994, 2004; Renema and Troelstra, 2001) especially on coral rubble with open interstitial spaces, where it lives attached to the sides of the pieces of rubble. In its shallowest occurrences *A. radiata* avoids highest irradiance and hydrodynamic energy levels by living up to 15 cm deep in the interstitial spaces between rubble (Renema, 2006a).

6.1.1.5. Amphistegina quoyi

6.1.1.5.1. Recognition. Biconvex, almost planispiral, almost symmetrical in the plane of coiling. Peripheral margin angular. Test surface smooth. Pillars develop between the septa especially on the dorsal side, but are not or only minimally expressed as pustules on the test surface. Chamber sutures straight to falciform, deflecting almost 90 degrees (in opposite direction of coiling) over the peripheral 2/3–3/4 of the spiral wall. Chambers narrow. Aperture very small and peripherally placed. Narrow umbo on either side of the test.

The taxonomic status of *Amphistegina quoyi* was discussed by Debenay (1985), who interpreted it as a separate species based on the lower number of chambers per whorl, smaller diameter and larger perforations of the test. Subsequently, most authors regarded these characters as ecophenotypic variation within *A. radiata*. Whereas I cannot exclude the possibility of ecophenotypic variation, the distinct environmental preferences of both *A. radiata* and *A. quoyi*, as well as the fact that the vast majority of specimens are attributable to either species are reasons why, for the moment, I refer to them as separate taxonomic entities. It should be noted that there are differences in the geographic distribution of *A. quoyi* and *A. radiata*.

6.1.1.5.2. Geographic range. Due to the taxonomic uncertainty associated with this species, its distribution is not well known. Occurrences in the Red Sea (Hottinger et al., 1993 as *A. aff radiata*), New Caledonia (Debenay, 1985, 2012) and the Great Barrier Reef (pers. obs.) suggest a wide distribution in the Central Indo-Pacific.

6.1.1.5.3. Habitat. Due to taxonomic uncertainty the ecological preferences of *A. quoyi* are not clear. Confirmed records occur on sandy substrate, but shallower than *A. papillosa* (pers. obs. Great Barrier Reef).

6.1.1.6. Amphistegina papillosa (Fig. 11)

6.1.1.6.1. Recognition. Biconvex, very low trochospiral (almost planispiral), almost symmetrical in the plane of coiling. Peripheral margin acute. Test surface with hemispherical to ovate pustules on both sides. Chamber sutures falciform, sometimes postulate or even lobate, deflecting 90 degrees (in opposite direction of coiling) over the peripheral 2/3–3/4 of the spiral wall, usually raised (especially on the ventral side). Intersutural pustules numerous, restricted to the alar extension over the previous chamber, oriented in 1–2 rows. Sutures more lobate at the ventral side, often difficult to trace. Chambers wide. Aperture very small and peripherally placed. Narrow umbo most pronounced on the ventral side of the test (based on Hottinger et al., 1993; Debenay, 2012). Regional variation in morphology includes the number and distribution of the pustules. For example, specimens from Indonesia have pustules on both the spiral and apertural side of the test, whereas in specimens from the Great Barrier Reef pustules are more irregularly shaped, and most abundant on the spiral side (Fig. 11).

6.1.1.6.2. Geographic range. *Amphistegina papillosa* is widely distributed in the Indo-Pacific, and occurs from the Red Sea in the west (Larsen, 1976) to at least New Caledonia in the east (Debenay, 1985; Debenay, 2012), and from southern Japan (Hohenegger, 1994) in the north to the Capricorn group (southern Great Barrier Reef) in the south (Renema et al., 2013).

6.1.1.6.3. Habitat. *Amphistegina papillosa* is, together with *A. bicirculata*, the deepest occurring *Amphistegina* species and can be found in clear water down to 150 m water depth (Hohenegger, 2004), but more frequently is restricted to ~100 m or less (Renema, 2006b; Hansen and Buchardt, 1977). In turbid reef environments, such as the Spermonde Archipelago, the shallowest depths at which *A. papillosa* was observed ranged from 20 to 30 m water depth in mid-shelf reefs (Renema and Troelstra, 2001). It is found on carbonate rich, sandy substrates, and is more tolerant to terrestrial influence than *A. bicirculata*, the deepest occurring species in the *A. lessonii*-group (Fig. 5; Renema, 2006b).

6.1.1.6.4. Remark. Debenay (2012) reports an as yet undescribed species from New Caledonia, which is also a member of the *A. radiata*-group, and can be confused with *A. papillosa*. This species is distinguished from other species in the *A. radiata*-group by the evolute spiral side of the test (Debenay, 2012), and was found in even deeper environments than *A. papillosa*.

6.2. Family Calcarinidae

This family includes the genera *Calcarina*, *Neorotalia*, *Bacylogypsina*, *Baculogypsinoides*, and *Schlumbergerella*.

6.2.1. Genus Calcarina

Trochospiral. Chambers square to rectangular, not elongate peripherally. interlocular space between the septa covered. Apertural face with multiple rimmed apertures. All species develop spines on the spiral sites between chambers. In some species they do not extend beyond subsequent whorls (the *C. hispida*-group e.g., Fig. 19), but in others they do (the *C. spengleri*-group, e.g., Fig. 13). Spines are canaliculated, either with a few large canals at the proximal part of the spine fanning (*C. hispida*-group) out or canaliculated throughout with reticulated canals of equal thickness (the *C. spengleri*-group; Renema and Hohenegger, 2005).

6.2.1.1. Calcarina gaudichaudii (Figs. 12, 13)

6.2.1.1.1. Recognition. Largest species of the genus *Calcarina*, diameter up to 3 mm without spines; 4–20 thick, tapering spines of varying length are arranged radially along the periphery of the test. The test is covered by widely spaced, smooth tubercles on both the dorsal and the umbilical sides. These tubercles are surrounded by 1–3 rows of openings to the enveloping canal system, which change gradually into the structure on the spines. Inside the openings to the canal system, there are short spikes. Thick lateral chamber walls obscure the chamber sutures except in the last few chambers, which have a rounded shape and smooth surface. The spines are canaliculate throughout, furrowed, with oblique ridges on each furrow.

There is considerable geographical variation in the morphology of this species (Figs. 12, 13). Specimens with long spines (0.5–0.75 times test diameter) have 4–8 spines and occur in the western part of the range of *C. gaudichaudii*, whereas specimens with short spines have 14–20 spines and occur in the eastern part of the range (Renema and Hohenegger, 2005). Additionally, there is considerable variation in the size and number of tubercles on the test surface. Specimens from the Central Philippines showed more tubercles than those from Japan (Fig. 13). Furthermore, there is considerable variation in the internal

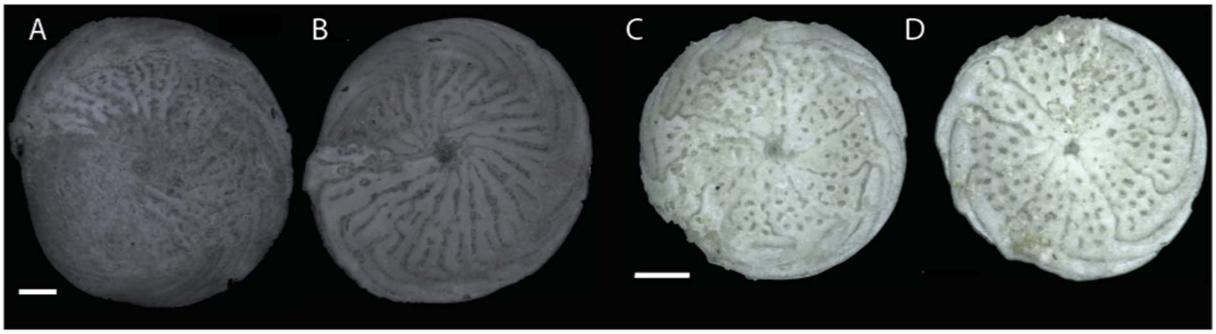

Fig. 11. *Amphistegina papillosa*. A, B: Hydrographer's Passage (Queensland, Australia); C, D: Spermonde Archipelago (SW Sulawesi, Indonesia) Scale bar 200 μm.

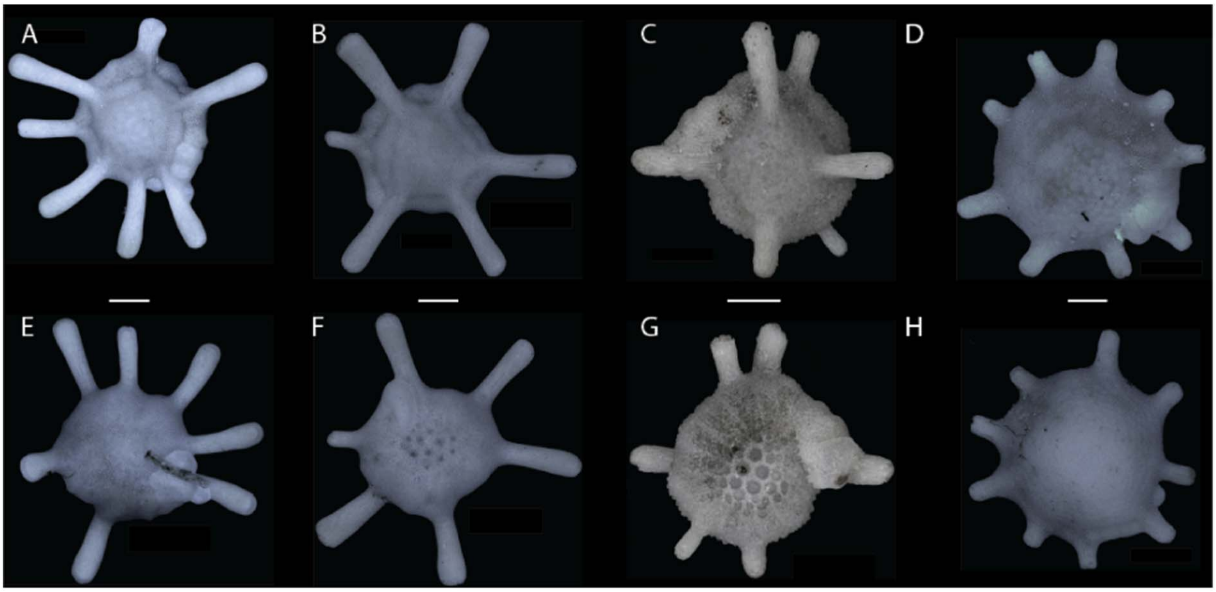

Fig. 12. *Calcarina gaudichaudii*. A,E, Kudikajima (Okinawa, Japan); B,F Cabilao Island (Bohol, the Philippines); C,G Maratua (East Kalimantan, Indonesia); Adorius Island (Palau). Scale bar 500 µm.

structure of populations, including the thickness of the chamber wall, the number of chambers per whorl, and the height of these chambers (Fig. 13A–C vs Fig. 13D–F). Both length of the spines and the amount of surface ornamentation have been associated with ecophenotypical variation in other taxa of *Calcarina*. Taxonomy, recognition, and geographic variation of *C. gaudichaudii* was discussed by Renema and Hohenegger (2005).

6.2.1.1.2. Geographic range. In southern Japan *C. gaudichaudii* reaches its northernmost distribution (Fig. 14) on Okinawa (Sugihara et al., 2006), furthermore it occurs from the central Philippines (Mindoro, Cebu, Mindanao), Palau (Hallock, 1984, identified as *C. spengleri*; Hohenegger, 1996) to the Marshall Islands. In Indonesia *Calcarina gaudichaudii* occurs from the Sulawesi Sea (Renema, 2006a) and Timor Sea (pers. obs.) to the east and is lacking in the Makassar Strait, Java Sea, and South China Sea.

6.2.1.1.3. Habitat. *Calcarina gaudichaudii* lives at very shallow depths on the reef flat, including the reef edge. It prefers epiphytic substrates on either turf-forming red algae (*Jania* or *Gelidiopsis*), sea grasses or calcareous coralline algae, and is recorded below stones. In lower energetic environments (back reef), it can be found on sand as well. It is only found in reef systems surrounded by deep, oceanic waters with minimal terrestrial influence (Renema, 2006a).

6.2.1.2. *Calcarina spengleri* (Figs. 15, 16)

6.2.1.2.1. Recognition. Intermediately sized species, up to 1.5 mm in diameter (excluding spines) with 3–7 intermediate to long, robust, blunt spines and a smooth test with centrally some granulated bosses, but no externally protruding spikes (Fig. 15). There are multiple,

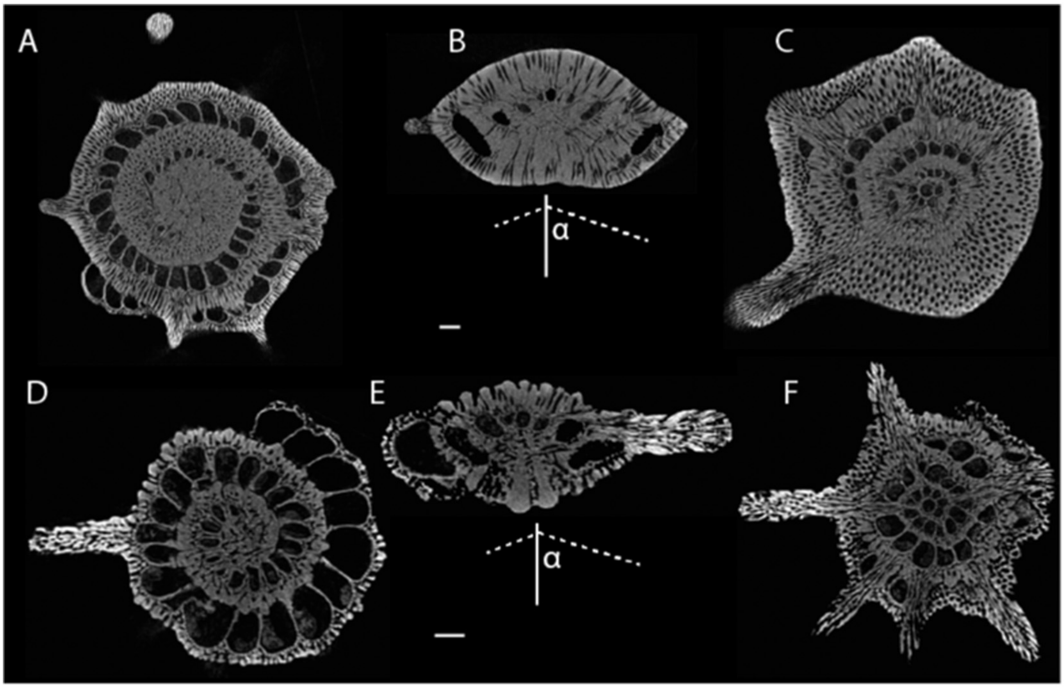

Fig. 13. Thin sections of *Calcarina gaudichaudii* A–C Adorius Island (Palau); D–F Maratua (East Kalimantan, Indonesia). Scale bar 200 µm.

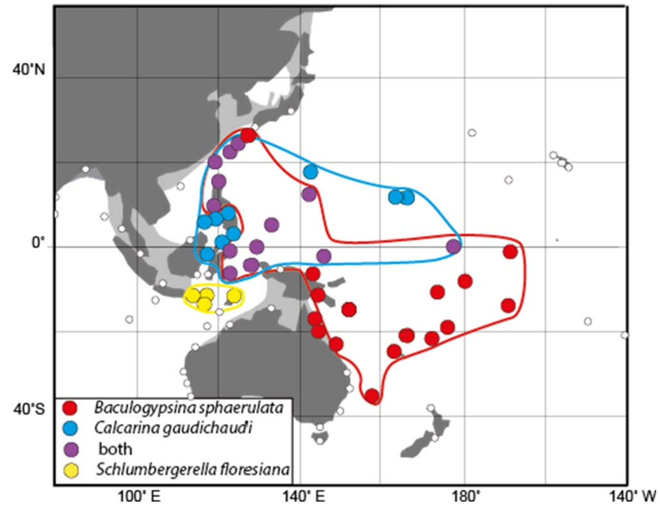

Fig. 14. Geographic ranges of three species that occur in high densities on the reef flat of blue-water reefs: *Calcarina gaudichaudii*, *Baculogypsina sphaerulata*, *Schlumbergerella floresiana*. Note that in Japan *Baculogypsina sphaerulata* has a more northern distribution limit, whereas in the western North Pacific Ocean *C. gaudichaudii* occurs farther to the north.

variably arranged openings to the enveloping canal system between neighboring pustules. The spacing between these openings is 1–2 times their diameter. The chamber sutures are not externally visibly, except for the last 3–5 chambers. The last 2–3 chambers have deep sutures, and an angular crest on the dorsal side. In the sutures, some oblique ridges are present. The last few chambers appear distinct, seemingly swollen on the ventral side of the test. The total length and thickness at the base of the spines, as well as the size and number of the pustules, are variable. In thin section the chambers are narrow and high (Fig. 16). Shallow-living specimens have shorter spines than deep-living specimens. The name and recognition of this species is discussed in Renema and Hohenegger (2005).

6.2.1.2.2. Geographic range. *Calcarina spengleri* occurs in the Philippines, Indonesia, and the western North Pacific Ocean along the north coast of New Guinea, east to the Solomon Islands (Renema and Hohenegger, 2005).

6.2.1.2.3. Habitat. *Calcarina spengleri* has a preference for firm substrates, especially coral rubble covered by coralline algae. *Calcarina mayori* has a similar depth range, but is more abundant on turf algae and *Halimeda* as substrate (Renema and Troelstra, 2001; Renema, 2006a, 2008). It is found on reef slopes from 1 to 45 m water depth, but it usually increases in abundance below the wave base at ~5–10 m, depending on the exposure of the reef, and is most abundant from 15 to 25 m water depth. In the shallow part of its depth range, *C. spengleri* occurs deeper within the interstitial space between coral rubble, but it never occurs at the water-rubble interface or on top of rubble (Renema, 2006a).

6.2.1.3. Calcarina defrancei (Fig. 17)

6.2.1.3.1. Recognition. Intermediate sized, round *Calcarina* species characterized by numerous (8–15), straight, long spines placed radially along the peripheral margin of the test. Test surface makes a smooth impression, with small to large pustules in the center, depending on area and microhabitat. The shape and structure of the spines are most reminiscent of *C. spengleri* and *C. gaudichaudii*. Spine length varies within (Fig. 17C,D vs Fig. 17E,F) and between areas (Fig. 17A,B vs Fig. 17C–F). Japanese specimens appear to be larger (1–2 mm vs 0.5–1.2 mm respectively) and have more numerous spines (10–15 vs 8–13 respectively) than Indonesian specimens (Hohenegger et al., 1999; Renema, 2003, 2008).

6.2.1.3.2. Geographic range. *Calcarina defrancei* has a very patchy distribution within its geographic range, which runs from West Java to southern Japan and as far east as the Solomon islands. Within this range it was not found in the Makassar Strait and SE Sulawesi (Renema and Troelstra, 2001), but it was present in Bali (Renema, 2003), and West Java (Renema, 2008).

6.2.1.3.3. Habitat. The habitat preference of *C. defrancei* is as disparate as its geographic distribution. In the Kepulauan Seribu it is abundant on the reef flat, especially on rubble with the interstitial spaces filled by sediments, sometimes covered by algae. It was not found on the reef slope (Renema, 2008). In other areas, it is most abundant on the reef slope and rare on the reef flat (Hohenegger, 1994; Renema, 2003, 2006a) and occurred at 3 to 25 m water depth, where it also had a preference for rubble with interstitial spaces filled by sand (Hohenegger, 1994; Hohenegger et al., 1999; Renema, 2006a). In East Kalimantan and Bali (Renema, 2003, 2006a) it is associated with areas of upwelling along the outer reef margin or the outer barrier reef of the carbonate shelf.

6.2.1.4. Calcarina hispida (Figs. 18, 19). The name *C. hispida* is widely applied to most hispid *Calcarina* species, frequently including *C. mayori*. There has been considerable uncertainty about the taxonomy of this group. Some authors place all taxa in a single taxon (either *C. mayori* or *C. hispida*), sometimes with morphological varieties. A number of additional species were recognized but not named by Renema (2008). This grouping is applied here, although no consistent morphological difference between *C.* sp. 2 in Renema (2008) and *C. hispida* s.s. was found, and these are both here included in the latter species. An additional deep-living species (*C.* cf. *guamensis*) is also included in the *C. hispida* -group. Mamo (2016) described the specimens previously referred to as *C. hispida* from the Great Barrier Reef as *C. capricornia*, and that is followed here.

6.2.1.4.1. Recognition. This taxon includes the holotype of *C. hispida* Brady, 1876. It is a relatively small species with short spines, the spikes are long, dense and equally distributed over the test, giving it a hispid appearance after which it is named.

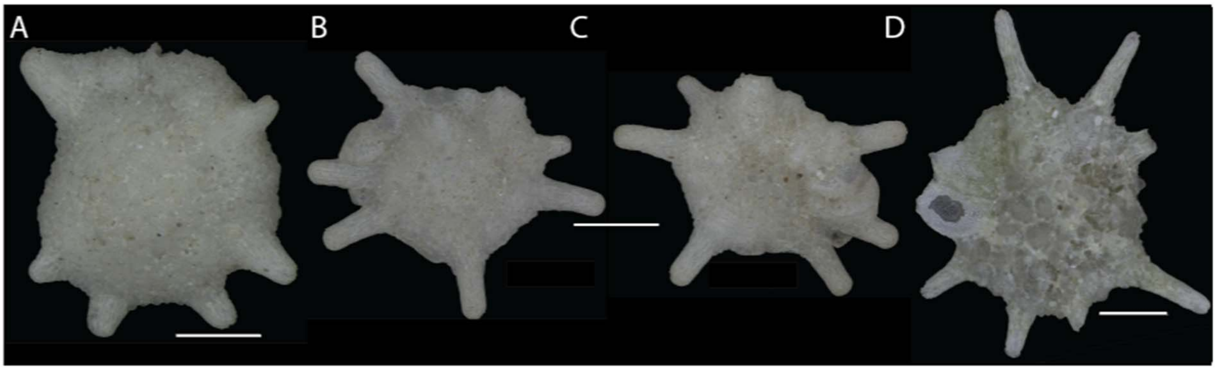

Fig. 15. *Calcarina spengleri*. A) Spermonde Archipelago (SW Sulawesi, Indonesia); B,C, D) Kepulauan Seribu (Java, Indonesia). Scale bar 500 µm.

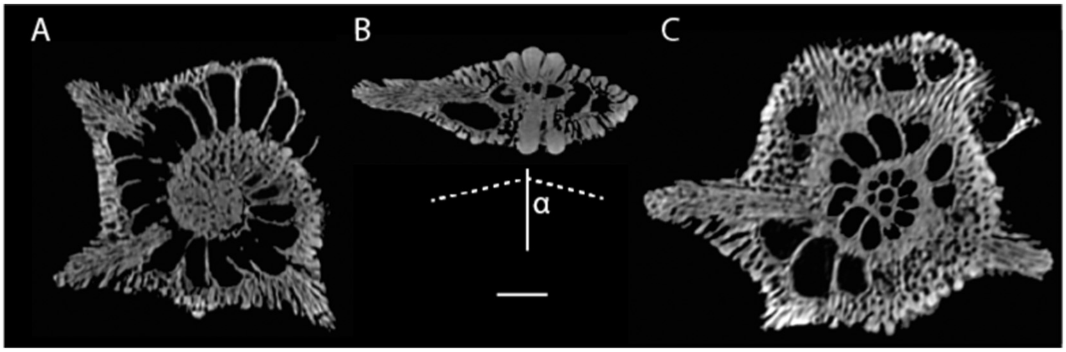

Fig. 16. *Calcarina spengleri*. Thin sections of *Calcarina spengleri* from the Spermonde Archipelago (SW Sulawesi, Indonesia). Scale bar 200 µm.

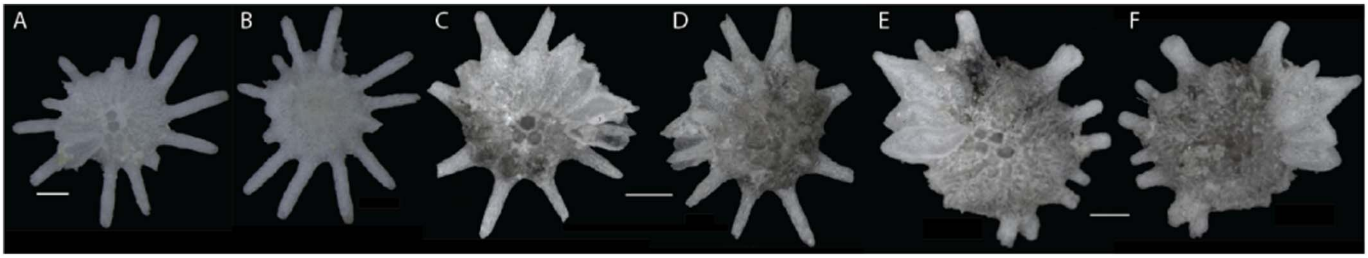

Fig. 17. *Calcarina defrancei*. A, B) Berau Shelf (East Kalimantan, Indonesia); C–F) Kepulauan Seribu (Java, Indonesia). Scale bar 200 µm.

There is distinct morphological variation between the China Sea (Hainan-Philippines-Japan-Guam) specimens and the central Indonesian specimens. The latter were included as *Calcarina* sp.2 in Renema (2008, 2010). The Indonesian specimens have wider chambers that are more pointed towards the periphery. It has fewer spines that are more regularly shaped, and the spikes are shorter (Fig. 18A–C, F).

6.2.1.4.2. Geographic range. Calcarina hispida is found from the Java Sea and northeast Kalimantan (Indonesia), Hainan (China, where it was reported as *C. hainanensis* (Zheng and Zheng, 1978), north to Japan (Kudikajima, Okinawa; Sugihara et al., 2006) and in the North Pacific Ocean as far east as Guam and Saipan.

6.2.1.4.3. Habitat. Calcarina hispida occurs abundantly at the base of filamentous algal mats at exposed sides of the reef crest (Sugihara et al., 2006; Renema, 2002, 2006a); in similar habitats further towards the reef moat it occurs in lower density (Sugihara et al., 2006). It is found in very shallow water of not > 5 m depth. Interestingly, Hallock (1984) reported *C. hispida* (or at least specimens that fit this description) in slightly deeper settings, especially channels between 10 and 20 m water depth where there were strong currents. Confusion with *C. mayori* cannot be excluded though.

6.2.1.5. Calcarina capricornia (Figs. 20, 21)

6.2.1.5.1. Recognition. This is a large, globular *Calcarina* closely resembling *C. hispida* in external morphology, and was recently

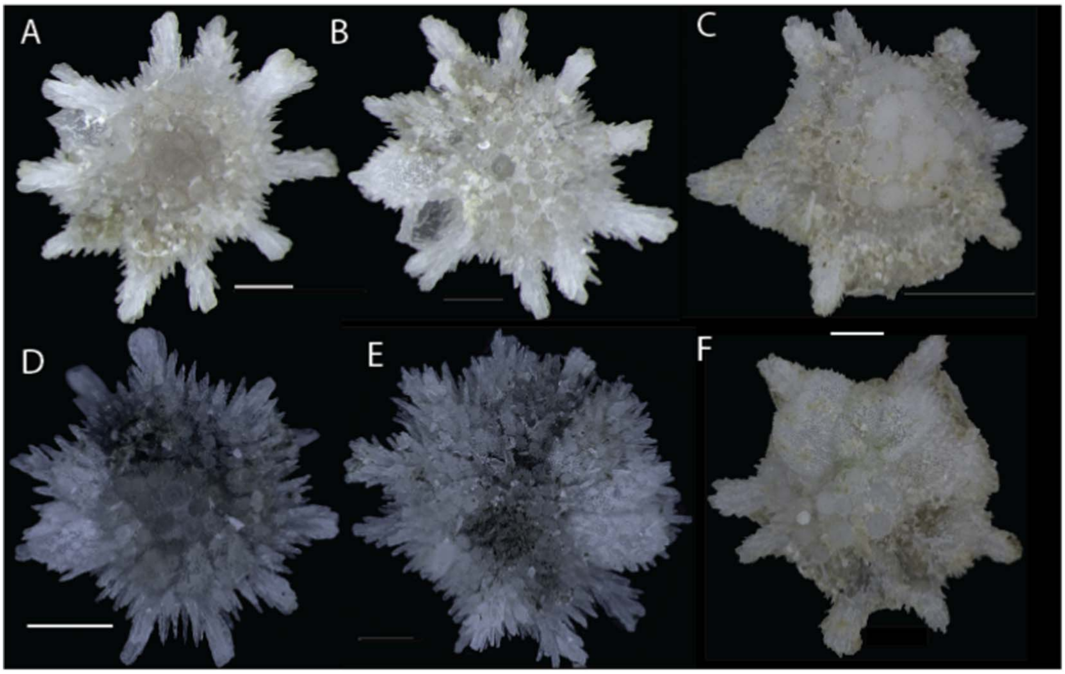

Fig. 18. *Calcarina hispida*. A,B) Berau Shelf (East Kalimantan, Indonesia) C,F) Kepulauan Seribu (Java, Indonesia); D,E) Kudikajima (Okinawa, Japan). Scale bar 200 µm.

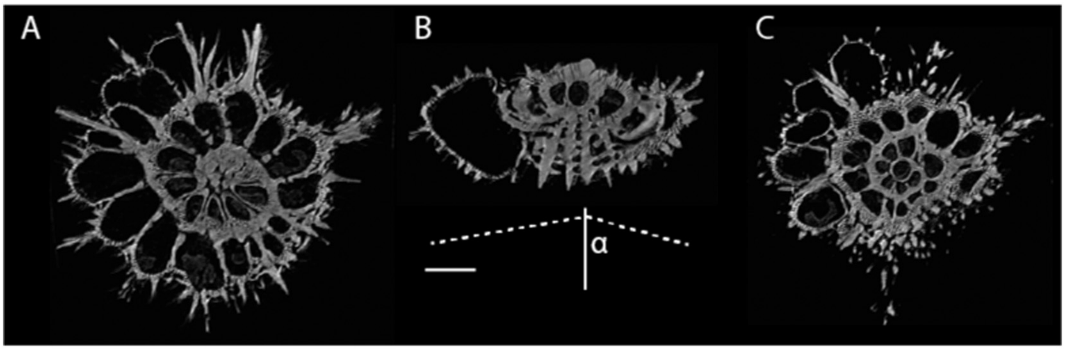

Fig. 19. Thin sections of *Calcarina hispida* from Kudikajima (Japan). Scale bar 200 µm.

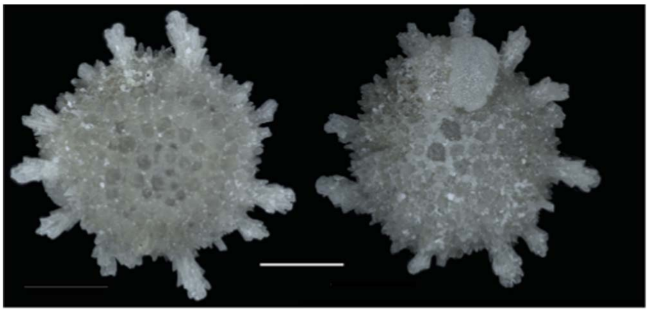

Fig. 20. *Calcarina Capricornia*. Sykes Reef (Queensland, Australia). Scale bar 500 µm.

described as a species on its own (Mamo, 2016), solving confusion on the taxonomic status of this Coral Sea endemic (reported as *C. spengleri* by Lobegeier, 2002 and as *C. hispida* by many other authors). *C. capricornia* has a coarsely hispid test with numerous bosses on both the ventral and spiral side, separated by single rows of coarse canal openings surrounded by spikes (Fig. 20). In *C. hispida* (and related taxa), the spiral side does not have these bosses, nor the canaliculation between them. Numerous (8–13), thin and hispid spines, which sometimes bifurcate, are canaliculated throughout. Canals are thick at the base of the spine and fan out towards the tip of the spines.

In vertical section the high trochospiral coiling stands out compared to all other species of *Calcarina* (Fig. 21). The successive chambers make an angle of 55–70° with the coiling axis in vertical section (α in Fig. 23), whereas in all other species of *Calcarina*, α > = 75°. Additional characters distinguishing both species include more chambers in the initial whorl (9–11 in *C. capricornia* vs 7–9 in *C. hispida*).

6.2.1.5.2. Geographic range. Calcarina capricornia occurs along the entire length of the GBR from Lady Musgrave Island in the south to Raine Island in the north (e.g., Jell et al., 1965; Baccaert, 1987; Lobegeier, 2002; Yamano et al., 2000; Mamo, 2016).

6.2.1.5.3. Habitat. It is the most abundant epiphytic foraminifer on most species of reef-flat macro-algae and is particularly abundant on filamentous algae (Jell et al., 1965; Lobegeier, 2002; Yamano et al., 2000). The turf-algae, *Laurencia* sp., and the fleshy chlorophyte, *Chlorodesmis fastigiata*, are filamentous algae that provide an entangled three-dimensional habitat (Lobegeier, 2002). These filamentous algal species are restricted to the nutrient-rich reef rim, where densities are highest. Lower densities occur on the reef flat in tidal pools to the windward reef edge where this algal community is abundant (Lobegeier, 2002). In this habitat it was often accompanied by *Baculogypsina sphaerulata*. In the GBR *C. capricornia* only occurs on mid- and outer-shelf reefs.

6.2.1.6. Calcarina cf. guamensis (Fig. 22)

6.2.1.6.1. Recognition. This *Calcarina* is of intermediate size, strongly flattened and pustulous in the center of the test. Short spikes occur around the margin of the test. Numerous short, blunt and flattened spines often are flaring and might develop a fringe between them.

6.2.1.6.2. Geographic range. This species has only been observed in East Kalimantan (Indonesia; Renema, 2006b) and Okinawa (Japan; Hohenegger, 1994). It is very similar to specimens described as *C. guamensis* by McCulloch (1977) from Guam.

6.2.1.6.3. Habitat. All records are from 40 to 75 m water depth on coarse sand substrates. This is the deepest occurring calcarinid, and the only calcarinid with a preference for sandy substrates. As such, it is unique, but always rare, both in number of sites where it has been reported from, and because of its low density at these sites (Renema, 2006b).

6.2.1.7. Calcarina mayori (Figs. 23, 24)

6.2.1.7.1. Recognition. Medium-sized species. Diameter without

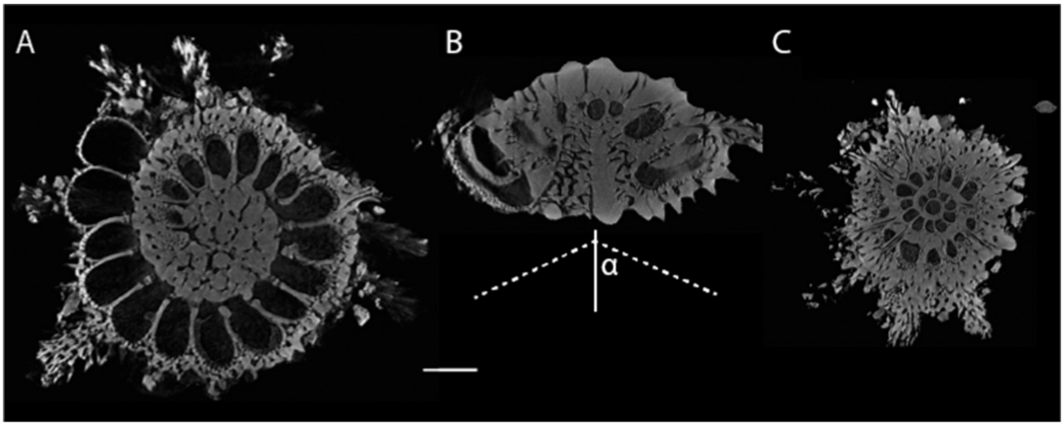

Fig. 21. Thin sections of *Calcarina capricornia* from Newton Island (Queensland, Australia). Scale bar 200 µm.

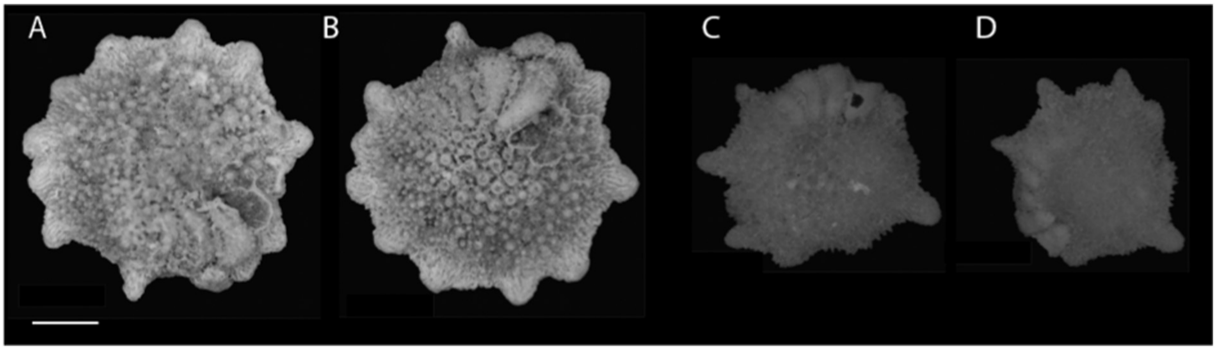

Fig. 22. *Calcarina* cf. *guamensis*. Berau shelf (East-Kalimantan, Indonesia). Scale bar 200 μm.

spines not larger than 1 mm, 3–6 short to intermediate, thin, straight to club-shaped spines. The test is covered with coarse pustules and short, protruding spikes. There is only one row of openings to the canal system between the tubercles, and there is a distinct change in the character of the openings to the canal system between the test and the spines. The canal openings are small, separated by 2–3 times the diameter of the canal opening. In adult specimens, sutures of the last 5–7 chambers are faintly visible on the umbilical side; these chambers have fine, randomly distributed pores without spikes. The size and the extent over the test of the tubercles is variable.

6.2.1.7.2. Geographic range. Calcarina mayori is the most widely distributed *Calcarina* species. It has been reported from East Sumatra to New Caledonia and from the Great Barrier Reef to southern Japan.

6.2.1.7.3. Habitat. Calcarina mayori is found on reef slopes on either rubble covered by crustaceous red algae or epiphytically on leafy red or green algae. It does not occur in highly energetic environments, and is usually restricted to > 10 m water depth in exposed reefs, but can occur shallower in more inshore reefs. The down-slope limit is usually restricted by the availability of firm substrates. In areas where substrate availability extends beyond its depth range, the maximum depth at which *C. mayori* was found alive is ~60 m (Hohenegger, 2004; pers. obs. Great Barrier Reef). *Calcarina mayori* is abundant in inshore reef systems, such as the Kepulauan Seribu (Indonesia; Renema, 2008, 2010), where it is more abundant than *C. spengleri*.

6.2.1.8. Calcarina calcarinoides (Fig. 25)

6.2.1.8.1. Taxonomic note. This species was reported as *Calcarina calcar* from southern Japan (e.g., Hohenegger, 1994; Hohenegger et al., 1999; Sugihara et al., 2006). These publications place the taxon as *Calcarina calcar* d'Orbigny in the genus *Calcarina*. Hottinger et al. (1991) described the internal structure of *Pararotalia*, *Neorotalia*, and *Calcarina* and demonstrated that the internal structure of *Neorotalia calcar* lacks the multiple interseptal laminae and has an apertural face with a single basal aperture, and should be placed in *Neorotalia*. After comparing the types of *N. calcar* with material provided by Drs Fujita and Hohenegger of their *Calcarina calcar* (Fig. 25), I conclude that these specimens represent a species of *Calcarina*, and as a consequence that the species name *calcar* is not available for this species. Zheng and Zheng (1978) described *C. calcarinoides* from the Xisha islands (China), and these specimens are very similar to the Japanese and Taiwanese specimens I studied.

6.2.1.8.2. Recognition. Both the spiral and umbilical side are coarsely perforate with a number of large pustules especially at the umbilical side. The last few (2–4) chambers are separated by deep sutures. Each chamber has a short, sharp, spine protruding from the proximal margin.

6.2.1.8.3. Geographic range. So far this species is only reported from the western part of the South China Sea north to Tane-ga-shima Jima (southern Japan; Zheng and Zheng, 1978; Li and Wang, 1985; Hohenegger, 1994; Sugihara et al., 2006).

6.2.1.8.4. Habitat. This species is especially abundant on the (inner) reef flat (Sugihara et al., 2006), where it occurs on firm

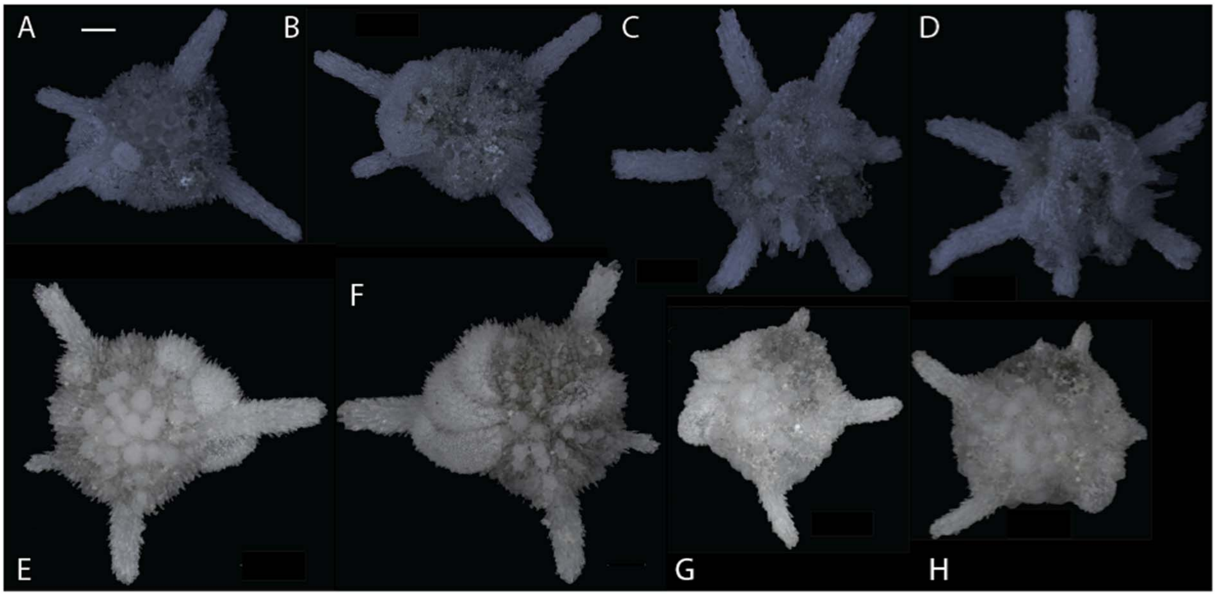

Fig. 23. *Calcarina mayori*. A–F Spermonde Archipelago (SW Sulawesi, Indonesia); G,H Kepulauan Seribu (Jakarta, Indonesia). Scale bar 200 μm.

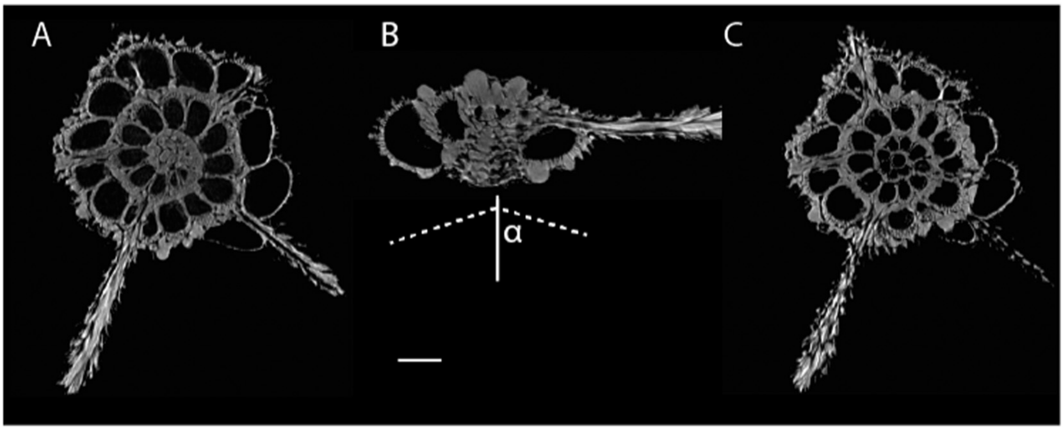

Fig. 24. Thin sections of *Calcarina mayori* from Pari Island (Java, Indonesia). Scale bar 200 µm.

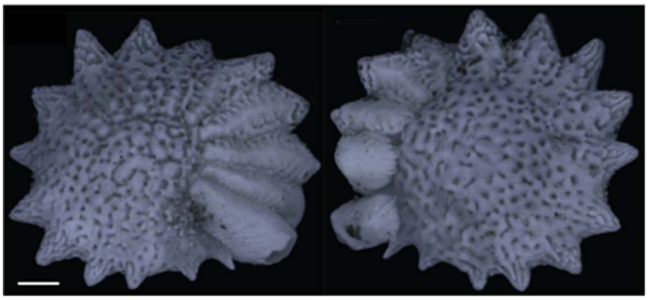

Fig. 25. *Calcarina calcarinoides*. Ishigaki island, Japan. Scale bar 200 µm.

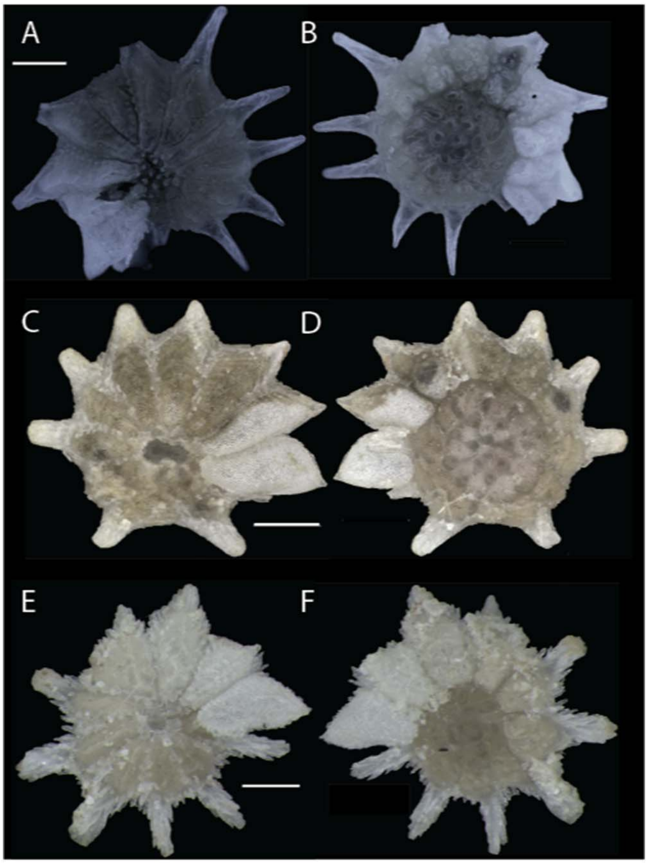

Fig. 26. *Neorotalia*. A, B *N. calcar* Adorius Island (Palau); C, D *N. calcar* Kudingkareng Keke (SW Sulawesi, Indonesia); E, F *N. gaimardi* Samalona (SW Sulawesi Indonesia). Scale bar 200 µm.

substrates and epiphytically on turf algae. In the northwestern South China Sea *C. calcarinoides* is restricted to oceanic reefs and is not found on reefs close to the coast (Li and Wang, 1985). It is most abundant at < 5 m depth, but has been found down to 30 m water depth on the reef slope (Hohenegger et al., 1999).

6.2.2. *Genus Neorotalia*

Trochospiral, evolute on the spiral side, involute on the umbilical side. Chambers are elongated, with a sharp ridge and thin spiral lamina. There is a single, rimmed main aperture as wells as multiple round to slit-shaped supplementary apertures. Spines grow at the distal end of most chambers, and have spinal canals surrounding a massive core (only in the oldest visible spines). A detailed description of the internal structure of *Neorotalia* and the differences with *Pararotalia* and *Calcarina* are provided by Hottinger et al. (1991).

6.2.2.1. *Neorotalia calcar (Fig. 26A–D, Fig. 27B)*

6.2.2.1.1. Recognition. Peripheral outline is stellate, lenticular, and more or less equally biconvex in peripheral view (Hottinger et al., 1993). Chambers are radially elongated and peripherally pointed at the anterior margin of most chambers in the final whorl, and most chambers develop a canaliculated spine. Chambers are sharply triangular with deeply depressed sutures on the umbilical side of the test. There is substantial variation in how far the triangular edge of the chambers extends. The deep sutures are progressively covered by secondary lamination forming the intraseptal space (Hottinger et al., 1993). The umbilical area can be open, or filled with large pustules. Spiral side with well-developed pustules, which vary from large and round (e.g., Renema and Troelstra, 2001), to elongate to vermiculate (e.g., Hottinger et al., 1993) pustules.

6.2.2.1.2. Geographic range. Neorotalia calcar has a wide tropical distribution in the Indo West-Pacific, from the Red Sea to the Marshall Islands and New Caledonia (Langer and Hottinger, 2000), and is highly variable in morphology throughout its range. The northernmost distribution is in Iriomoto (southern Ryukyu Islands, Japan; Hatta and Ujié, 1992. Due to confusion with *Calcarina calcarinoides* its occurrence in the South China Sea and further north in Japan is uncertain (see above).

6.2.2.1.3. Habitat. Neorotalia calcar occurs on the outer reef flat and adjacent upper reef-slope and is restricted to the upper 10–20 m in most places where it has been found (e.g., Reiss and Hottinger, 1984; Renema and Troelstra, 2001; Renema, 2008). In most places it is abundant epiphytically on macro-algae (e.g., Reiss and Hottinger, 1984; Renema, 2003), but in SW Sulawesi it has a preference for sandy substrates at the leeward side of sand cay reefs, locally associated with sparse seagrass (*Halophilus*) occurrences.

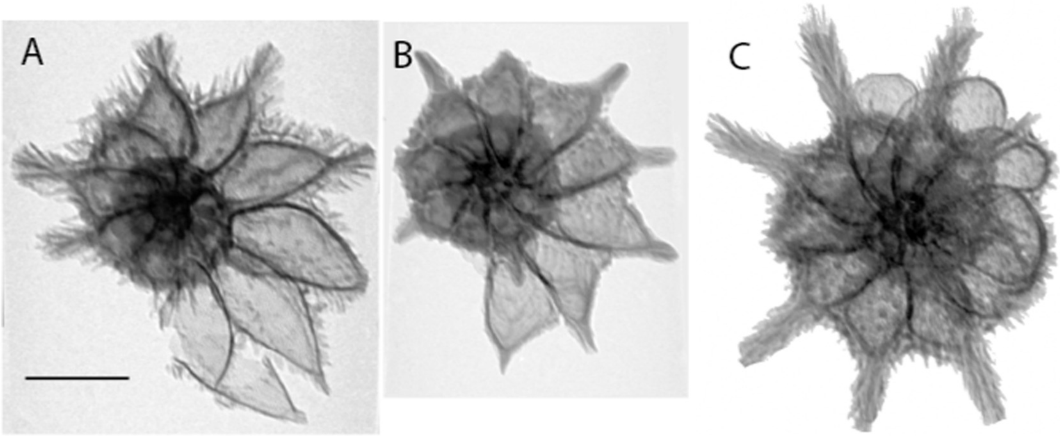

Fig. 27. X-ray images of A) *Neorotalia gaimardi* (Kepulauan Seribu, Java, Indonesia), B) *Neorotalia calcar* (Spermonde Archipelago, SW Sulawesi, Indonesia), and C) *Calcarina hispida* (Kepulauan Seribu Java, Indonesia), highlighting the structural difference between the genera *Neorotalia* and *Calcarina*. Scale bar 200 μm.

6.2.2.2. Neorotalia gaimardi (Figs. 26E,F; 27A)

6.2.2.2.1. Recognition. This species is figured by Renema (2008) as *Calcarina* sp1. It is a very characteristic, small-sized species. The initial spire is visible on the spiral side, and sutures of all chambers in the last whorl are visible on the umbilical side, although they become increasingly covered by small pustules. On the umbilical side there are a number of coarse pustules, but no distinct openings to the canal systems are discernable. Short, blunt spines form at the peripheral margin of each chamber.

6.2.2.2.2. Geographic range. This species has only been recorded from central Indonesia, ranging from West Java to West Papua and from East Kalimantan to Flores. I have not observed this species in suitable habitats from neighboring regions, but given that it is a poorly known species that is abundant in relatively under-sampled habitat, its actual distribution might be wider and include, for example, parts of the South China or Andaman Seas.

6.2.2.2.3. Habitat. Neorotalia gaimardi is found on the reef flat and slope in both nutrient-rich (Kepulauan Seribu) macro-algal (*Turbinaria* and *Sargassum*) dominated settings (Renema, 2008), on turf algae on the reef flat extending down slope to as deep as 35 m water depth (Renema, 2010). In the Berau region is was restricted to the reefs surrounded by deep oceanic water, and did not occur on the reef flats or slope of the shelf reefs (Renema, 2010).

6.2.3. Genus Baculogypsina

Smooth, test with 4–6 long sharp spines more or less in a horizontal plane (Fig. 28). Outer surface smooth consisting of finely perforate chamberlet walls, separated by pustules. The initial spiral is planispiral, from which the spines originate. Spines are canaliculated, and do not or hardly increase in width in equatorial section. The lateral chamberlets are small, thin-walled and form a very regular stack.

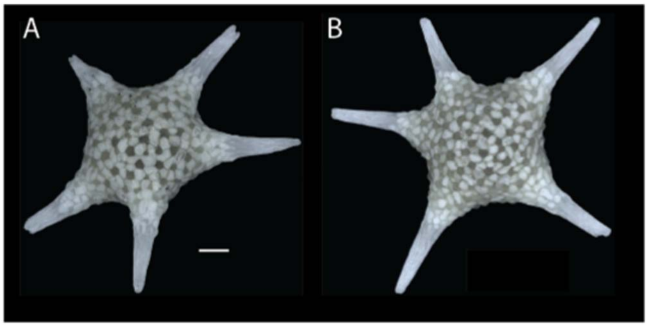

Fig. 28. *Baculogypsina sphaerulata*. Esperitu Santo (Vanuatu). Scale bar 200 μm.

6.2.3.1. Baculogypsina sphaerulata (Fig. 28)

6.2.3.1.1. Recognition. Star shaped with 4–6 thin, sharp spines, usually arranged in a single plane. *Baculogypsina*, *Baculogypsinoides* and *Schlumbergerella* all have globular tests as the result of stacks of lateral chamberlets alternating with pustules. Test surface smooth, with alternating small pustules surrounded by rimmed, hexagonal, finely perforated chamberlet walls. Spines with parallel groves.

6.2.3.1.2. Geographic range. The geographic range of *Baculogypsina sphaerulata* encompasses the tropical North and South Pacific Oceans east to Samao (Langer and Hottinger, 2000), it is absent in most of the Philippines and in the western part of the Indonesian Archipelagos, where it was found in southeast Sulawesi and north of Waigeo (Fig. 14). Its northernmost occurrence is Tane-ga-shima Jima (Sugihara et al., 2006) in Japan and its southernmost occurrence Lord Howe Island. In Japan *B. sphaerulata* occurs farther north than *C. gaudichaudii* (Fig. 14), whereas in the western North Pacific Ocean *C. gaudichaudii* occurs farther north than *B. sphaerulata* (Fig. 14).

6.2.3.1.3. Habitat. Baculogypsina sphaerulata is found on exposed reef flats in blue-water reefs. It has a preference for solid substrates, and is also found attached to filamentous and turf macro-algae. On reef flats it can occur in very high densities, and contribute substantially to carbonate production (Yamano et al., 2000; Woodroffe and Morrison, 2001; Lobegeier, 2002; Fujita et al., 2009, 2016; Doo et al., 2012) and the maintenance of cays (Dawson et al., 2014) to such an extent that mass-culturing has been suggested as a method to maintain coral cays to counter future sea-level rise (Hosono et al., 2014).

6.2.4. Genus Baculogypsinoides

Baculogypsinoides stands out as a massive, usually tetraedrical-shaped, calcarinid with blunt spines. The initial chambers are trochospiral, and juveniles can be mistaken for *Calcarina*. Stacks of thick-walled, somewhat irregular, lateral chamberlets follow the initial spire and are separated by pillars. The spines are canaliculate and originate from the initial chambers. The outer appearance is hispid.

6.2.4.1. Baculogypsinoides spinosus (Fig. 29)

6.2.4.1.1. Recognition. Test globular with up to four large, massive and canaliculated spines in a tetrahedral orientation. Test surface pustulose, especially centrally. Between the pustules, irregularly shaped lateral chamberlet walls with large pores are present. The large lateral chamberlets form in alternating stacks and there are more lateral chamberlets around the test marginal site than in the centre of the test. Massive spines with channels. The initial chambers are trochospirally arranged.

6.2.4.1.2. Geographic range. The northernmost boundary of the geographic range of *B. spinosus* is between Okinawa and Tanegashima

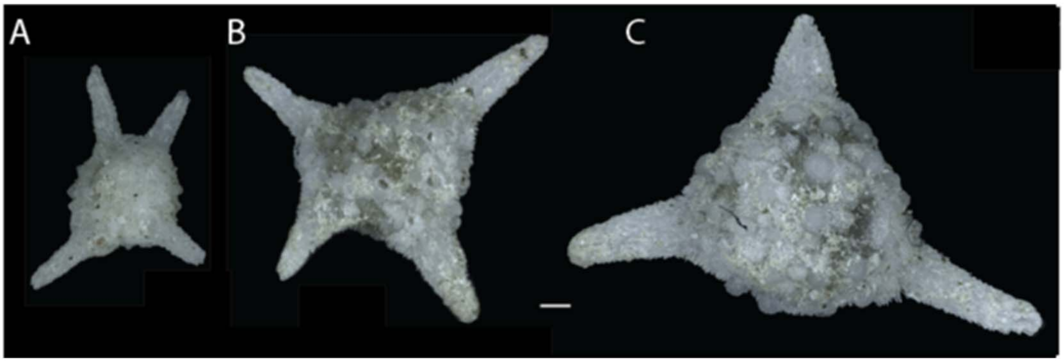

Fig. 29. *Baculogypsinoides spinosus*. Samalona (SW Sulawesi, Indonesia). Scale bar 200 μm.

(Sugihara et al., 2006). Farther south it occurs in the South China Sea (e.g., Hainan; Zheng and Zheng, 1978), the Philippines and the Indonesian Archipelago. There are no records from the Indian Ocean side of Sumatra, but it is locally abundant in the Java Sea (Renema, 2008). The eastern distribution boundary is not as clearly known. It was found as far east as the Raja Empat islands and the Bird's Head (West Papua) (pers. obs.), and is not reported from any location farther east.

6.2.4.1.3. Habitat. Baculogypsinoides spinosus is a deep-living calcarinid, preferring firm substrates and macro-algae (Renema and Troelstra, 2001). There is variation between regions in both substrate types used and depth distribution. Whereas in Japan (Hohenegger et al., 1999) and the Spermonde Archipelago (Renema and Troelstra, 2001) this species was found mostly on the deeper part of the reef slope. In the Berau Shelf (Renema, 2006a) and Kepulauan Seribu (Renema, 2008) it was found abundantly on the upper part of some reef slopes, associated with abundant macro-algae. In Japan it was the only calcarinid observed on sandy substrates (Hohenegger et al., 1999), but such habitat has not been reported elsewhere.

6.2.5. Genus *Schlumbergerella*

Unlike all other calcarinid genera, the spines of *Schlumbergerella* do not have a canal system, but consist of elongated walls of adjacent stacks of chamberlets, originating in the initial chambers (Hofker, 1970). Externally these massive spines are covered by parallel grooves. In the megalosphere there are three large initial chambers forming a globular initial part of the test ('raspberry type' embryonic apparatus according to Hofker, 1970), followed by regular stacks of thin-walled chamberlets alternating with pillars. The initial spire in the microsphere is planispiral. Externally *Schlumbergerella* is characterized by a globular appearance with 3–6 short spines, with porous lateral chamberlet walls alternating with massive pustules (Fig. 30).

6.2.5.1. *Schlumbergerella floresiana* (Fig. 30A, B)

6.2.5.1.1. Recognition. Test large, massive and globular with four usually short, pointed spines. Lateral chamberlets smaller than in *S. neotetraedra*.

6.2.5.1.2. Geographic range. This species occurs from Bali to Flores in the Lesser Sunda Islands.

6.2.5.1.3. Habitat. It was found at all sites around Bali in water depth < 20 m. It does not have a preferred substrate, and can live on coarse sand, rubble and epiphytically on algae in the reef moat (Renema, 2003).

6.2.5.2. *Schlumbergerella neotetraedra* (Fig. 30C)

6.2.5.2.1. Recognition. Similar to *S. floresiana*, which some authors regard as conspecific. However, as discussed by Hofker (1970), the test surface between the spines is concave instead of convex, the spines are much thicker due to the presence of lateral chamberlets around the spines and the lateral chamberlets are larger. Often the tips of the spines are bifurcated. Test surface is smooth and formed by irregularly shaped, perforated walls of chamberlets, alternating with large pustules.

6.2.5.2.2. Geographic range. So far this species has only been found around Bali. The original description is from Pleistocene reefs at Sumbawa (Tobler, 1918). I did not encounter the species at Flores and Komodo where *S. floresiana* was present. Hofker (1970) mentions *S. neotetraedra* from Jakarta Bay and the Kepulauan Seribu, but I have not found *Schlumbergerella* there (Renema, 2008), neither are there specimens from that region in Hofker's collection.

6.2.5.2.3. Habitat. Most specimens of *S. neotetraedra* occur at < 10 m water depth and have a preference for coral rubble with an open interstitial space and covered by coralline algae. It was predominantly found in areas with very high hydrodynamic energy (spur-and-groove systems) (Renema, 2003).

6.3. Family Nummulitidae

Planispiral test with marginal cord. Genera defined by traditional morphology are divided by coiling mode (involute, pseudo-evolute, evolute) and the presence/absence of chamberlets and annular chambers (e.g., Banner and Hodgkinson, 1991). Hottinger (1977b) was the

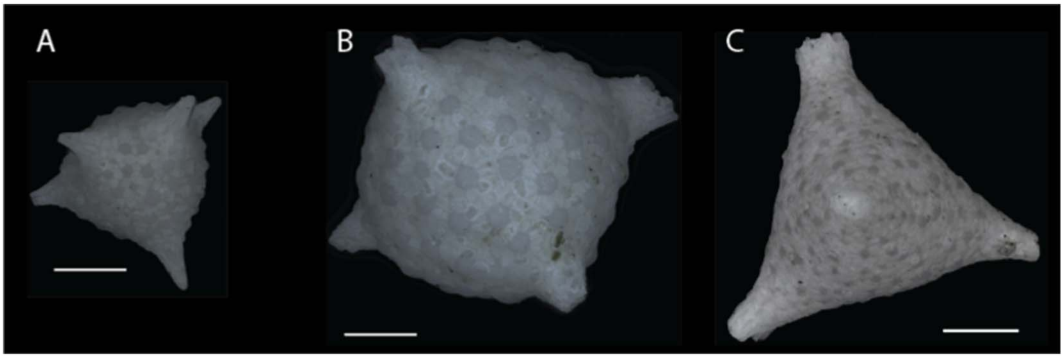

Fig. 30. *Schlumbergerella*. A,B: *Schlumbergerella floresiana* Tulamben (Bali, Indonesia); C *Schlumbergerella neotetraedra* (Kesumasari (Bali, Indonesia)). Scale Bar 500 μm.

first to recognize that several of these characters are environmentally influenced, and that convergent evolution resulted in polyphyletic genera. He preferred to use the shape of the intercameral stolons and the septa to discriminate nummulitid genera, as well as morphological characters such as the presence of trabeculae. These structures, here interpreted as short imperforate surface traces of the underlying branches of the septal canal leading to septal pores (sensu Haynes et al., 2010). In species in which the septal pores are distributed along the septal trace, trabeculae are not present, but in species in which the septal pores (also) occur at some distance from the septal trace they are visible as short imperforate bars on the test surface. The presence of trabeculae was used to define the genus *Nummulites* (Hottinger, 1977b), and this character still forms the basis for the separation of (*Palaeo*) *nummulites* and *Operculinella* (Hohenegger et al., 2000). However, trabeculae have later also been found in other genera, such as *Assilina* (Sengupta and Mukhopadhyay, 2008), and in the extant *Operculinella cumingii* and *Operculina* sp., indicating that this character developed multiple times during the evolution of the Nummulitidae and should be downplayed in the classification of this group.

Recent phylogenies based on molecular data are consistent with the finding that several of the characters used for the traditional generic classification evolved multiple times (Holzmann and Hohenegger, 2003). Because it is beyond the scope of this paper to do a full revision of the family, here I use a classification into *Operculina*, *Heterostegina*, *Cycloclypeus*, and *Operculinella* (Table 1), until a thorough revision of the suprageneric classification is completed, ideally including molecular, morphological, and fossil data.

6.3.1. Genus Operculina

Operculina is (sub)evolute, has a lax spire and no secondary chamberlets. The apertural face consists of a single slit-shaped primary aperture at the base, and a row of secondary apertures on the septal wall.

Hottinger (1977b) showed that there are at least two morphologically distinct groups in this genus, one with (*O. ammonoides*- group) and one without (*O. complanata*-group) a folded septal flap. He placed those in separate genera, *Operculina* and *Planoperculina*. *Planoperculina* has *Operculina heterosteginoides* as type-species based on two character-states 1) the folded septal flap and 2) the regular stolon pattern (Hottinger, 1977b). However, Hohenegger et al. (2000) argued that these characters are variable, often even within specimens. In some subsequent papers *Operculina* in the *ammonoides* group (without the septal flap) have been placed in the (up to then restricted to the Early-Middle Eocene) genus *Assilina*, which also does not have a septal flap. Coiling pattern and cell ultrastructure are different between *O. ammonoides* and *Assilina*. I have opted to use *Operculina* for all (sub)evolute forms without or with at most partially secondary chamberlets, and to be very conservative in naming taxa, as a more thorough study will probably reveal that there are several cryptic species.

6.3.1.1. Operculina ammonoides

6.3.1.1.1. Recognition. *Operculina ammonoides* does not have a folded septal flap (Hottinger, 1977b). Coiling can be almost evolute (with only a very small part of the spiral laminae extending over the previous whorl to entirely involute, at least in the early whorls. The septal trace is formed by a series of papillae (granulated). The size of these papillae usually decreases in later chambers, proximal papillae are larger than distal ones, and sometimes the initial one is much larger than all others. The spiral wall may be finely perforate throughout, or small, interseptal pustules may be present, sometimes even expressed as surface structures. Other sets of parameters that have been proposed to identify species are coiling parameters, analogues to differentiation between species in the fossil record (e.g., Hohenegger et al., 2000). Coiling can be almost evolute (with only a very small part of the spiral laminae extending over the previous whorl; Fig. 31A) to entirely involute, at least in the early whorls (Fig. 31C). The septal traces are granulated. The size of the papillae usually decreases in later chambers, proximal papillae are larger than distal ones, and sometimes the initial one is much larger than all others. The spiral wall may be finely perforate throughout, or small, interseptal pustules may be present, sometimes even expressed as surface structures. Other sets of parameters that have been proposed to identify species are coiling parameters, analogues to differentiation between species in the fossil record (e.g., Hohenegger et al., 2000).

However, several of these characters have also been associated with ecophenotypical variation (e.g., Pecheux, 1995), and consistent boundaries separating species are yet to be discovered. Clarifying species boundaries is further hampered by inconsistent use of names between authors, resulting in taxonomic confusion. As a result some studies consider the *O. ammonoides*-complex as a single species (e.g., Hottinger et al., 1993; Pecheux, 1995; Langer and Hottinger, 2000; Renema and Troelstra, 2001), whereas others include two (e.g., Hohenegger et al., 2000) or more (Debenay, 2012) species.

Operculina ammonoides has a proloculus size in the A-form of 20–140 μm (usually 40–70 μm). B-forms are considerably larger (3–5 mm) and almost always close to evolute (Fig. 31D,E,H).

Ecophenotypical variation includes thicker shells, less rapidly opening spiral, and larger proloculus sizes (Pecheux, 1995). Regional variation includes the 'angle of backward curve' (sensu Hohenegger et al., 2000), which is consistently small in Indonesian specimens (< 35°, usually < 25°), a bit higher in specimens figured by Pecheux (1995) and Hottinger et al. (1993) (20–45°) from the Red Sea, and by Debenay (2012) from New Caledonia, and increasing from 20° in the initial whorl to 60–80° in later whorls in southern Japan (Hohenegger et al., 2000). In the Indonesian and Red Sea specimens septa are initially straight, and bend backwards in the peripheral 20–30% of the chamber height (Renema and Troelstra, 2001; Hottinger et al., 1993). In specimens from Okinawa and New Caledonia, the septa are curved backwards gradually over almost the entire length of the septa (Hohenegger et al., 2000; Debenay, 2012).

Hohenegger et al. (1999) additionally recognized *O. discoidalis*, based on a tighter coil and straight less backward bent septa

Table 1
Characters used for the recognition of the main taxonomic groups in the Nummulitidae.

Coiling	Characters		Genus
Involute	Spiral laminae extent at least to the poles, alar prolongations present	Trabeculae present	*Operculinella*
Quasi-evolute	Spiral laminae extent at least to the poles, no alar prolongations	Trabeculae present	*Operculina* sp.
Subevolute	Spiral laminae extent partially over the previous whorl (usually only very limited), and do not reach the pole		*Operculina ammonoides*
Evolute	Spiral laminae do not extend over the previous whorl	Folded septal flap	*Operculina complanata*
		Secondary chamberlets	*Heterostegina*
		Secondary chamberlets and annular chambers	*Cycloclypeus*
Maturo-evolute	Initially involute, turning into evolute in the last whorls; secondary chamberlets		*Heterostegina depressa*

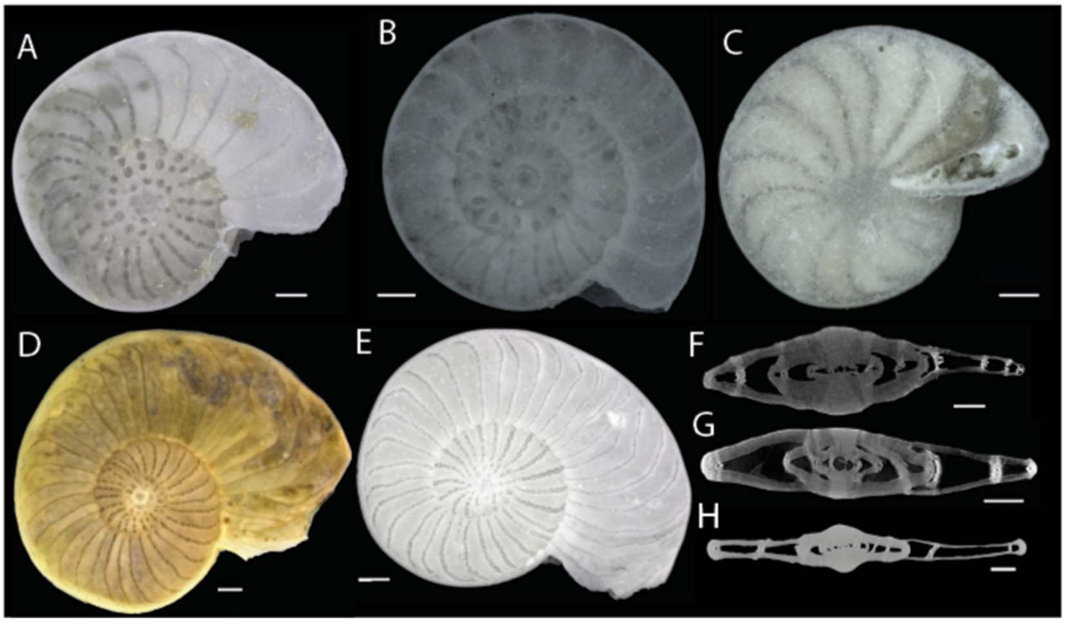

Fig. 31. *Operculina ammonoides* from the Spermonde Archipelago illustrating the intraspecific variability. Specimens A, D, E are from sandy substrate at the reef base, B and C from rubble with sand on the lower reef-slope. Specimen H is the same as specimen D. A, B, C, F, G A-forms; D, E, H B-form. Scale bar 200 μm.

(usually < 25°, maximally 40°). Debenay (2012) reports four species of the *O. ammonoides*-group from New Caledonia, including *O. ammonoides* and *O. discodalis*, and in addition *O. philippinensis* and *O. gaimardi*. These species are mostly differentiated based on surface ornamentation, shape of the septa, and chamber size.

6.3.1.1.2. Geographic range. *Operculina ammonoides* is very widely distributed over the entre Indo-Pacific. Its range is circumscribed by Moreton Bay (southern Queensland; Narayan and Pandolfi, 2010), Fiji, Funafuti, Hawaii (Langer and Hottinger, 2000), southern Japan (Hohenegger et al., 2000), south almost to Perth in Western Australia (James et al., 1999), and in the Indian Ocean from Mozambique to the Red Sea (Langer and Hottinger, 2000). Regional variation in morphological characters questions whether this is a single, very variable species, or multiple cryptic species.

6.3.1.1.3. Habitat. *Operculina ammonoides* can be found in a wide range of environments. It is the first soft-substrate species to occur in turbid nearshore environments (Renema and Troelstra, 2001), and has the capacity to transform these muddy substrates to a coarse carbonate sand suitable for a wider range of LBF taxa, such as *Dendritina*, *Parasorites*, and *Amphistegina papillosa* (Renema, 2006b). In these soft-substrate environments widely coiled, flat specimens are found. In the Spermonde Archipelago the flat, sand-preferring morphotype is extremely abundant, whereas the thick solid substrate preferring morphotype is not present. To the contrary, in Bali the reverse was observed (Renema and Troelstra, 2001; Renema, 2003).

The lower boundary of its depth range is around 2% surface light intensity (Hohenegger et al., 1999). Within the same window of light intensity, *O. ammonoides* can also be found on coral rubble (Hohenegger et al., 1999; Pecheux, 1995; Renema, 2008). Maximum depth of occurrence is deeper around the equator than close to the northern and southern limits of its distribution.

6.3.1.2. Operculina cf. complanata (Fig. 32)

6.3.1.2.1. Recognition. A thin-shelled species of *Operculina* that grows up to 5 mm in diameter. The test is entirely evolute with a rapidly opening spire. Most of the spiral laminae are covered in raised pustules that vary in size with depth, and are more pronounced in deeper-living specimens (Hohenegger et al., 2000). The ‘angle of backward bend’ (sensu Hohenegger et al., 2000) increases from 40° to 100° in Japan, but the septa are more straight in the GBR (30–60° increase). The main difference with *O. ammonoides* is that the septa are not granulated. Furthermore, the septa have a folded septal flap that is most pronounced in later formed chambers (Hottinger, 1977b; Hohenegger et al., 2000). The proloculus size is ~80–120 μm.

6.3.1.2.2. Geographic range. In older literature there has been considerable confusion with other species in the genus *Operculina*, especially *O. ammonoides* (see, for example, the synonymy list in Hottinger, 1977b), which makes the distribution limits uncertain.

Operculina cf. *complanata* has been reported from large parts of the western North and South Pacific Ocean, from southern Japan (Hohenegger et al., 2000) through Indonesia, including the Java Sea (Renema, 2008), to Papua New Guinea (Langer and Lipps, 2003), and from the Great Barrier Reef (Renema et al., 2013) through to New Caledonia (Debenay, 1988; as *O. bartschi* in Debenay, 2012). The distribution farther to the east is poorly documented.

6.3.1.2.3. Habitat. *Operculina* cf. *complanata* has been found in habitats receiving 0.3–12% surface irradiation (Hohenegger et al., 2000) on sandy substrates (Hohenegger et al., 2000; Renema, 2006b; Renema et al., 2013). Rare occurrences on the Sunda Shelf and inter-reef areas of the Spermonde Archipelago show that this species tolerates exposure to a limited amount of sediment (Fig. 5).

6.3.1.3. Operculina heterosteginoides (Fig. 33)

6.3.1.3.1. Recognition. A thin-shelled, evolute *Operculina* distinguished from all other species of extant *Operculina* by its partial development of septula. Otherwise the species is variable and the spiral wall can be ornamented by surface expressions of the partial septula, which is sometimes used to distinguish multiple species (e.g., Hohenegger et al., 2000).

6.3.1.3.2. Geographic range. Despite my more narrow definition of the species, the geographic range reported here is wider than that reported in Langer and Hottinger (2000). *O. heterosteginoides* is known from southern Japan (Hohenegger et al., 2000), Indonesia (Renema, 2006b), and the Great Barrier Reef (Renema et al., 2013) south to the Fraser Shelf (pers. obs., Fig. 33).

6.3.1.3.3. Habitat. *Operculina heterosteginoides* is restricted to poorly illuminated habitats receiving 0.3%–2.5% surface light intensity, and prefers medium- to fine-grained sand substrates (Hohenegger et al., 2000; Beavington-Penney and Racey, 2004). In the Great Barrier Reef and Berau Shelf, this species is restricted to the

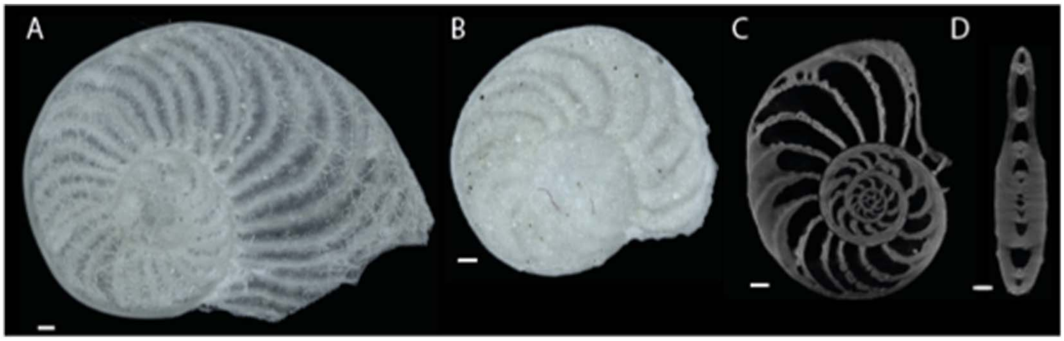

Fig. 32. *Operculina* cf. *complanata*. A, C, D Hydrographer's Passage (Queensland, Australia); B: Samalona (SW Sulawesi, Indonesia). Scale bar 200 μm.

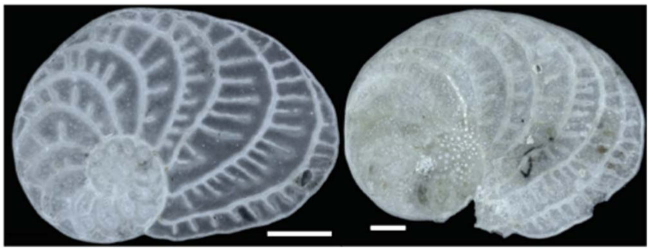

Fig. 33. *Operculina heterosteginoides*. Fraser Shelf (Queensland, Australia). Scale bar 200 μm.

outer shelf area, out of reach of terrestrial influence (Fig. 5).

6.3.1.4. *Operculina* sp. (Fig. 34)

6.3.1.4.1. Recognition. A robust species with a folded septal flap, and a spiral wall with numerous interseptal pustules, but no or at most very rare pustules on the septa. The shell is much larger and thicker than in regular *O*. cf. *complanata*, with a diameter of up to 6 mm in A-forms, but approaching 3 cm in B-forms (Fig. 34). Large specimens are undulated and have a thickened central area. In large specimens pustules are restricted to the initial whorls. Septa are strongly, but gradually curving backwards. Angle of backward bent increases to 70–80° in the final whorl (A-form). Test surface is smooth, with the sutures and pustules not being expressed by thickness differences, but the marginal cord often appears to be thickened. This species has a more rapidly opening spire than *O*. cf. *complanata* and a larger proloculus (200–250 μm) in the A-forms. This species was reported as *O. bartschi* Cushman by Collins (1958), and as *Operculina* sp. 1 by Renema et al. (2013).

6.3.1.4.2. Geographic range. Only known from the outer shelf-slope of the Great Barrier Reef between Cooktown (Collins, 1958) and Townsville (Renema et al., 2013).

6.3.1.4.3. Habitat. Both records are from the lower part of the photic zone (50–70 m), with a preference for coarse stable, carbonate-sand substrates (Collins, 1958; Renema et al., 2013).

6.3.2. Genus *Heterostegina*

This genus is characterized by the presence of secondary chamberlets. There is a mature-evolute group (Banner and Hodgkinson, 1991) and an evolute group. The latter is sometimes referred to as *Planostegina*, but this name is not available as the type species is from the Miocene of Austria, and is part of a group that went extinct in the Middle Miocene.

6.3.2.1. *Heterostegina depressa* (Fig. 35)

6.3.2.1.1. Recognition. Medium-sized maturoevolute nummulitid with secondary chamberlets. The alar prolongations are not subdivided into secondary chamberlets (Fig. 35). Shallow-living specimens are smaller and thicker than deep-living specimens, but otherwise this is one of the, morphologically, least variable species of LBF.

6.3.2.1.2. Geographic range. Circumtropical species that roughly occurs between 30° N and 30° S. The southernmost record in the South Pacific Ocean is from Moreton Bay (southern Queensland; Palmieri, 1976; Narayan and Pandolfi, 2010) and in the Indian Ocean from Rottnest Island (Western Australia; James et al., 1999) and Mozambique (Langer and Hottinger, 2000). The northernmost records are from Tanegashima in southern Japan (Sugihara et al., 2006) and Midway Atoll (Weinmann et al., 2013b).

6.3.2.1.3. Habitat. *Heterostegina depressa* is a species that has a wide depth range, and is found in the middle part of the photic zone (Hohenegger, 2006). It has a preference for solid substrates (Hohenegger, 1994; Renema and Troelstra, 2001; Renema, 2006a, etc.), especially for those with open interstitial space and cover by coralline algae (Renema, 2008). Despite this wide depth range, suggesting that it has a wide tolerance to light levels, Nobes et al. (2008) found that photosynthetic yield is highest in low light levels. In shallow environments *Heterostegina depressa* shelters in the interstitial space between rubble, showing that it can position itself in optimal

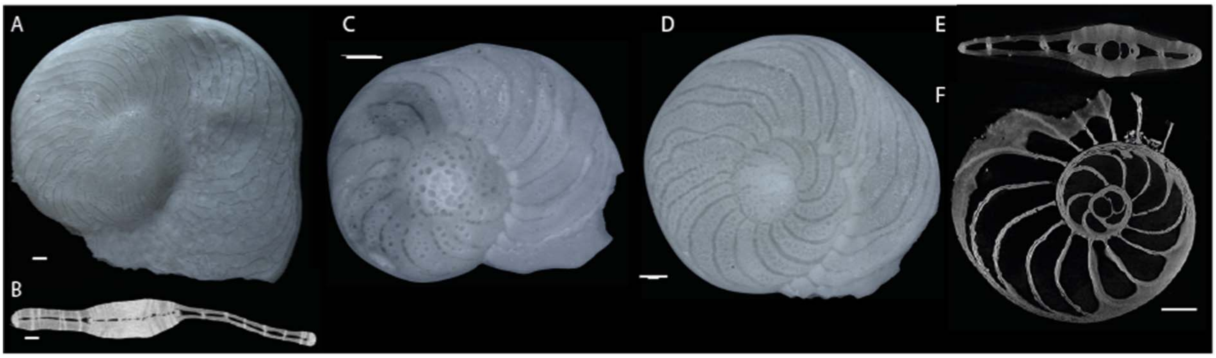

Fig. 34. *Operculina* sp. from Hydrographer's Passage (Queensland, Australia). A,B B-form, C–F A-form. Scale bar A, B 1 mm; C–F 500 μm.

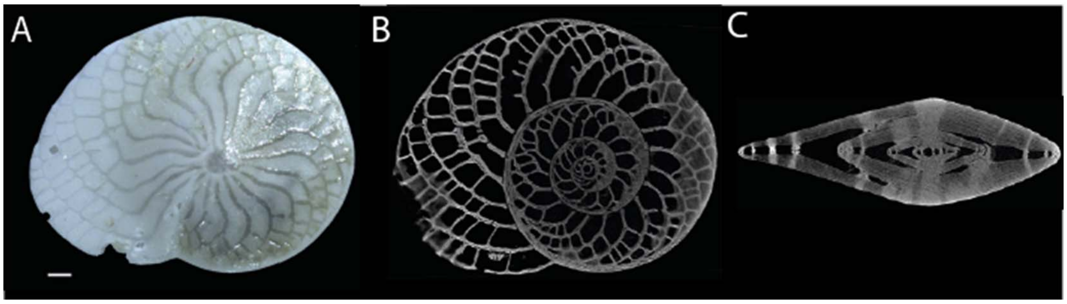

Fig. 35. *Heterostegina depressa*. Spermonde Archipelago (SW Sulawesi, Indonesia). A) external view; B) horizontal thin section; C) vertical thin section. Scale bar 200 µm.

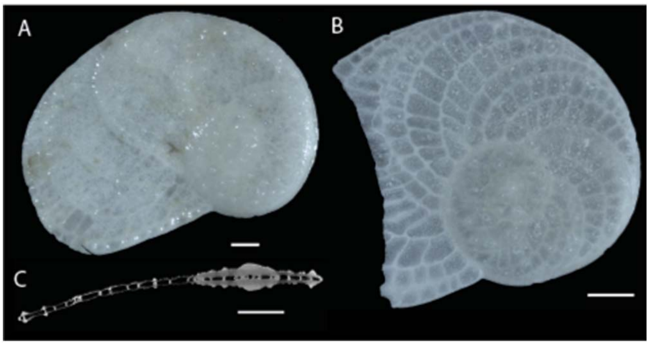

Fig. 36. *Heterostegina operculinoides*. Hydrographer's Passage (Queensland, Australia). A: external view of a thick specimen, B) external view of a thin specimen; C) vertical thin section. Scale bar 200 µm.

light conditions by finding shelter among the coral rubble. In deeper environments and on vertical reef-walls it is found on top of the rubble-water interface.

6.3.2.2. *Heterostegina operculinoides* (Fig. 36)

6.3.2.2.1. Recognition. An evolute *Heterostegina*. Very thin shell, with regularly spaced secondary chamberlets that are longer than wide. There is variation in the ornamentation from very thin with hardly any pustules, to heavy ornamentation with pustules.

6.3.2.2.2. Geographic range. *Heterostegina operculinoides* has been reported from all over the Indo-Pacific, from the Red Sea to Mauritius, and from New Caledonia to northern Japan (Langer and Hottinger, 2000).

6.3.2.2.3. Habitat. *Heterostegina operculinoides* prefers sandy substrates in the oligophotic zone. It is typical of the deepest assemblages where it co-occurs with *Cycloclypeus carpenteri* and *Amphistegina bicirculata* (Hohenegger et al., 2000; Renema, 2006b; Renema et al., 2013). It has a strong preference for (carbonate) sand substrates. Compared to other oligophotic species, *H. operculinoides* is more tolerant to turbid conditions, which is shown in a distribution over the outer shelf in front of river deltas, whereas species with a comparable light tolerance only occur on the shelf edge (Renema, 2006b; Fig. 5).

6.3.3. Genus *Cycloclypeus*

Cycloclypeus is the largest extant benthic foraminifera and is represented by a single extant species, *C. carpenteri*. The B-forms can grow to 10 cm in diameter, but most commonly do not grow beyond 5–6 cm diameter. The asexually derived A-forms usually do not grow larger than 1 cm in diameter.

6.3.3.1. *Cycloclypeus carpenteri* (Fig. 37)

6.3.3.1.1. Recognition. *Cycloclypeus* is an evolute heterosteginid with a relatively large embryonic apparatus (0.25–0.4 mm), 1 chamber without chamberlets and 2–3 (rarely 4) heterostegine chambers before the first annular chamber (Renema, 2015).

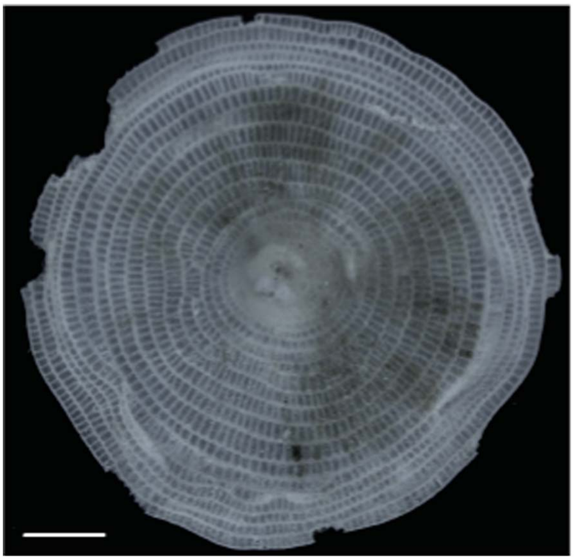

Fig. 37. *Cycloclypeus carpenteri*. Hydrographer's Passage (Queensland, Australia). Scale bar 1 mm.

6.3.3.1.2. Geographic range. *Cycloclypeus* occurs from East Kalimantan and SE Sulawesi north to southern Japan and south to the southern Great Barrier Reef and New Caledonia (Renema, 2015). It has furthermore been recorded from numerous western Pacific atolls and from the Maldives (Langer and Hottinger, 2000). However, *C. carpenteri* was not recorded in the Andaman and Java Seas, and Makassar Strait, despite intensive sampling in these areas.

6.3.3.1.3. Habitat. *Cycloclypeus* lives within the lower part of the photic zone (Hohenegger et al., 2000; Renema, 2006b; Renema et al., 2013). Koba (1977) found that its range encompassed those areas of the South China Sea within the photic zone, with year-round temperatures at the sediment-water interface higher than 20 °C, and below the storm wave-base. In East Kalimantan *C. carpenteri* occurred from 55 to 100 m water depth on the outer platform-slope (Renema, 2006b). In Japan it occurred in slightly deeper environments (Hohenegger et al., 2000). In the Great Barrier Reef *Cycloclypeus* is also abundant on the outer slope and occurs rarely inside the reef barrier (Tudhope and Scoffin, 1988; Renema et al., 2013). In Vanuatu *Cycloclypeus carpenteri* is abundant from 35 to 60 m water depth. Whereas in most areas *Cycloclypeus* is laying on top of coarse sand, in Vanuatu it occur on fine rubble covered by algae between which it is laying or sometimes found in a position at a low angle with the sediment-water interface. All brown coloration of the symbionts was concentrated in the part of the test that is standing out. With more and more data gathered by Remote Operated or Autonomous Underwater Vehicles (ROV and AUV), it becomes clear that *Cycloclypeus* can be as abundant on solid substrate as it is on sand. On both substrates it can occur in high densities on top of the substrate (e.g., Bridge et al., 2011).

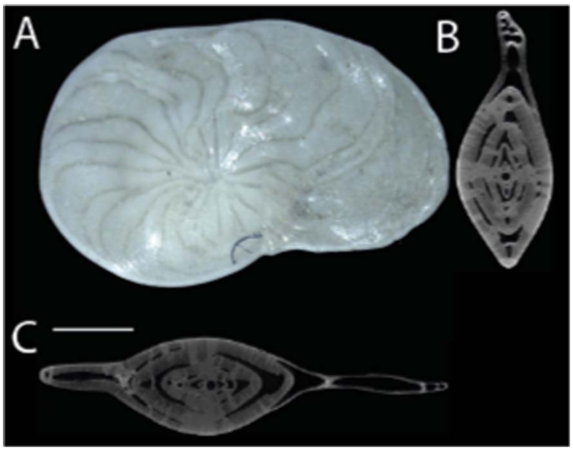

Fig. 38. *Operculinella cumingii*. Spermonde Archipelago (SW Sulawesi, Indonesia), all the same specimen. A: external view; B: vertical section over the short axis; C: vertical section over the long axis. Scale bar 1 mm.

6.3.4. Genus Operculinella

Involute nummulitid with a thin marginal cord and undivided chambers. Alar prolongations extend almost to the centre of the test. The apertural face shows a single slit-shaped basal aperture, with very few or no secondary apertures. Trabeculae, poreless bars caused by the presence of underlying secondary channels, are present. In later whorls the anterior septal flap is folded.

Up to the 1990s all extant involute nummulitids with undivided chambers were considered a single species (e.g., Hottinger, 1977b; Langer and Hottinger, 2000). Hohenegger et al. (2000), however, demonstrated that *N. venosus* and *O. cumingii* are separate species. The generic classification of the two species needs revision, but is maintained for the sake of stability. Because the trabeculae were overlooked in *O. cumingii*, in earlier publications (e.g., Hohenegger et al., 2000; Renema, 2006b), this is not a good character. In larger specimens of *O. cumingii* folded septal flaps develop on the septa, something that is not seen in *Nummulites*.

6.3.4.1. Operculinella cumingii (Fig. 38)

6.3.4.1.1. Recognition. Involute, tightly coiled in the initial whorls, opening up to lax in the last whorls. The chamber lumen is very high and of constant thickness, crescent shaped, and strongly curved backward. Width of the chambers varies considerably, as does the degree to which the chambers curve backwards. Damage repair is frequent, adding to the irregular appearance of the chamber shape. Alar prolongations are thick and extend at least 1/4–7/8 over the previous whorl. The longer the alar prolongation is, the stronger the chamber curves backwards. There is a tendency that narrow chambers have longer alar prolongations.

The proloculus of A-forms is small, 40–80 μm. There is a single, slit-shaped aperture in earlier chambers, with secondary apertures appearing from the 38–40th chamber onwards.

O. cumingii differs from *N. venosus* by its more flaring last whorl and the progressive decrease in length of the alar prolongations. The septa, especially in the flaring last whorl, are a bit irregular and covered by a folded septal flap. It is most easily distinguished from *N. venosus* by its higher angle of backward bend of the septa (Hohenegger et al., 2000), which increases progressively in *Operculinella cumingii*, and is fairly constant in *N. venosus*.

6.3.4.1.2. Geographic range. The taxonomic confusion makes it difficult to access the distribution of both *N. venosus* and *O. cumingii*. Confirmed records of *O. cumingii* are from southern Japan (e.g., Hohenegger et al., 2000) and central Indonesia (e.g., Renema, 2006b). It appears that this species is confined to a relatively small area from central Indonesia to southern Japan.

6.3.4.1.3. Habitat. *Operculinella cumingii* prefers soft substrates, specifically fine- to coarse-grained carbonate sand (Hohenegger et al., 2000; Renema, 2006b). It occurs in regions between 1.2 and 25% surface irradiation (Hohenegger et al., 2000). Furthermore, *O. cumingii* has a low tolerance for terrigenous material (Fig. 5), and was only found on the outer shelf-slope of the Berau carbonate shelf, where carbonate production by foraminifera outnumbers terrigenous sediment deposition (Renema, 2006b).

6.3.5. Genus Nummulites

Involute nummulitid with a thin marginal cord and undivided chambers. Alar prolongations extend almost to the centre of the test. The apertural face shows a single slit-shaped basal aperture, with very few or no secondary apertures. Trabeculae, poreless bars caused by the presence of underlying secondary channels, are present. The anterior septal flap is not folded. Future revision of the supra-specific classification of the nummulitids likely to place this species in a different genus, but for reasons of stability I opted to place this species in the genus *Nummulites* (following Hohenegger et al., 2000).

6.3.5.1. Nummulites venosus (Fig. 39)

6.3.5.1.1. Recognition. Lenticular, planispirally coiled test with radial septal traces that curve backward, but not as strongly as in *O. cumingii*. The test is tightly coiled, spire opening more rapidly in the last whorl of larger specimens. There is a small umbilical pillar. The alar prolongations are thick, and extend to the central pillars. In the more flaring (but never as strong as in *O. cumingii*) last chambers of larger specimens, the alar prolongations extend only partially over the previous whorl. There are 15–18 chambers in the last whorl. The proloculus size of A-forms is 100–150 μm.

6.3.5.1.2. Geographic range. As noted previously, the taxonomic confusion makes it difficult to determine the distribution of both *N. venosus* and *O. cumingii*. Confirmed records of *N. venosus* are available from the western shores of the North Pacific Ocean and Great Barrier Reef (Hohenegger et al., 2000; Renema and Troelstra, 2001; Renema, 2006b; Renema et al., 2013). Records of either *N. venosus* or *O cumingii*

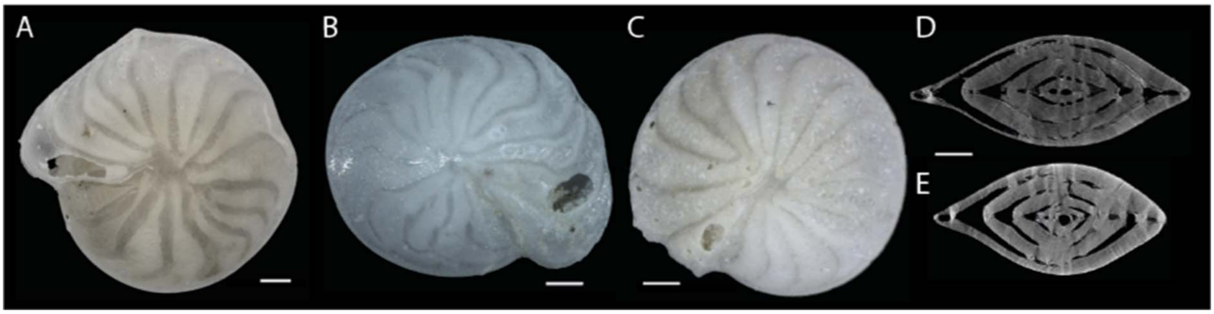

Fig. 39. *Nummulites venosus*. *A* Berau Shelf (East Kalimantan, Indonesia); B, D, E) Spermonde Archipelago; C) Hydrographer's Passage (Queensland, Australia). A–C external view, D and E vertical sections of the same specimen (perpendicular to each other). Scale bar 200 μm.

are available from many sites in between these localities (Langer and Hottinger, 2000).

6.3.5.1.3. Habitat. Most detailed information on habitat preference of *Nummulites venosus* is available from the western North Pacific Ocean (Hohenegger et al., 2000). It prefers coarse sand substrates (Hohenegger et al., 2000; Beavington-Penney and Racey, 2004) below the wave base (Hohenegger et al., 2000). Here it has a depth distribution from 15 to 85 m water depth with maximum occurrence at 35–60 m water depth (Hohenegger et al., 1999, 2000; Beavington-Penney and Racey, 2004). In Indonesia a much more restricted depth range was observed. In both the Spermonde Archipelago and Berau Shelf *N. venosus* was observed below wave base to a maximum water depth of 40–50 m. It has a medium tolerance for clastic sediment input, limiting its distribution to the outer part of the shelf (Fig. 5) (Renema and Troelstra, 2001; Renema, 2006b). It is rare at the outer shelf-margins in both areas (Renema and Troelstra, 2001; Renema, 2006b).

7. Anthropogenic challenges to LBF assemblages on coral reefs

Coastal zones are regionally affected by overfishing and pollution, and anthropogenic climate change is likely to exacerbate these effects globally (Hughes et al., 2017). Ocean warming and ocean acidification will exert increased pressure on tropical marine ecosystems, and coral reefs will in the future occur in new configurations (Hughes et al., 2017). Although not contributing to the three-dimensional reef structure, LBF are important carbonate producers, especially on the reef flat (Yamano et al., 2000; Fujita et al., 2009; Dawson et al., 2014), and in the inter-reef area and on deeper reef-slopes (Renema, 2006b). In the latter they have the capacity to alter physical properties of the environment (grain size, carbonate content). However, how will local and global environmental stressors affect LBF? So far, this has mostly been explored in experimental set-ups, including only a limited number of species, usually from shallow reef-slope environments.

Under lab-controlled conditions, populations of *Amphistegina lobifera* from reef sites located along a temperature and nutrient gradient of the northern Great Barrier Reef showed that populations collected from the inner-shelf sites (highest nutrient levels, largest temperature variation) were consistently able to acclimate to both parameters after 30 days (Prazeres et al., 2016b). In contrast, foraminifera collected from reef sites located in the mid- and outer-shelf zones were significantly more sensitive to elevated temperatures and nitrate (Prazeres et al., 2016b). Growth experiments, to the contrary, show reduced growth in higher-nutrient conditions, possibly due to release of symbionts in higher-nutrient environments (Uthicke and Altenrath, 2010). In-situ growth of two diatom-bearing benthic foraminiferal species (*Amphistegina radiata*, *Heterostegina depressa*) was significantly lower on inshore reefs compared to offshore reefs in the Great Barrier Reef (Uthicke and Altenrath, 2010). Increased concentrations of dissolved nitrogen were associated with reduced growth (Uthicke and Altenrath, 2010).

Transplanting dinoflagellate-bearing *Marginopora* into higher-nutrient conditions, as well as exposure to higher nutrient concentrations in an experimental set up, resulted in reduced growth rates (Reymond et al., 2013a). *Marginopora* is one of the taxa indicative of 'blue-water' conditions, and thus might be more sensitive to nutrients than diatom-bearing *Calcarina* or *Heterostegina*. The latter are the most tolerant species to higher nutrients in field conditions (e.g., Renema, 2006a, 2008), and no response to increased nutrient concentration was observed in experimental conditions (Schmidt et al., 2011).

Atmospheric carbon dioxide (CO_2) concentrations are nearly 40% above pre-industrial levels, and are likely to increase even further (IPCC, 2013). Uptake of atmospheric CO_2 in the surface ocean has reduced the pH (ocean acidification) and is expected to have negative impacts especially on calcifying organisms. Experimental studies using LBF give ambiguous results. Vogel and Uthicke (2012) found that, in diatom-bearing *Amphistegina radiata* and *Heterostegina depressa*, growth rates were not affected by decreased pH, whereas in the dinoflagellate-bearing *Marginopora* sp., calcification increased. In contrast, Fujita et al. (2011) found increased calcification rates in mildly decreased pH in diatom-bearing *Calcarina gaudichaudii* and *Baculogypsina sphaerulata*, before calcification rates decreased at the lowest pH levels, and that dinoflagellate-bearing *Amphisorus* decreased calcification in all decreased pH settings. The latter was also found in the dinoflagellate-bearing *Marginopora* from the GBR, where increased nutrients amplified this effect (Reymond et al., 2013a). In a meta-analysis Doo et al. (2014) concluded that, in porcellaneous, dinoflagellate-bearing foraminifera, calcification decreased with decreasing pH, while hyalineous, diatom-bearing species either show no effect or increased calcification rates with decreased pH.

The effect of ocean warming has been demonstrated to result in bleaching in at least some species (e.g., Talge and Hallock, 2003; Schmidt et al., 2011). The genus *Amphistegina* is especially sensitive to bleaching, which shows as light colouration and mottling of the test, rather than becoming totally white. Consequently, experimental studies involving exposure to higher temperatures have largely targeted the effect on, and efficiency of the photosymbiotic system, and also have produced widely different results. Depending on the study LBF were found to be sensitive to ocean warming (e.g., Schmidt et al., 2011; Webster et al., 2016) or able to acclimate to increased seawater temperatures (e.g., Prazeres et al., 2017; Titelboim et al., 2016).

Most of these studies, however, report additive effects when two stressors are combined (e.g., Doo et al., 2014, and references therein; Webster et al., 2016; Prazeres et al., 2017). Furthermore, opposing results, sometimes even within the same taxon, but especially between the two main groups of LBF, highlight the complexity of these environmental responses. Generally speaking it appears that the diatom-bearing hyaline LBF are better able to accommodate the tested environmental changes than the dinoflagellate-bearing porcellaneous groups. Thus, those groups that are most similar to corals also show the most similar response to environmental change. The groups that are the most prolific carbonate producers (Amphisteginidae, Nummulitidae, and Calcarinidae) are least affected by the environmental parameters that have been tested.

The response to environmental change on coral reefs, however, is only partly a response to gradually changing conditions, to which LBF are more sensitive than reef corals (Hallock et al., 2003). Superimposed on this gradual change, abrupt changes in benthic habitat will also be reflected in the LBF composition (Renema, 2010). LBF are especially sensitive to (changes in) substrate type (Reiss and Hottinger, 1984; Hohenegger, 1994; Renema, 2006a, 2008), and changes in the benthic habitat structure are associated with changes in available substrate, and, hence, LBF assemblage composition (Fig. 40; Renema, 2010). Changes in the benthic habitat structure of reefs in response to ocean warming, ocean acidification, and nutrification (Hughes et al., 2017) might have a much larger effect on the community composition of LBF than the sensitivity of individual taxa to environmental change (Fig. 40).

8. The use of LBF as environmental indicators?

In 2003 Hallock et al. introduced the FoRAM index (FI) which relies on the weighted contribution of LBF to the total benthic foraminiferal assemblage to indicate water quality. This is an easy to use tool to gain insight into the water quality of reefal areas (Hallock et al., 2003). The FI has been widely applied in reef settings in the Caribbean, where it was originally defined, the Indo-Pacific (e.g., Schueth and Frank, 2008; Narayan and Pandolfi, 2010; Reymond et al., 2013b; Pisapia et al., 2017), and the Mediterranean (e.g., Koukousioura et al., 2011). The method was described in detail, including a sampling and sample processing protocol, based on reference sets from the Florida Keys in the western Atlantic bioprovince (Hallock et al., 2003). Evaluation of the results in FI studies is hampered in part by non-standardised application

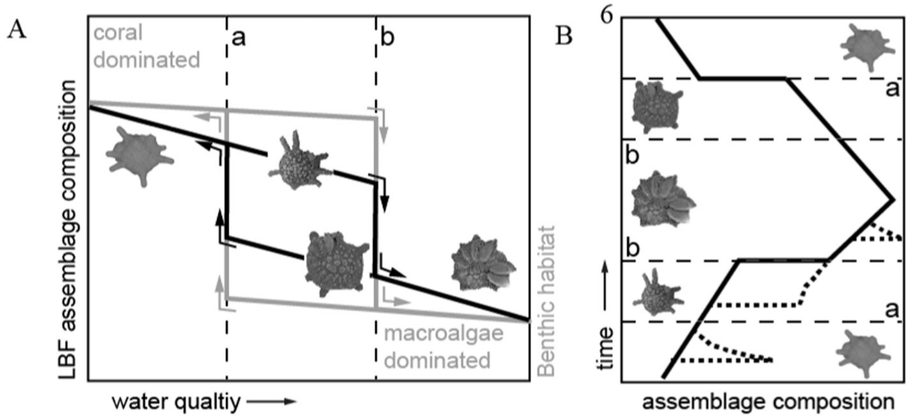

Fig. 40. Hypothetical model demonstrating the interplay between water quality, the benthic habitat, and LBF assemblage composition on the reef slope. A) Benthic habitat responds non-linearly to water quality change, and changes abruptly from coral dominated to algal dominated at threshold b, or at a disturbance event between thresholds a and b. Due to the hysteresis effect (Done, 1992; Hughes, 1994) the reverse happens at threshold a, or when there is a disturbance between threshold a and b. Benthic foraminifera have shorter generation times, and respond more directly to changes in water quality. However, changes in the benthic habitat also have a large impact on assemblage composition, and even though the LBF themselves do not display any thresholds in response, the thresholds in the benthic habitat are reflected in the assemblage composition of the LBF. B) Temporal change in the LBF assemblage, the black line matches the black line in A), whereas hatched lines represent the response to disturbance events.

(e.g., using different mesh sizes when sieving; Narayan and Pandolfi, 2010), and sampling on different parts of the reef (Schueth and Frank, 2008), yet maintaining the same cut-off values. However, also some methodological issues arise when applying the FI in different regions of the Indo-Pacific. As shown above (Fig. 40) benthic foraminifera assemblages not only respond to changes in water quality, but are also dependent on the benthic habitat structure. The way the FI is calculated does not reflect replacements in the LBF assemblage of species characteristic for high coral-cover reefs, or by species that prefer macro- or turf algae. Hallock (2012) already remarked on the unique occurrence of calcarinids in reefal LBF communities in the Indo-Pacific.

In the IWP calcarinids are important in the environmental quality discussion. The *Calcarina-Amphistegina* ratio is a candidate for an easy to calculate index. Replacement of *Amphistegina lobifera* by *Neorotalia gaimardi* and *C. hispida* was observed on reef flats, and associated with a change of dominant benthic cover from corals to algae (Renema, 2010). Furthermore, in sediment cores taken on the reef slope in the Great Barrier Reef, higher percentages of *Calcarina* spp. were observed in locations nearer to the shore (Reymond et al., 2013b). The disadvantage of this ratio, however, is that some understanding of the local community is needed. For example, in Indonesia *Calcarina gaudichaudii* is abundant on blue-water reefs and *Calcarina spengleri* replaces *C. mayori* on the reef slope when the substrate is dominated by rubble and crustose coralline algae. On the Great Barrier Reef, *C. capricornia* can be extremely abundant side-by-side with *Amphistegina lobifera* on mid-shelf and outer-shelf reefs (Lobegeier, 2002; Prazeres et al., 2016a). At such sites the *Calcarina/Amphistegina* ratio will be high, even though conditions are sufficient for coral growth. In contrast, also in nearshore environments, the *Calcarina/Amphistegina* ratio on the reef flat will be high, but these environments include the species *Neoritalia gaimardi*, *Calcarina defrancei* and sometimes *C. hispida* or *C. mayori*.

Depth gradients are related to light intensity, and in reef types were the benthic substratum is shaded by the presence of macro-algae, deeper-living taxa can be found in shallower habitats (Renema, 2010). The most distinct contrast in these conditions is between *C. spengleri* and *C. mayori*. The first species prefers rubble covered by crustaceous coralline algae, whereas *C. mayori* occurs in highest density on reefs with turf and macro-algae (Renema, 2010). Otherwise these species have very similar depth distributions. In Indonesia to southern Japan the *C. mayori*/*C. spengleri*-ratio could potentially be used as an indicator for the amount of macro-algae on the reef within the distribution range of *C. spengleri*.

9. Conclusions

The overall structure of LBF assemblages is roughly comparable over the Indo-Pacific, with the exception of the eastern tropical Pacific. In all reef systems there is separation between reef-flat, reef-slope, and reef-base/inter-reef assemblages. Of these the reef-slope assemblage is least diverse and least differentiated along environmental and geographical gradients. Diversity differences between areas arise to a large extent from differences in reef-flat to reef-crest environments, and the deep inter-reef and reef-base environments. The benthic habitat is in all areas the dominant driver in local LBF assemblage composition. This can be deconstructed into at least three, interrelated, components: substrate type, water quality, and sediment stress. These are not mutually exclusive. For example, both higher nutrient availability and sediment stress result in a higher abundance of certain groups of calcarinids.

In all studied shelf systems, there is a strong nearshore-offshore differentiation in LBF assemblage composition, especially in the inter-reef assemblages. LBF diversity increases either stepwise (Trophic Resource Continuum model, Hallock, 1988; Renema and Troelstra, 2001), or linearly (Hohenegger et al., 1999) with distance from shore and thus with decreased light attenuation. The largest turnover in assemblage composition was observed between the nearshore, where symbiont-bearing foraminifera are not present on the reef base, and the mid-shelf zones. In the former the benthic assemblage is dominated by benthic foraminifera with chloroplast husbandry or that are not light dependent (Renema and Troelstra, 2001; Renema, 2006b). In the mid-shelf to barrier zone, the inter-reef benthic foraminifera assemblage is dominated by nummulitids (especially *Operculina*), and *Amphistegina*. With increasing distance from shore, taxa that are less tolerant to terrestrial influence appear in the LBF assemblage. I argue that there are two groups of deep-living taxa, those tolerating terrestrial influence (e.g., *Operculina complanata*, *Heterostegina operculinoides*), and those that only occur in areas that are not subject to terrestrial influence (e.g., *Cycloclypeus*).

In the shallow parts of the reef, nearshore-offshore gradients are more complex. The largest faunal break is on the outer shelf, where a distinct assemblage is characteristic for blue-water reefs. On their reef flat, the calcarinids, *Calcarina gaudichaudii*, *C. hispida*, *C. capricornia*, and *Baculogypsina sphaerulata* are especially abundant. In brown water reefs these taxa are typically rare to absent. On the reef flat of nearshore and shelf reefs *Amphistegina lobifera* is the most abundant taxon when the substrate is dominated by rubble or rubble with sand. *Calcarina spengleri*, *Amphistegina radiata* and *Heterostegina depressa* are important species on the reef slope on rubble. As soon as turf or macro-algae become more abundant *Neorotalia gaimardi* (on the reef flat) and *Calcarina mayori* and *Baculogypsinoides spinosus* (on the reef slope) become the most important taxa (Renema, 2010; Reymond et al., 2013a). This sensitivity to the condition of the benthic habitat can result in temporary or permanent changes in the LBF assemblage composition as the result of disturbances in coral-reef environments (Fig. 40).

In conclusion, yes, there is great potential in the use of symbiont-bearing foraminifera assemblage composition. Perhaps even more so than previously thought, given the prior bias to reefal environments and the very poor representation of reef-base and inter-reef studies. The context of the sampling should be very clear though, and reference should be made to local conditions.

10. Future directions of LBF research

- *Resolve taxonomic uncertainty*. Comparison between regions depends on a solid taxonomical framework consisting of well-defined species. A better understanding of ecophenotypical, morphological, and molecular phylogenetic variation within, and between species is needed to improve the power of LBF-based environmental assessments in the past and present. At the moment both improved morphological methods (e.g., microCT-scanning), and the more frequent use of genetic approaches providing an independent test for the description of morphospecies results in a better assessment of phenotypic variation in LBF species. In each of the major groups discussed in this paper, the Amphisteginidae, Calcarinidae, and Nummulitidae, most species display both extensive ecophenotypic and geographic variation. Only by integrating detailed morphological descriptions along environmental gradients, and replicated over their range, will it be possible to obtain an objective insight into LBF distribution, environmental tolerance, and potential changes in the future distribution of species.
- *Improve understanding of deep-living species, especially in inter-reef areas.* How reef-base and inter-reef species will respond to changes in environmental parameters is largely unstudied, even though these contribute the largest proportion of LBF biomass, and substantially to reef system carbonate production. Surprisingly few data are available on these habitats and how environmental change may affect them.
- *Gain better insights into the role of the prokaryotic and eukaryotic endobionts in the adaptive potential of LBF.* Some experimental studies have addressed composition and role in calcification and metabolism of endosymbiotic eukaryotes in LBF (Lee and Anderson, 1991; Pawlowski et al., 2001a, 2001b; Lee, 2006). Even less is known about the prokaryotic endobionts in LBF. Bourne et al. (2013) found that LBF were host to the most diverse endobiotic prokaryote community among photosymbiotic organisms. Webster et al. (2016) found that the endosymbiotic community of LBF was most sensitive to decreased pH and warming. However, because the function of these endobionts is poorly understood, it is impossible to know whether this means that LBF will be the first to disappear as the result of global change (as suggested by Webster et al., 2016), or that they have the highest adaptive potential. Indications for the past are no guarantee for the future, but during past greenhouse climates, for example during the Paleogene, characterized by warmer climates (Pearson et al., 2001) and higher atmospheric CO_2 concentrations (Anagnostou et al., 2016) than at present, LBF were the dominant component in tropical carbonates (e.g., Wilson and Rosen, 1998; Pomar et al., 2012).
- *Standardise sampling and processing methods to increase comparability between studies*. LBF assemblage composition has a large potential to develop into an easy to use tool in environmental assessments (Hallock et al., 2003; Hallock, 2012). However, because of regional differences in the species pool, and the non-standardised application of the method, for example with respect to sieve fractions included, comparability between studies is limited. Further investigation into the indirect non-linear response as a result of changes in the benthic habitat (Fig. 40), should reveal how this influences FI. Potentially other indices, such as the *Calcarina hispida/Amphistegina* ratio, or the *Calcarina mayori/C. spengleri* ratio might be regionally useful as well.

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