VRIJE UNIVERSITEIT

LARGER FORAMINFERA AS MARINE ENVIRONMENTAL INDICATORS

ACADEMISCH PROEFSCHRIFT

ter verkrijging van de graad van doctor aan
de Vrije Universiteit Amsterdam,
op gezag van de rector magnificus
prof. dr. T. Sminia,
in het openbaar te verdedigen
ten overstaan van de promotiecommissie
van de faculteit der Aard- en Levenswetenschappen
op maandag 9 december 2002 om 10.45 uur
in het auditorium van de universiteit,
De Boelelaan 1105

door

WILLEM RENEMA

geboren te Apeldoorn

Promotor: prof.dr. J.E. van Hinte
Copromotor: dr. S.R. Troelstra
dr. C.F. Winkler Prins

Larger foraminifera as marine environmental indicators

Willem Renema

Renema, W. Larger foraminifera as marine environmental indicators. — Scripta Geol., 124: 1-260, 114 figs., 13 pls; Leiden, November 2002.

Willem Renema, Nationaal Natuurhistorisch Museum, PO Box 9517, 2300 RA Leiden, The Netherlands; Renema@naturalis.nl

Key words — Foraminifera, Spermonde Shelf, Sulawesi, Cabilao, Philippines, Recent, Palaeogene, diversity.

Contents

1. General introduction and abstract

"Larger benthic foraminifera" are large, single celled organisms living under similar conditions as zooxanthellate corals, in shalllow tropical seas. Just like other reef associated taxa the diversity of larger benthic foraminfera is highest in the border region between the Pacific and Indian Ocean, the Indo-West Pacific (IWP).

Since foraminifera have calcareous tests and occur in huge numbers, they fossilise easily. Other taxa on which stratigraphical schemes have been built, e.g., planktonic foraminifera and nannoplankton, are not as abundant in tropical shallow marine carbonates and in these settings larger foraminfera have been used for stratigraphical purposes.

The Recent distribution of larger foraminifera has mainly been studied in pristine areas with a deep photic zone. Distribution of larger foraminfera in such areas probably differs from those on mesotrophic carbonate shelfs. The latter are also more likely to preserve and dominate carbonate production during the Cenozoic in tropical southeast Asia (Wilson, 2002).

The present thesis aims at:

- Describing the Recent distribution over various reefs and carbonate platform.
- Identifying the most important parameters that determine the occurrence of species of larger benthic foraminifera.
- Determining whether the distribution of empty tests of larger benthic foraminifera reflects the distribution of the living protists, and determining whether the occurrence of larger benthic foraminifera can be used for palaeoenvironmental analysis.
- Use these models to interpret the fossil record.

Two main groups of foraminifera, differing in test structure, house symbionts, lamellar perforate foraminifera and imperforates. Hyaline shells have a higher transparency because the calcite crystals have their longest crystallographic axis perpendicular to the outer test wall. Transparency of the test is much lower in imperforate foraminifera, in which the crystals are randomly oriented with an outerlayer with the crystal axis parallel to the outer test wall (Haynes, 1965, 1981; Hallock, 1999). In order to profit from photosynthesising endosymbionts, the symbionts need to be irradiated through the test wall.

In this introduction I will first give a summary of the parameters determining larger benthic foraminiferal distribution over reefs and carbonate platforms and their strategies to cope with these conditions. The second part of the introduction comprises of a brief summary of the chapters.

The material is deposited in the National Museum of Natural History (Leiden, The Netherlands) with registration numbers prefixed RGM.

Parameters

The distribution of larger benthic symbiont-bearing foraminifera is determined by a complex set of often inter-related parameters Fig. 1.1 summarises these parameters and the way they interact with foraminifera.

Two parameters limit the geographical distribution of larger benthic foraminifera occurrence, these are temperature and nutrient availability, of which the latter is affected by the first. Housing symbionts is only profitable in conditions where organic matter is concentrated in particles (Hallock, 1981c). The host collects and digests particulate organic matter, and the symbiont feeds on the waste product of the host. Excess energy produced by the symbiont is again used by the host (Hallock, 1981c). Laboratory experiments show that 10-90% of the energy of larger symbiont-bearing foraminifera is provided by the symbionts (ter Kuile, 1991).

The role of photosynthesis in calcification is not clear. Ter Kuile (1991) holds that photosynthesis consumes CO_2, producing CO_3^{2-} and thus enhances calcification.

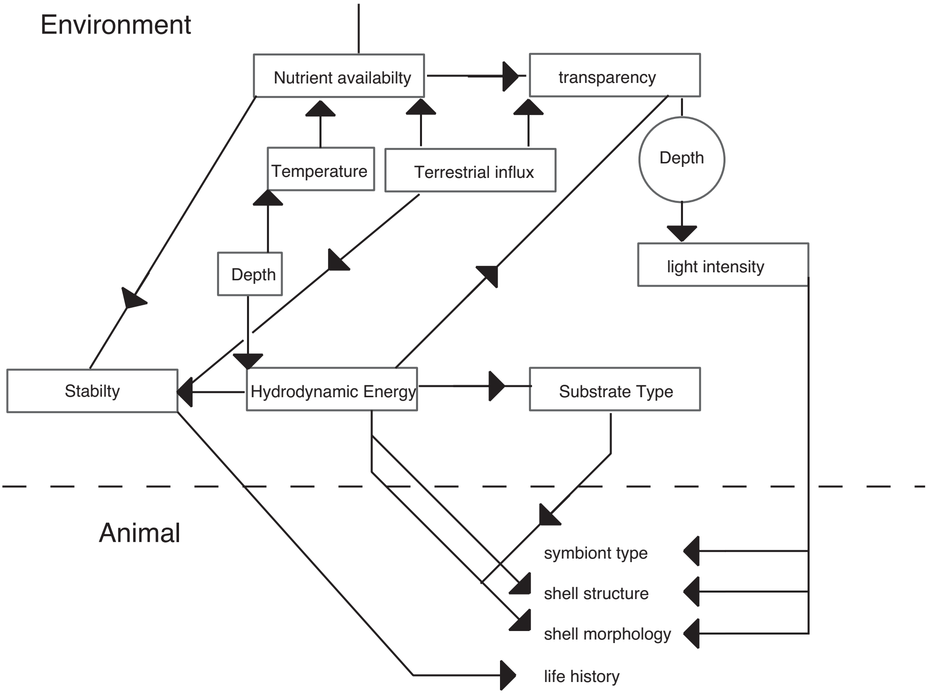


Fig. 1.1. Schematic representation of the environmentalparameters influencing the distribution of larger foraminifera and properties of the foraminfera to deal with these conditions.

McConnaughley (1989) and McConaughley & Whelan (1997) have proposed the reverse interpretation, though. They postulate that lack of CO_2 limits photosynthesis in warm, shallow aquatic environments and that calcification provides protons that make CO_2 readily available (Hallock, 2001).

Carbon cycling in perforate foraminifera supplies 10% of the carbonate incorporated in the skeleton, while feeding is mainly used as a source for nutrients (ter Kuile *et al.*, 1987; ter Kuile & Erez, 1987; ter Kuile, 1991). In imperforate foraminifera the carbon uptake for calcification and photosynthesis occurs in two separate flows, and thus one does not affect the other (ter Kuile, 1991). The dependence on light for their symbionts limits larger benthic foraminifera to the photic zone.

In warm water, the metabolic rate of larger foraminifera is higher than in cool water. In invertebrates metabolic rate doubles with a 10 degrees increase in temperature. Thus it is more likely to find sufficiently oligotrophic conditions in tropical than in temperate seas. Larger symbiont-bearing foraminifera are restricted to a climatic belt limited by the 16°C isotherm in the coldest month (Langer & Hottinger, 2000).

In most studies on the distribution of larger foraminifera depth is the most important directly measurable environmental parameter. However, depth only affects the distribution of foraminifera indirectly (Fig. 1.1). At first, light intensity decreases with depth dependent on the transparency of the water column. Transparency in its turn is influenced by nutrient availability and terrestrial influx. In areas with high terrestrial influx, transparency will be lower because of the higher concentration of both inorganic and organic particles. The nutrients discharged over the coastal zone increase the abundance of planktonic organism, thus decreasing transparency.

Furthermore, both temperature and hydrodynamic energy decrease with depth. So far, the geographic distribution has mainly been studied in relation to sea surface temperature (SST). Hollaus & Hottinger (1997) interpreted the truncation of the occurrence of *Amphistegina lessonii* as due to temperature requirements of the symbionts.

Hydrodynamic energy both directly and indirectly affects the occurrence of larger foraminifera (Fig. 1.1). In areas with continuous battering of high waves or strong currents, larger benthic foraminifera are swept away or broken into pieces. In soft sediment areas, waves disturb the sediment too often, so that foraminifera are not able to stay on top of the sediment 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 *Palaeonummulites 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.

Strategies

Larger benthic foraminifera have several ways to deal with the environmental conditions. Since larger benthic foraminifera are a polyphyletic group, there is a wide variety in shell structure and morpholgy. The occurrence of several types of symbionts in taxa further affects the distribution of species. Imperforate foraminifera are generally restricted to shallower depth than perforate (Hottinger, 2000). Furthermore, in 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).

There are four main types of endosymbionts recorded in larger foraminifera. Each of them is found in a limited set of taxa which usually houses only one type of symbiont. The perforate nummulitids, amphisteginids and calcarinids and the imperforate alveolinids all house diatoms. Peneroplids house rhodophytic algae, most soritids have dinoflagellate symbionts and *Parasorites* and *Laevipeneroplis* house chlorophytes. Because each symbiont type uses its own range of the light spectrum, the foraminifera hosts are restricted in their depth distribution. Chlorophytes (using orange light) are restricted to the shallowest areas, diatoms and dinoflagellates can live in the deepest settings. For example, the chlorophyte *Fragilaria shiloi* was rarely isolated from hosts collected at more than 25 m depth (Lee & Anderson, 1991). 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 & Anderson, 1991). The symbionts were also depth limited. By hosting different species of endosymbiont, a larger foraminifera species can occur in a large depth range and still optimally profit from its symbionts.

Both within and between species test shape varies in response to environmental parameters. Test shape is a compromise between hydrodynamic energy resistance and light and metabolic requirements (Haynes, 1965; Hallock *et al.*, 1991b). In shallow water irradiation levels are too 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 or by thickening of the test wall. 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, 1997; 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 a foraminifera should not break and not be swept away or 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 protoplasm sheath (*Heterostegina depressa*), pseudoplasm plugs at the end of spines (calcarinids) or changes in morphology of the apertural faces (amphisteginids).

The Spermonde Archipelago

In Chapters 2 and 3 the occurrence of larger benthic foraminifera at the Spermonde Shelf is described. The Spermonde Shelf is a mesotrophic carbonate shelf, with considerable terrestrial influence because of run-off of the river Jene Berang in the south of the area. Water depth increases offshore untill the barrier at the edge with the Makassar Strait. Sand cay reefs occur all over the shelf (Fig. 2.1). Twenty species of larger foraminfera were found in the living fauna, occurring in six assemblages. One of these assemblages was geographically limited to the most nearshore area, while the others occurred in all other zones, but at increasing depth going offshore. In the reefbase assemblage more species were present in the outershelf zone. This pattern was explained by including, next to nutrient availability and irradiation level, environmental variability cq. predictability as an important parameter determining the occurrence of larger benthics at the Spermonde Shelf.

Chapter 4 compares the occurrence of living larger benthics with the distribution of empty tests in the sediment. In general, the distribution of dead tests and living foraminifera is similar. Foraminifera living at the reef base (and especially members of the Nummulitidae) have a higher preservation potential and their distribution over the shelf fits the models best. The empty tests of solid substrate dwelling species have been found only in samples taken on the reef itself. The distinction between leeward and exposed assemblages as found in the living assemblages was obscured because species living at the exposed slope are transported to the leeward slope after death.

In Chapter 5 the distribution on a reef in the Phillipines (Cabilao, near Bohol and Cebu) is described and compared with the Spermonde Archipelago. The reefs around Cabilao are markedly different from the reefs at the Spermonde Shelf. Some habitats, such as unlithified sediment below the fair weather wavebase are (almost) absent or limited in extend. Other habitats, such as sheltered reef flats with macroalgae were abundant at Cabilao, but have not been found at the spermonde Archipelago. Apart from many similarities, there are some marked differences in the larger foraminiferal fauna. For example, at Cabilao the highest density was found at the reef flat, whilst at the Spermonde Shelf the reef flat was usually barren and the highest densities were found at the reef base. The reef base assemblage found in the Spermonde, was totally absent. Also, for example, the distribution of *Calcarina spengleri* shows that a different combination of environmental parameters can result in a shift in habitat of a species.

The fossil record

The second part deals with fossil settings. The genus *Nummulites* has been studied intensively in the former Tethys Ocean west of the Arabic peninsula. Allthough many species in this genus have been described from Indonesia, the last overview of occurrences of *Nummulites* in Indonesia was published in 1932 (Doornink, 1932) and dealt only with Java. New insights in taxonomy, stratigraphy and accurate descriptions of European occurrences of simple chambered nummulitids made it possible to make a revision of the genera *Nummulites, Palaeonummulites, Assilina* and *Pseudocamerinoides* in Indonesia.

Of over 70 species have been placed in these genera 16 are considered valid. Taxa previously recorded as *Assilina orientalis, A. leymeriei, A. granulosa, A. spira, A. exponens* and *A. umbilicata* are reassigned to *Planocamerinoides* whilst *Nummulites taballarenis, N. pengaronensis, N. beaumonti, N. crasseornatus* and *N. variolarius* are reclassified to *Palaeonummulites.* Six species of *Nummulites*, three of *Planocamerinoides* and seven of *Palaeonummulites*, including two new taxa, *Palaeonummulites* nov. spec., and *Nummulites* nov. spec. are described and illustrated from Eocene-Oligocene strata of the Indonesian Archipelago.

Biogeographic implications of these changes are that previous records of the genera *Assilina* and *Ranikothalia* turned out to be erroneous and that the genera *Nummulites, Palaeonummulites* and *Pseudocamerinoides* are much less speciose than elsewhere in the Tethys Ocean.

This notion was built upon in Chapter 7, in which the diversity in southeast Asia was compared to that in Europe, north Africa and Oman. These regions were chosen since revisions of the above mentioned genera were available for these regions (Schaub, 1981; Racey, 1995). Both species number as morphologic diversity turned out ot be much lower in southeast Asia than any of the other regions. Similar patterns were found in other Eocene groups, such as *Alveolina* and orthophragminids.

This was further documented by comparing the generic diversity of Cenozoic larger benthic foraminifera between Europe and Southeast Asia. The generic diversity was in accordance with the previously described pattern: during the Eocene diversity was low in Southeast Asia and much higher in Eurpe. Diversity in the Indo-Malayan region steadily increased from the end of the Eocene onwards. The Eocene-Oligocene boundary shows an increased turnover of larger benthic foraminifera in Southeast Asia, with a net increase in the number of genera during the Oligocene. Followed by a rapid decrease from the Early Miocene onward in Europe, and from the Middle Miocene onward in the Indo-Malaysian region.

However in Europe, net extinction occurred at the Eocene-Oligocene boundary and was followed by a steady decrease in genus number during the Oligocene to Miocene. The larger foraminiferal data support those shown by corals, but also show that diversity steadily increased from the Eocene onwards in the Indo-Malayan region. The combination of low diversity and relatively little morphological variation suggests that environmental conditions were not optimal for larger foraminifera.

In the final chapter, all results are combined and are used to correlate patterns as seen in the fossil record with known tectonic, oceanographic and climatologic events. From this it can beconcluded that:

Distribution patterns of larger foraminifera show that diversity and distribution is limited by an interplay of temperature and nutrient availability, fine tuned by sealevel fluctuations. The Eocene-Oligocene faunal turnover can mainly be attributed to oceanographical/climatological related changes (SST, nutrient availability), while with the extinction of the Miocene faunas tectonics related factors (availability of shallow marine habitat and increased terrestrial run off) play a more important role.

The faunal turnover around the Eocene-Oligocene boundary was driven by an increased fertility of surface waters, increased upwelling rates and increased transport of terrestrial dust into surface waters. Both upwelling and the input of wind-blown terrestrial dust have a pronounced seasonal component, resulting in a more variable system, thus limiting the opportunities for K-selected species.

Cenozoic larger foraminifera faunas can be divided into three periods of high diversity, characterized by increased adult dimorphism. The time interval in which these three faunas occur differ between the west and east Tethys. The increase in adult dimorphism and species diversity occurred more than 10 million years earlier (in the Palaeocene) in Europe than in Indonesia. The extinction of the Late Oligocene-Early Miocene fauna happened later in Indonesia than in Europe and the Recent fauna is not present at all in Europe (Fig. 8.5).

In the Eocene, the Indonesian fauna was characterised by immigration of genera from the west, that sometimes locally evolved into new species, but hardly any lineages of species are recognisable.

The opening of the Makassar Strait, starting in the middle Lutetian, was an important event for the evolution of a diverse shallow marine fauna in the Indo-Malayan region. From this time large shallow marine environments away from upwelling zones became available for colonisation, thus increasing the potential habitat for larger foraminifera.

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

Willem Renema & Bert W. Hoeksema, Nationaal Natuurhistorisch Museum, PO Box 9517, 2300 RA Leiden, The Netherlands; Jan E. van Hinte, De Laraissestraat 78-I, 1071 PH Amsterdam, The Netherlands.

Previously published as:
Renema, W., Hoeksema, B.W. & Hinte, J.E. van, 2001. Larger benthic foraminifera and their distribution patterns on the Spermonde shelf, South Sulawesi. *Zoologische Verhandelingen Leiden* **334**: 115-149.

Introduction

During most of the Cenozoic, larger benthic foraminifera contributed much to the carbonate production on tropical shelves (Hallock, 1981b; 1997). At the Great Barrier

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

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

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

Larger foraminifera can regulate the amount of light reaching their symbionts in two ways, finding shelter in shaded areas (for example between sea grass or macroalgae leaves) or by moving their symbionts inside the shell away from the light. The latter method requires a dark non reflecting surface, such as rubble covered by algae or sea grass leaves (Hottinger, 1997).

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

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

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

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

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

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

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

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

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

Area

The Spermonde Archipelago is situated on a shallow carbonate shelf bordered in the east by the south-western peninsula of Sulawesi and in the west by the Makassar Strait. The shelf is approximately 40 km wide and increases gradually in depth until a maximum depth of about 60 m is reached just before the discontinuous barrier (Fig. 2.1). Cay-crowned reefs and shoals occur in rows parallel to the coast. In the outershelf area these reefs remain submerged and do not develop cays. Cay crowned reefs develop in seas with high hydrodynamic energy. Reef debris is swept on the reef flat, usually forming shingle ramparts, bordering a shallow reef flat at the exposed side, and an island on the leeward side (Guilcher, 1988). The reef flat in between the coral rubble rampart and island usually is very shallow (not more than 0.5 m at low tide). The reef flanks at the windward side are covered with dense coral growth, while the leeward reef slope consists of a sandy slope (Fig. 2.2).

At the Spermonde Archipelago, the shape of the reefs is determined by a monsoon

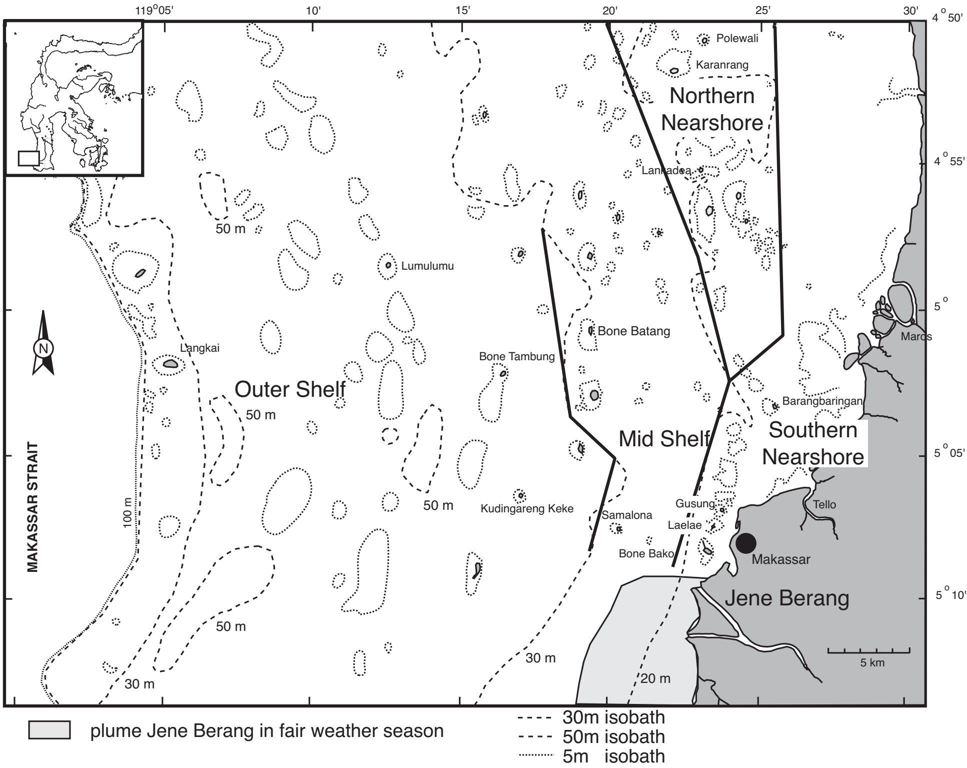


Fig. 2.1. Map of the research area showing all islands that have been visited during this study. Zone 1a: Southern Near Shore, 1b: Northern Near Shore; 2: Mid Shelf; 3+4: Outer Shelf

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

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

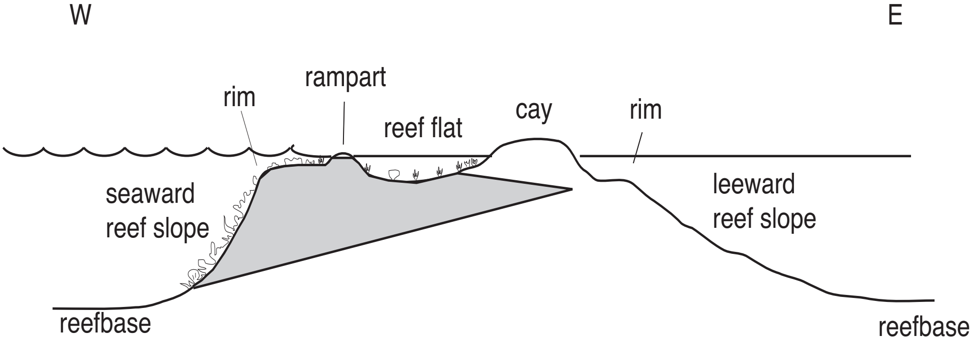


Fig. 2.2. Schematic section through a typical sand cay reef as found in the Spermonde Archipelago. Elements used in the text are indicated. Scale differs for each island and area. Grey area is a projection of the coral cover on the northern and southern side of the reef. The coral cover reaches till about 24 m depth in the Outer Shelf Zone, but only till 6 m dept in the Southern Nearshore Zone.

nutrient levels that do not vary throughout the year (Erftemeijer, 1993).

Further than four kilometres offshore, the sediments contains 75-85% carbonate, increasing to 85-95% around the barrier (Verheij, 1993). Secchi depth increases going off shore, reaching its maximum value (30 m) during the dry season around Langkai, on the barrier reef at the shelf margin (Erftemeijer, 1993). During the wet season high turbidity and terrigenous input decreases light penetration, with secchi depth half those of the in dry season (Verheij, 1993).

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

On the basis of geography, geomorphology and distance to the shore, the Spermonde was divided into four shelf zones (van Vuuren, 1920). These zones differ in biotic and abiotic parameters (de Klerk, 1983; Moll, 1983; Hoeksema, 1990; Erftemeier, 1993). Not all authors use the same zonation. Moll (1983) ignored the first zone, whereas Verheij (1993) combines the second and third zone. Hoeksema (1990), using free-living corals, recognises all four zones. In the present study a slightly modified zonation is used, clarifying the terrestrial impact on the distribution of larger foraminifera. In order to compare results, the classification of the shelf zones resembles those given by van Vuuren (1920) and Hoeksema (1990). Zone 1A (Southern Nearshore

Table 2.1. Samples taken in the Spermonde area, 0 = sample taken, but did not contain larger foraminifera, 1 = sample taken containing larger foraminifera, 2 = two samples taken containing larger foraminifera.

	1A					1B					2													3+4															
depth	2	3	6	9	12	3	6	9	12	15	1	1,5	2	3	4	6	9	12	15	18	21	24	27	1	2	3	4	6	7	9	10	12	15	18	21	24	27	30	33
exposed																																							
Laelae		1	1	1	1																																		
Gusung		1	1	1	0																																		
Baranberingan	1	1	1	1	0																																		
Polewali						1	1	1	1	1																													
Karanrang						1	1	1	1	1																													
Lankadea						1	1	1	1	1																													
Bone Baku														1	1	1	1	1	1	1																			
Samalona														2		2	1	1	1	1	1	1	1																
Bone Batang														1		1	1	1	1	1	1	1																	
Kudingareng Keke																									1	2	1	1		1		1	1	1	1	1	1	1	1
Bone Tambung																										1			1		2		1	1	1	1	1	1	1
Lumulumu																										1		1		1		1	1	1	1	1	1	1	1
Langkai																								1	1	1		1		1		1	1	2					
leeward																																							
Laelae		1	1	1	0																																		
Gusung		1	1	1	0																																		
Baranberingan																																							
Polewali						1	1	1	1																														
Karanrang						1	1	1	1																														
Lankadea						1	1	1	1																														
Bone Baku																1	1	1	1	1																			
Samalona														1		1	1	1	1	1	1	1																	
Bone Batang											1	1	1	1		1	1	1	1	1	1	1																	
Kudingareng Keke																										1		1				1	1	1	1	1	1	1	
Bone Tambung																										1	1	1		1		1	1	1	1	1	1	1	1
Lumulumu																										1		1		1		1	1	1	1	1	1	1	1
Langkai																										2		1		1		1	1	1	1	1	1	1	1

Zone) is bounded by the 20 m isobath and within 4 km from the shore, while zone 1B (Northern Nearshore Zone) is also bordered by the 20 m isobath, but the islands are more than 4 km from the shore. Zone 2 (Mid Shelf Zone) has a maximum depth between 20 m and 30 m, all other islands were situated in the combined zone 3+4 (Outer Shelf Zone).

Methods

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

Hundred and eighty six samples have been collected at the leeward (east) and seaward (west) sides of 13 reefs (named on Fig. 2.1) at 3 m depth intervals. Of these samples, 182 contained living larger foraminifera. Three islands were sampled in the Southern Nearshore, Northern Nearshore and Mid Shelf Zones, and four islands where sampled in the Outer Shelf Zone (Table 2.1).

Presence/absence data are used to determine ecological preferences of species. A species is considered present if at least five specimens occur in a sample of 200-300 specimens. The presence/absence data are compared with the random distribution in all samples on the parameters leeward slope vs seaward slope and firm vs. sandy substrate using a chi^2 test.

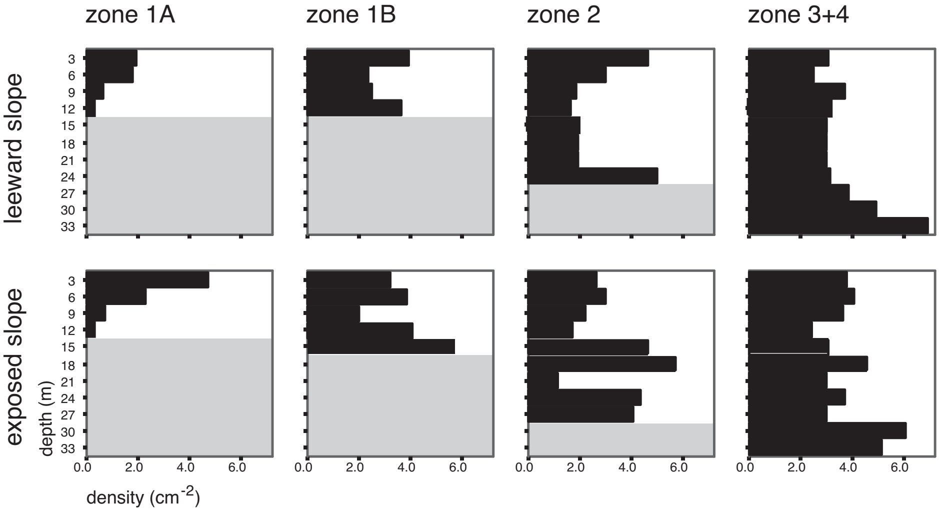


Fig. 2.3. Bar diagram showing the average density of larger benthic foraminifera on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

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

Results

On both the leeward and exposed sides of zone 3+4 reef slopes, densities were slightly higher than in the other areas (Fig. 2.3), reaching up to 6 foraminifera cm^{-2}. Except for the Southern Nearshore Zone (1A), highest densities were found in the deepest (reef base) samples. Due to depth variations of the shelf bottom around reefs, this pattern is not clear in the Mid Shelf Zone (2). Reef base samples contain 4-6 foraminifera cm-2, slope samples 1-3 specimens cm^{-2}.

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

In total 21 larger foram species have been found. They will be discussed systematically in the following section. Per species, a short description with the most important characters and symbiont type will be presented, with remarks on occurrence at the Spermonde Shelf and comparative distribution data from other areas reported in the literature.

Table 2.2. Chi^2 values and the falsification change of the null hypothesis that the samples in which a species occurred was the same as the total set of samples analysed. The fourth and seventh column gives an indication which slope direction (E = Exposed, L = Leeward) or substrate type (H = solid, Z = soft) is over-represented.

soort	**chi-square**	P	E<>L	**chi-square**	P	H<>Z
Operculina ammonoides		2		1.0	<0.001	Z
Nummulites venosus		11.7			<0.005	Z
Alveolinella quoyii						
Amphistegina papilosa	5.43	<0.05	E	8.10	<0.005	Z
Elphidium craticulatum	9.39	<0.005	E			
Dendritina ambigua	4.45				<0.05	Z
Parasorites orbitolitoides	27.0				<0.001	Z
Calcarina gaudichaudii	42.0	<0.001	E	21.8	<0.001	H
C. hispida						
Baculogypsinoides spinosus	25.6	<0.001	E			
Peneroplis pertusus						
Spirolina arietina						
Neorotalia calcar	22.9	<0.001	L			
Peneroplis planatus	19.9	<0.001	L			
Laevipeneroplis proteus						
Amphisorus hemprichii	33.9	<0.001	E	35.0	<0.001	H
Amphistegina radiata	64.0	<0.001	E	33.5	<0.001	H
Heterostegina depressa	40.5	<0.05	E	35.0	<0.001	Z
Sorites orbiculus						

Systematic account

Suborder Miliolina

Family Peneroplidae

Peneroplis planatus (Fichtel & Moll, 1798)

Pl. 1, figs. a-b.

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

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

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

Distribution — *P. planatus* is the most abundant peneroplid of this study with den-

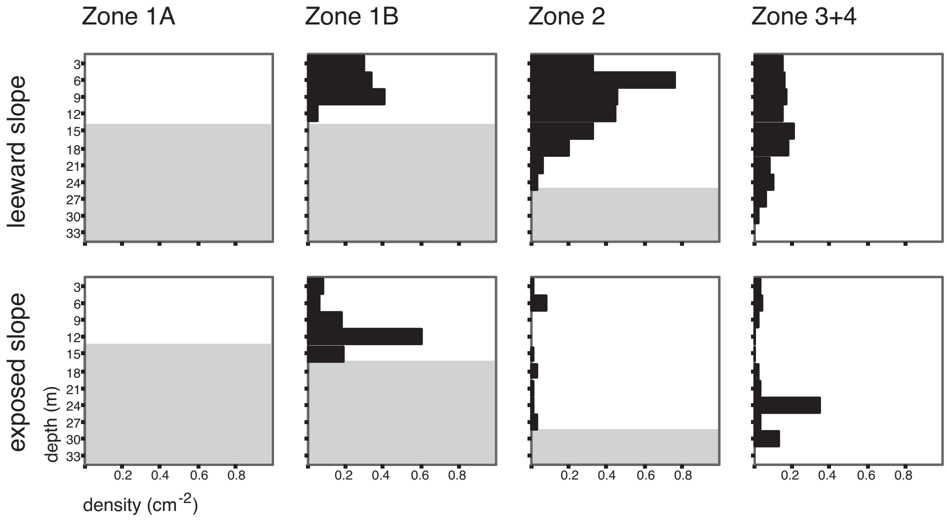


Fig. 2.4. Bar diagram showing the average density of *Peneroplis planatus* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

sities up to 0.7 cm^{-2}. It occurred significantly (chi^2 test, $p < 0.001$, Table 2.2) more abundant on the leeward reef slopes than on the exposed slopes. *P. planatus* did not show a clear preference for substrate type. Samples with a high abundance of this species were often taken in the vicinity of the sea grass *Halophilus ovalis*. Although no specimens were seen living on sea grass leaves, some were found attached to its root system. The highest densities have been found at 3-12 m depth in the Northern Nearshore and Mid Shelf area (Fig. 2.4), in the Outer Shelf Zone, the maximum depth at which *P. planatus* was found is 30 m.

Discussion — Just like at the Spermonde (Fig. 2.4), at Okinawa, life specimens were found at 0-30 m depth, with the highest density in the upper 10 m (Hohenegger *et al.*, 1999), but Hallock (1984) observed it at Palau from 1-5 m depth only.

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

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

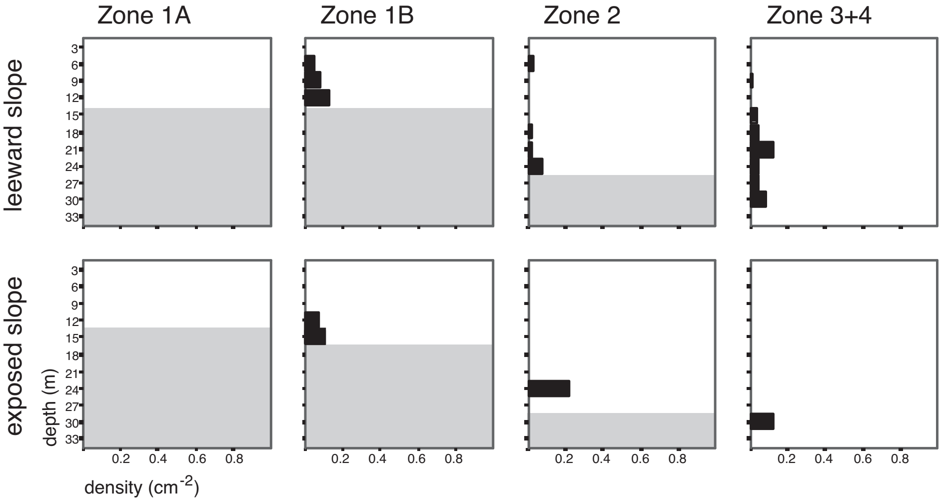


Fig. 2.5. Bar diagram showing the average density of *Dendritina ambigua* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

Dendritina ambigua (Fichtel & Moll, 1798)
Pl. 1, figs. c-d.

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

Affinities — The congeneric *D. zenghae* Ujuiie at the Spermonde Archipelago is more evolute, always showing a clear umbilicus and a smooth surface. Last whorl in large specimens is flaring, increasing in size and arched, so that it has a flattened periphery. Large specimens of *Dendritina* can be mistaken for *Laevipeneroplis proteus* (d'Orbigny, 1839), which has a larger umbilicus, a row of pores on the aperture surface and chlorophytic symbionts (Leutenegger, 1984) (Pl. 1, figs. e-f).

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

Distribution — On the Spermonde Shelf, *D. ambigua* showed a significant preference for sandy sediments (chi^2 test, $p < 0.05$, Table 2.2) as well, but no preference for either leeward or seaward slope was found. *D. ambigua* is found at depths ranging from 10-30 m in reef base samples and in some shallower samples on the leeward side around reefs all over the shelf, except in the southern Nearshore area (Fig. 2.5). It usually occurred in areas on the shelf bottom where organic detritus and algae accumulated.

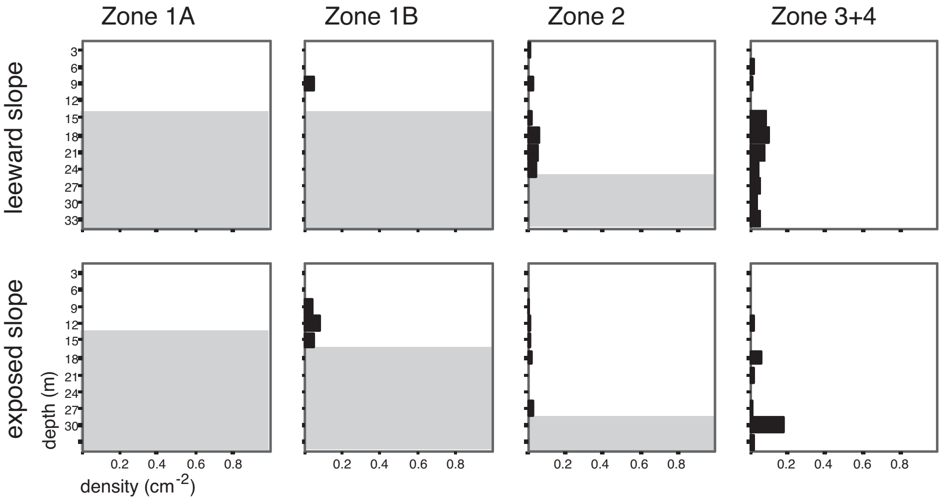


Fig. 2.6. Bar diagram showing the average density of *Parasorites orbitolitoides* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

D. zhengae was only found in two samples in very low densities. It was photographed at the reef base of several Mid Shelf and Outershelf reefs, together with *Operculina ammonoides* and *Parasorites orbitolitoides* (Fig. 2.20d, e).

L. proteus was found in one sample taken at the west side of the outer shelf reef Langkai at 2 m depth, where it co-occurred with *Amphisorus hemprichii* on macroalgae that were attached to coral rubble in a very highly hydrodynamic setting.

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

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

Family Soritidae
Parasorites orbitolitoides (Hofker, 1930)
Pl. 1, figs. g-h.

Description — Test round, flat, and smooth. Its height hardly increases towards the periphery. First few chambers peneropline, later chambers annular. All chambers divided into chamberlets. Small, round apertures occur in one or two rows in a groove at the periphery (Loeblich & Tappan, 1987).

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

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

Distribution — In the Spermonde area, a similar distribution pattern as for *D. ambigua* is found. *P. orbitolitoides* has a significant preference for soft substrate (Table 2.2). The chlorophyte symbionts limit the depth distribution to shallow areas.

All samples in which *P. orbitolitoides* was found were taken at the reef base, with highest densities in the Northern Nearshore and Mid Shelf Zones (Fig. 2.6). Here it occurred most abundantly at places with organic detritus accumulations, which occasionally covered the sides of the foraminifera (Fig. 2.20f). In the Outer Shelf Zone, off Langkai, *P. orbitolitoides* was also found on a gently declining leeward slope.

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

Sorites orbiculus (Forskål, 1775)
Pl. 2, figs. a-b.

Description — Discoidal test, initial few chambers planispiral evolute, at an early stage succeeded by annular ones. Aperture form a single row of openings with protruding rims and 8-shaped apertures resulting from cross like oblique stolons (Loeblich & Tappan, 1987).

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

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

Distribution — *S. orbiculus* was found regularly, but always in very low densities at the Spermonde Archipelago (usually 1-5 specimens per sample). *S. orbiculus* did not show any preference for substrate type or slope direction (Table 2.2). Troelstra *et al.* (1996) found this species living abundantly on *Enhalus* sea grass-leaves, especially on the reef flat. Furthermore they state that this species is hardly found on solid substrates. The low abundance of *Enhalus* on the reef flat during the present study, explains why we found much lower numbers of *S. orbiculus* than Troelstra *et al.* (1996).

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

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

Amphisorus hemprichii Ehrenberg, 1839
Pl. 2, figs. c-d.

Description — *A. hemprichii* is the largest soritid found at the Spermonde Archipelago, reaching almost 1.5 cm in diameter. Test biconcave with thickened rims, aperture of numerous pores on the peripheral margin, elongated across the margin, and aligned in two alternating rows (Loeblich & Tappan, 1987). The test usually shows some radial lining on the test, especially in larger specimens.

Affinities — See *Sorites orbiculus*.

Symbiont type — Dinoflagellate, *Symbiodinium* spec.

Distribution — *A. hemprichii* significantly prefers solid substrates (chi^2 test, $p<0.001$, Table 2.2) and the exposed reef slopes (chi^2 test, $p <0.001$, Table 2.2) in the Spermonde Archipelago. It was observed attached to large boulders by a protoplasm sheath to prevent detachment and breakage (Fig. 2.20h). Around the margin, sediment grains were found stuck to this sheath. Large specimens occasionally occurred on soft substrate at the reef base. Its depth distribution depends on the distance to the shore (Fig. 2.7); the more offshore, the deeper the range of the reef slope and the deeper the lowest depth limit of the species. In the Southern Nearshore area, in the proximity of large river outlets, it does not occur despite the availability of suitable substrate. Around reefs in the Northern Nearshore Zone, *A. hemprichii* only occurred in the shallowest samples. At the Mid Shelf and Outer Shelf Zones A. *hemprichii* occurs alsmost as deep as the maximum depth of the suitable substratum (18 m at the west side of Langkai), or over 20 m depth (e.g., 22 m at Karang Kassi reef, 21 m at Bone Tambung reef). In the Northern Nearshore Zone, large specimens of *A. hemprichii* were also found at the reefbase, in between sea grass (*Halophilus*).

Discussion — This species has been reported from firm substrate, irrespective of depth from the reef crest until 60 m depth (Hohenegger, 1994; Hohenegger *et al.*, 1999; Troelstra *et al.*, 1996). Hohenegger (1996) reported *A. hemprichii* from Palau at 0-10 m depth only.

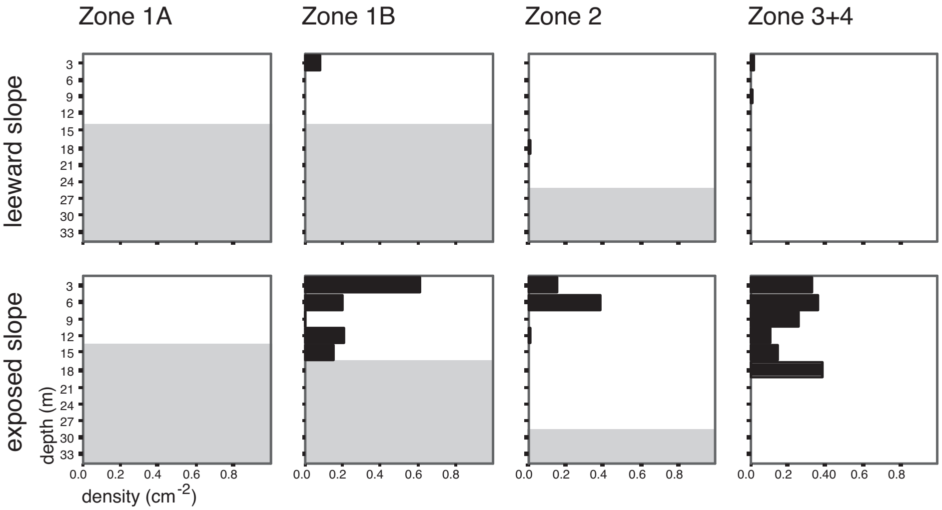


Fig. 2.7. Bar diagram showing the average density of *Amphisorus hemprichii* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

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

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

Family Alveolinidae
Alveolinella quoyii (d'Orbigny, 1826)
Pl. 2, fig. e.

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

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

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

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

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

Suborder Rotalida
Family Amphisteginidae
Genus *Amphistegina*

The genus *Amphistegina* is characterised by a low trochospiral, lenticular and inequeally biconvex test, that can be bi-involute or partially evolute on the spiral side. Chambers are strongly arched at the periphery (Loeblich & Tappan, 1987).

Amphistegina lessonii d'Orbigny, 1826
Pl. 2, fig. f.

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

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

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

Distribution — *A. lessonii* is the most abundant larger foraminifera in the area. It occurs in almost all samples, but the highest densities have been found on shallow, soft substrates (down to 25 m depth) (Fig. 2.8). The maximum depth at which *A. lessonii* occurred varied from 9 m at Lae Lae to 30-33 m around the Mid Shelf reefs

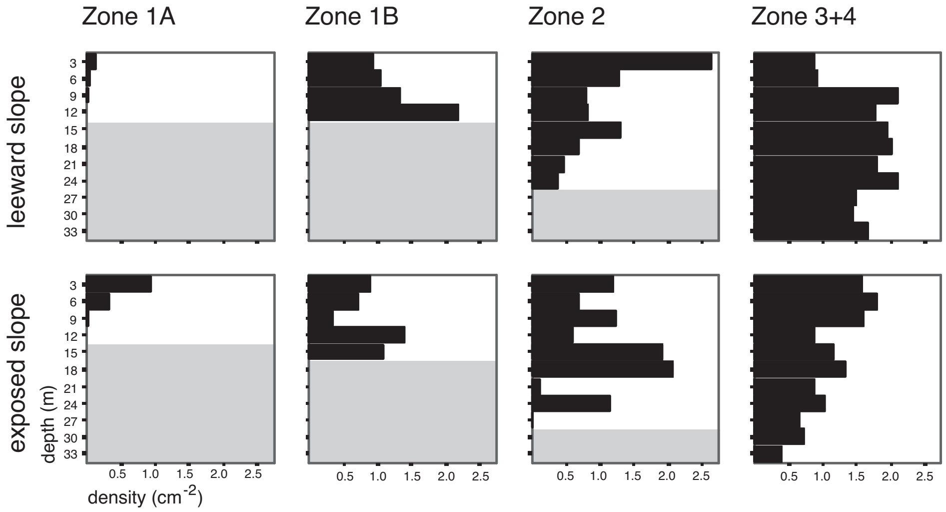


Fig. 2.8. Bar diagram showing the average density of *Amphistegina lessonii* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

(Fig. 2.8). This pattern is similar to what Troelstra *et al.* (1996) reported, but they found much higher densities on the reef flat.

Discussion — *A. lessonii* shows a very broad depth range in the Indo Pacific from 0-90 m (Hohenegger *et al.*, 1999), with highest densities around 10-25 m (Hallock, 1984; Hohenegger, 1996). It has been reported to have either a preference for sandy (Hallock, 1984) and solid substrate (Hollaus & Hottinger, 1997). Hansen & Buchardt (1977) found *A. lessonii* (empty shells and living specimens combined) from 0-85 m in the Gulf of Aqaba.

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

Amphistegina lobifera Larsen, 1976
Pl. 2, fig. h.

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

Affinities — See *A. lessonii*.

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

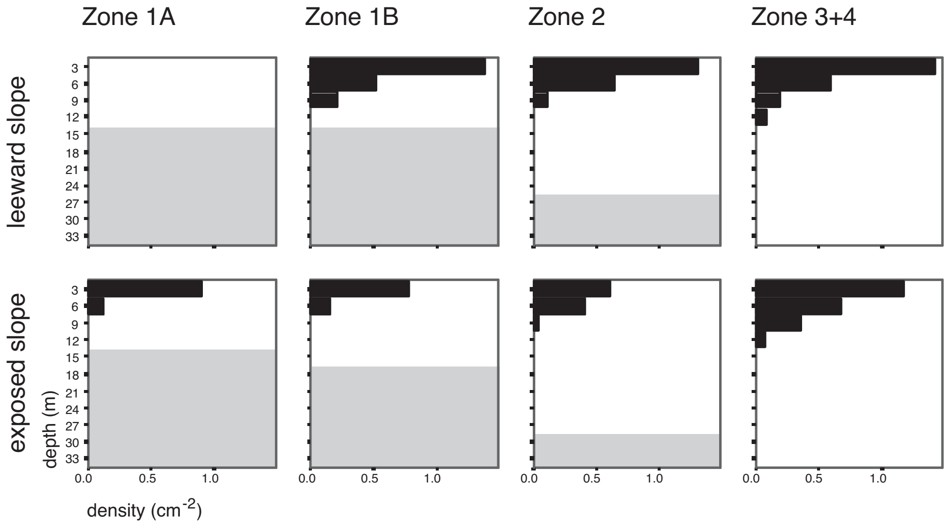


Fig. 2.9. Bar diagram showing the average density of *Amphistegina lobifera* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

Distribution — *A. lobifera* was the rarest *Amphistegina*-species found. It only occurred in the shallowest samples, on both the eastern and western reef sides (Fig. 2.9). No specimen was recorded from deeper than 12 m. The depth range of this species does not vary much between the four shelf zones, where it was found on both solid and soft substrates. On coral rubble, this species occurs below larger boulders covered with red algae. Here, *A. lobifera* occurred mainly on the sides, the largest specimens living closer to the boulder edges than small specimens.

Discussion — The highest densities of *A. lobifera* have been found at very shallow depths (Hallock, 1984; Hohenegger, 1994; Hohenegger, 1996; Hohenegger *et al.*, 1999). Because of its thick shell, this species can live in the highest light-energy levels of all species of *Amphistegina* (Hallock, 1981a). *A. lobifera* had the best ability to attach to solid surfaces in order to withstand high hydrodynamic energy (Hallock, 1981a; Hohenegger *et al.*, 1999). Similar to Hohenegger (1994) we did not find *A. lobifera* (or any other larger foraminifera) in high energy sands on the reef flats. *A. lobifera* was found on sheltered sandy substrates and in sheltered places between coral rubble covered by algae.

Amphistegina radiata (Fichtel & Moll, 1798)
Pl. 2, fig. g.

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

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

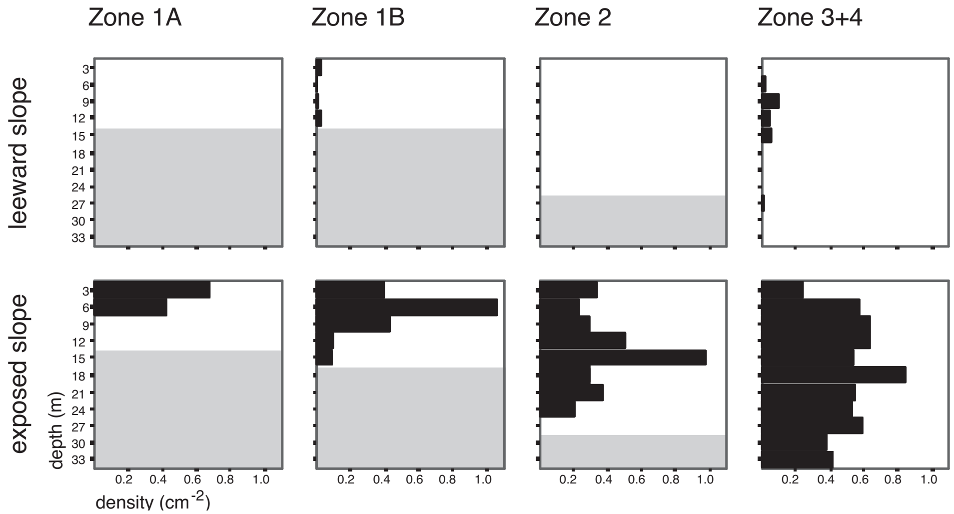


Fig. 2.10. Bar diagram showing the average density of *Amphistegina radiata* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

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

Distribution — In the Spermonde Archipelago this species is found at 2-33 m depth (Fig. 2.10). *A. radiata* significantly (Table 2.2) preferred both firm substrates and the western slope of the reefs. At shallow depths specimens occur hidden between coral rubble, especially the smaller ones. *A. radiata* does not replace *A. lessonii* with depth, but is rather characteristic for solid substrates. *A. radiata* is more abundant in the 2-30 m depth range on solid substrate, while *A. lessonii* is dominant on soft substrates at the same depths.

Discussion — *A. radiata* has been recorded from intermediate depths at solid substrates (Hohenegger *et al.*, 1999; Troelstra *et al.*, 1996). Hohenegger *et al.* (1999) explained its absence in shallow waters at the reef crest by its lesser ability to attach to the substrate than *A. lessonii* and *A. lobifera* because of small apertural fields. In the same area, Hohenegger (1994) found *A. radiata* on both solid and soft substrates in the shallow part of the range, and predominantly on soft substrates at greater depths. At Palau Hallock (1984) found that *A. radiata* replaced *A. lessonii* with depth.

At the Spermonde shelf, *A. radiata* and *A. lessonii* are found in the same depth range. *A. radiata* is found on the exposed side, while *A. lessonii* occurs both on the leeward side and the exposed side. Especially larger specimens of *A. radiata* are found abundantly on the surface of coral rubble (Fig. 2.20a). *A. lessonii* was always found in cryptic, sheltered places (when it was found at the exposed side). In deep areas, with no solid substrates, *A. radiata* was present, but *A. papillosa* was more common.

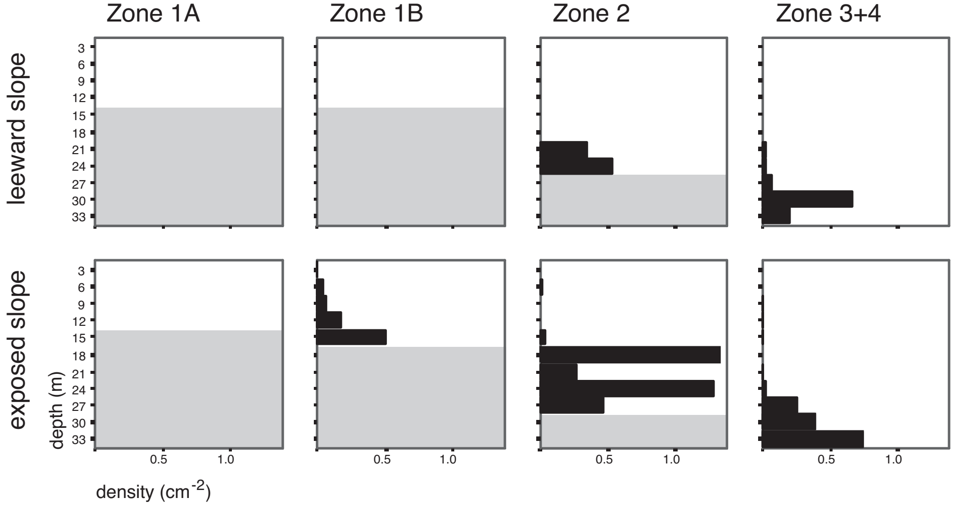


Fig. 2.11. Bar diagram showing the average density of *Amphistegina papillosa* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

Amphistegina papillosa Said, 1949

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

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

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

Distribution — In this study *A. papillosa* was the deepest living representative of its genus, occurring on the reef base in all zones, except for the Southern Nearshore Zone (Fig. 2.11). It was found at 6-15 m depth around Lankadea reef, 15-24 m around Samalona reef and 27-33 m (maximum depth of sampling) around Bone Tambung and other reefs in the outer shelf zone. It does not show a preference for slope orientation. *A. papillosa* has a significant preference for sandy substrates (chi^2 test, $p < 0.005$, Table 2.2).

Discussion — Of the amphisteginids found on the Spermonde Shelf, *A. papillosa* is the deepest living species. It has been reported from down to 120 m depth in the Gulf of Eilat (Hansen & Buchardt, 1977), but these authors made no differentiation between dead and living specimens. At Okinawa it has been reported alive from more than 100 m depth (Hohenegger, 1994). No substrate preference has been reported. Though the maximum depth at which *A. papillosa* is found in the Spermonde is much shallower, this species shows a similar distribution pattern as in other regions.

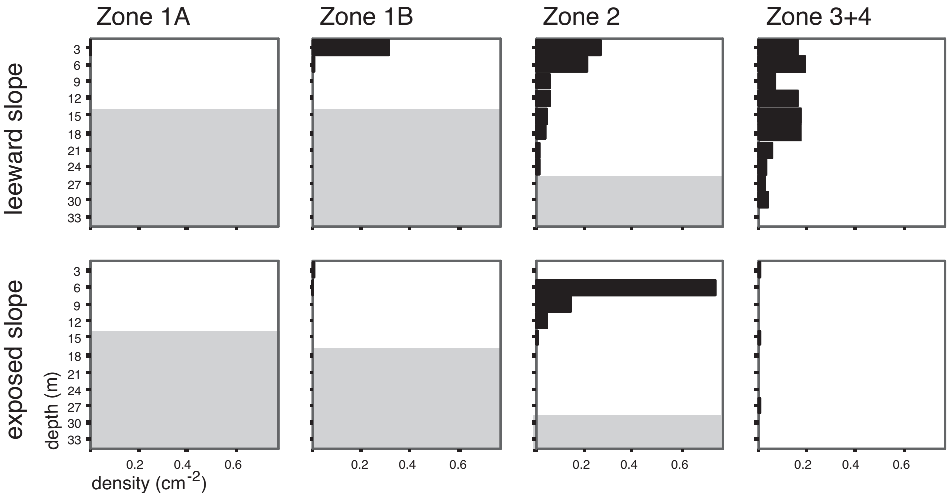


Fig. 2.12 Bar diagram showing the average density of *Neorotalia calcar* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

Family Calcarinidae
Neorotalia calcar (d'Orbigny, 1839)
Pl. 3, figs. e-f.

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

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

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

Distribution — *N. calcar* occurs on the reef edge and has no preference for substrate type in the Spermonde Archipelago. It lives in shallow water and is usually restricted to the upper 10 m (Fig. 2.12). *N. calcar* is significantly more abundant on the leeward slope than on the exposed slope (chi^2 test, $p < 0.001$). On the leeward slope, it may occur in deeper water (down to 30 m, Fig. 2.12).

Discussion — The occurrence of this species on the Spermonde Shelf is different from that in other regions from where it has been reported. Instead of having its highest density in the shallowest part of the reef flat, it is more abundant around the reef edge on the leeward side, where the highest densities in zone 1B, 2 and 3+4 are found

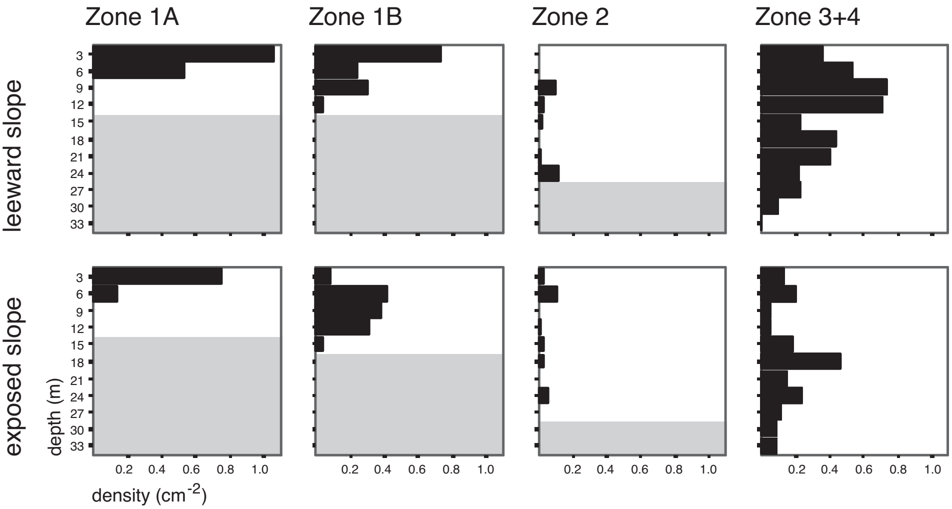


Fig. 2.13. Bar diagram showing the average density of *Calcarina hispida* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

down to 3, 6 and 18 m (Fig. 2.14), respectively. This species has been found in shallow water on thalli of macroalgae and on firm substrates in the beach region (Hallock, 1984; Hohenegger, 1994, 1996). Hohenegger *et al.* (1999) found a significant preference for solid substrates in two transects off Okinawa. Troelstra *et al.* (1996) found this species in very shallow water as well but with a much higher density on reef flats.

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

Calcarina hispida Brady, 1876
Pl. 3, figs. a-b.

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

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

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

Distribution — In our study *C. hispida* was the most abundant calcarinid foram. It occurred around reefs in most zones (Fig. 2.13), and was found in 2/3 of the samples. Only *A. lessonii* was found in more samples. *C. hispida* showed no preference for either substrate type or exposed/leeward side of the reefs. In most areas it occurred down to the maximum sampling depth at the reef base while the highest densities occurred at the lower part of the reef slope (Fig. 2.13).

C. hispida occurred in high densities in the southern Nearshore Zone, where this was the most abundant species on sandy substrate. Low densities were found on the Mid Shelf reefs (Fig. 2.13). On reefs in the Northern Nearshore and Outer Shelf Zone, *C. hispida* is abundant at both the leeward and exposed reef slope. On the leeward slope, it occurs on top of barren sediment.

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

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

Calcarina spengleri (Gmelin, 1791)
Pl. 3, fig. d.

Description — Test large, flat, and trochospiral with thick chamber walls giving rise to circular contours (Hohenegger *et al.*, 1999). In our study specimens with only few spines are more angular with usually only a limited number of long, rounded spines (4-6), showing some parallel striae. Test surface smooth with very small pores. The last chambers often are large with relatively deep sutures, especially at the spiral side.

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

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

Distribution — This species shows a significant preference for both the exposed slopes of the reefs and solid substrates (Fig. 2.20a). Its maximum abundance was at the middle of the slope (9-24 m in the zone 3+4, 3-12 m in zone 2, Fig. 2.14), where it lived below large boulders of rubble or in crevices. The density of this species decreases rapidly as soon as the substrate type at the exposed slope changes from coral rubble into sand. The maximum depth at which it has been recorded is 30 m.

Discussion — This species is characteristic for high hydrodynamic energy, shallow water (Röttger & Krüger, 1990). Hallock (1984) found this species in the upper 5 m (maximum density at 1 m), as did Röttger & Krüger (1990) and Röttger *et al.* (1990).

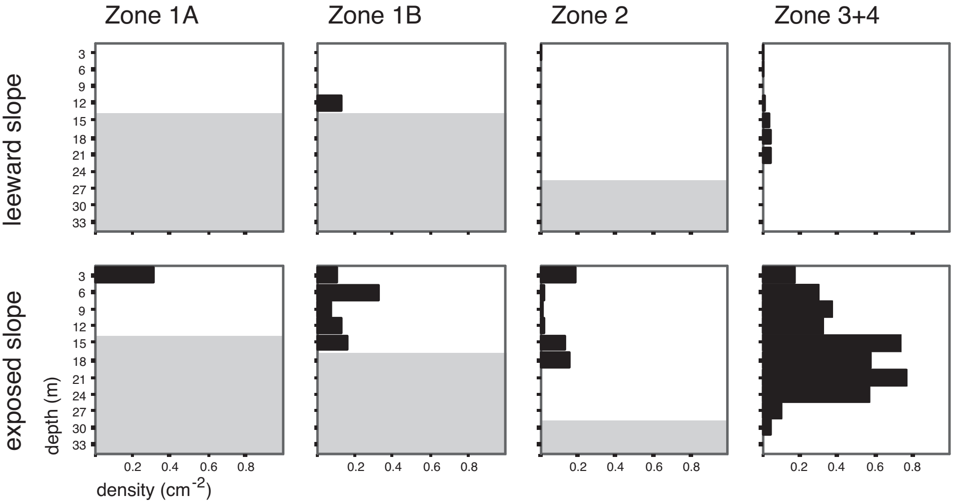


Fig. 2.14. Bar diagram showing the average density of *Calcarina spengleri* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

Hohenegger (1994) and Hohenegger *et al.* (1999) found it in slightly deeper water, of 0-20 m depth, while their maximum density was in crest pools at 0-10 m depth, where it was associated with algae.

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

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

Baculogypsinoides spinosus Yabe & Hanzawa, 1930
Pl. 3, fig. c.

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

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

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

Distribution — This large *calcar*inid occurs in a few samples, most of them on the

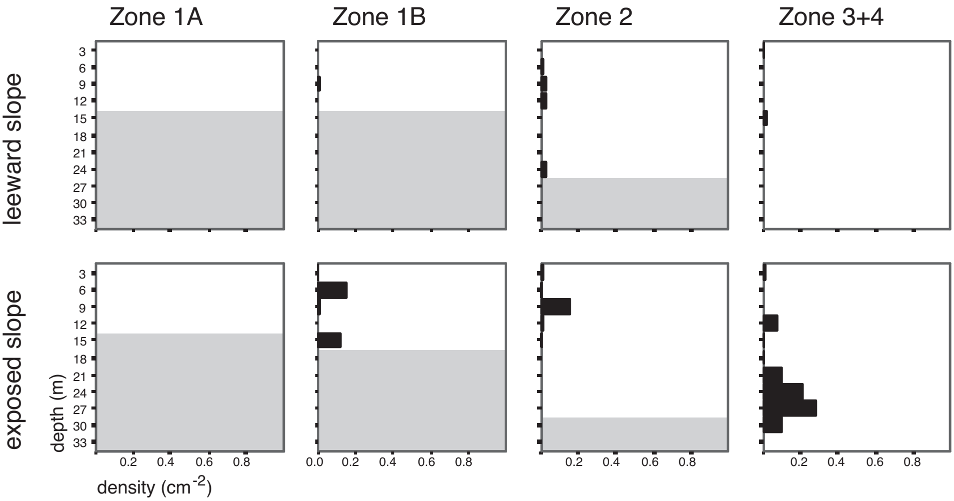


Fig. 2.15. Bar diagram showing the average density of *Baculogypsinoides spinosus* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

seaward slope of the reefs (Fig. 2.15). It occurs at the upper part of sandy reef bases just below the coral cover on the base of slope, where it lives attached just below the edges of large pieces of coral rubble (e.g., dead mushroom corals) covered by algae (Fig. 2.20b). This pattern is very similar to what Troelstra *et al.* (1996) found (listed as *Baculogypsina sphaerulata* (Parker & Jones, 1860)).

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

Family Rotalidae

Elphidium craticulatum (Fichtel & Moll, 1798)

Pl. 3, figs. g-h.

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

Affinities — Misidentification impossible.

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

Distribution — This species occurs all over the shelf. The highest densities were

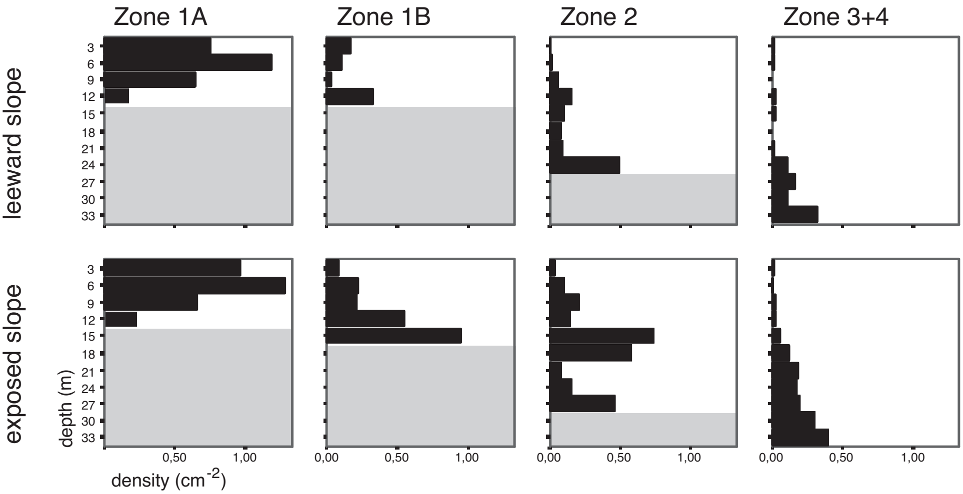


Fig. 2.16. Bar diagram showing the average density of *Elphidium craticulatum* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

found around nearshore reefs (zone 1A) where they co-occurred with *A. radiata* attached to algae on coral rubble and in the deepest samples taken in between the reefs (Fig. 2.20c). *E. craticulatum* can be found at any depth, and seems to occur mostly in conditions at the limits of the range of symbiont-bearing foraminifera (Fig. 2.16). This is related to the fewer restrictions of chloroplast husbandry over symbiont housing.

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

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

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

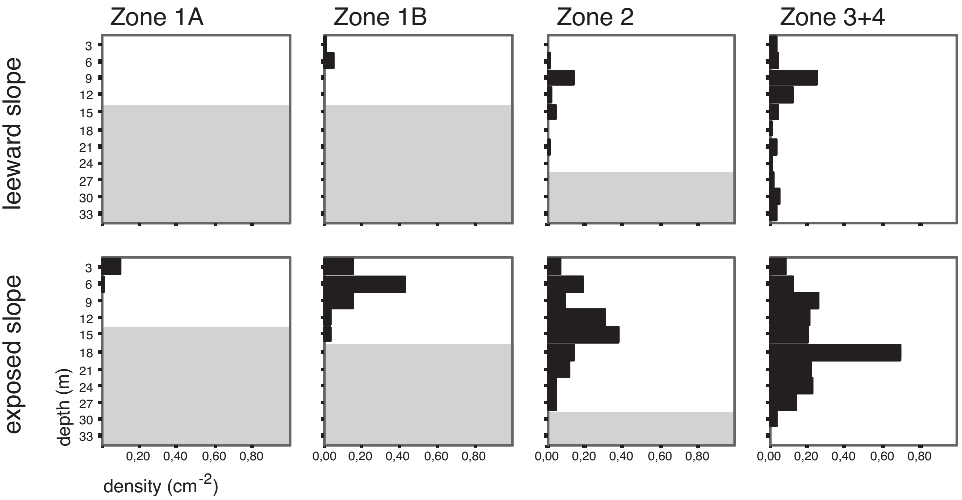


Fig. 2.17. Bar diagram showing the average density of *Heterostegina depressa* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

Family Nummulitidae
Heterostegina depressa d'Orbigny, 1826
Pl. 4, fig. a.

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

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

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

Distribution — *H. depressa* is common in the Spermonde Archipelago (Fig. 2.17), with a significant preference for seaward slope sides (chi^2 test, $p < 0.05$, Table 2.2) and for solid substrates (chi^2 test, $p < 0.001$, Table 2.2). The highest densities occur on the exposed slopes, and this species shows a marked increase in depth range going from the Southern Nearshore Zone to the Northern Nearshore Zone (Fig. 2.17). It is found hidden in sheltered places on coral rubble covered with coralline algae (Fig. 2.20b). On the sandy leeward sides and on sandy reef bases it occurs in very low densities (Fig. 2.17). Here, very large microspheric specimens were observed, some of which were found attached to echinoids.

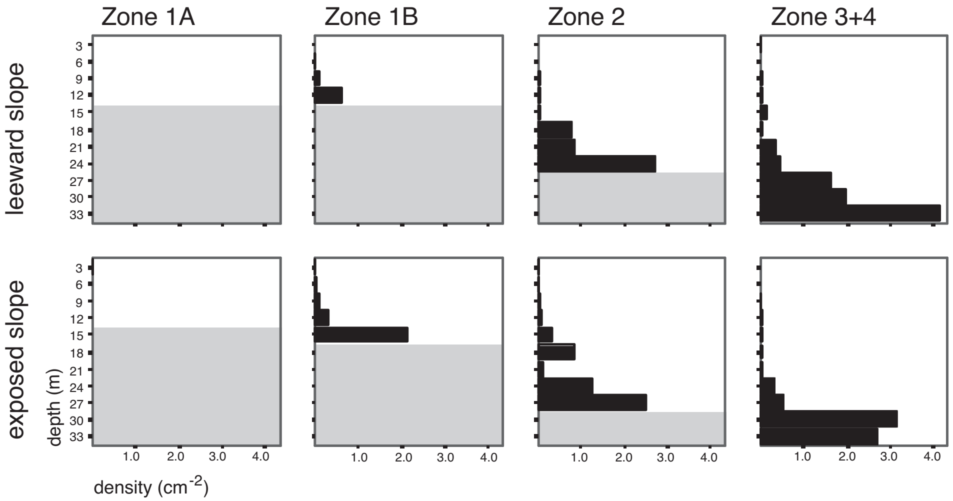


Fig. 2.18. Bar diagram showing the average density of *Operculina ammonoides* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

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

Operculina ammonoides (Gronovius, 1781)
Pl. 4, figs. b-c.

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

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

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

Distribution — At the Spermonde Archipelago, this is the most abundant species, occurring on various sandy substrates, to which it has a significant preference (Table 2.2), especially in patches at reef bases, except those at the Southern Nearshore area (Lae Lae, Baranberingan, Fig. 2.18). It was found dead in grab samples from < 54 m

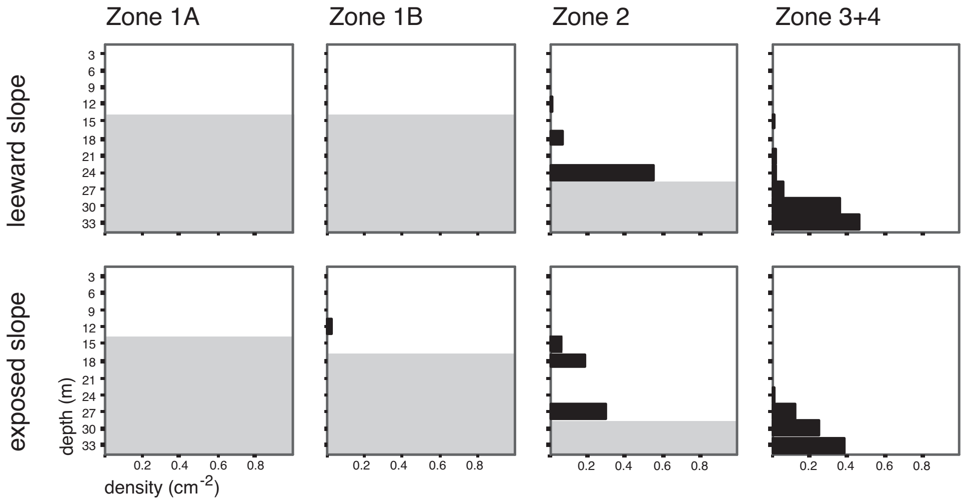


Fig. 2.19. Bar diagram showing the average density of *Palaeoummulites venosus* on the exposed and leeward slope of reefs in four zones of the Spermonde Archipelago. Shaded area was not sampled.

depth E of Langkai, and alive from not deeper than 45 m just west of Kudinkarengkeke. It occurred at slightly shallower depths on sandy leeward reef slopes (Fig. 2.18; 2.20 e, f). The minimum depth at which it has been found varies from 9 m in zone 1B to 21 m in zone 3+4 (Fig. 2.18).

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

Nummulitids that prefer even lower light intensities do not occur in the Spermonde Archipelago. Empty tests of *Operculina heterosteginoides* have been found, but *Heterostegina operculinoides* and *Cycloclypeus carpenteri* Brady are not present.

Palaeonummulites venosus (Fichtel & Moll, 1798)
Pl. 4, figs. d-e.

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

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

Symbiont type — Diatom (Leutenegger, 1984).

Distribution — At the Spermonde Archipelago, *P. venosus* is one of the species showing a preference for soft substrates at the reef base(chi^2 test, p <0.001, Table 2.2). *P. venosus* was collected in low densities at the deepest SCUBA sample depths (Fig. 2.19). It was not found around islands in the Southern Nearshore Zone. *Palaeonummulites venosus* was found nearest to the shore around Bone Baku (zone 2). Highest densities were recorded at the reef base around the outer shelf reefs (Bone Tambung, Kudinkarengkeke).

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

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

Discussion

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

1. The varying influence of terrigenous influx by rivers. Larger foraminifera occur at greater depth in zone 1B than in zone 1A. Both areas are shallower than 20 m, and differ only in the distance to the mainland shore. In zones 1B, 2 and 3+4 the maximum depth at which foraminifera have been found increases in offshore direction, together with parameters like maximum depth and the maximum depth of coral cover on reef slopes and the transparency of the water (secchi depth).

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

On the exposed sides, the shallowest samples were similar to those in the other zones, but *Elphidium craticulatum* occurred in higher densities. The samples at 6-9 m *contained E. craticulatum*, *Amphistegina radiata* and *A. lessonii*. *Heterostegina depressa* was absent. All species occurring in samples taken at the reef base in the other three zones, were absent from this zone as well.

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

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

Neorotalia calcar and *Peneroplis planatus* are both shallow water species living

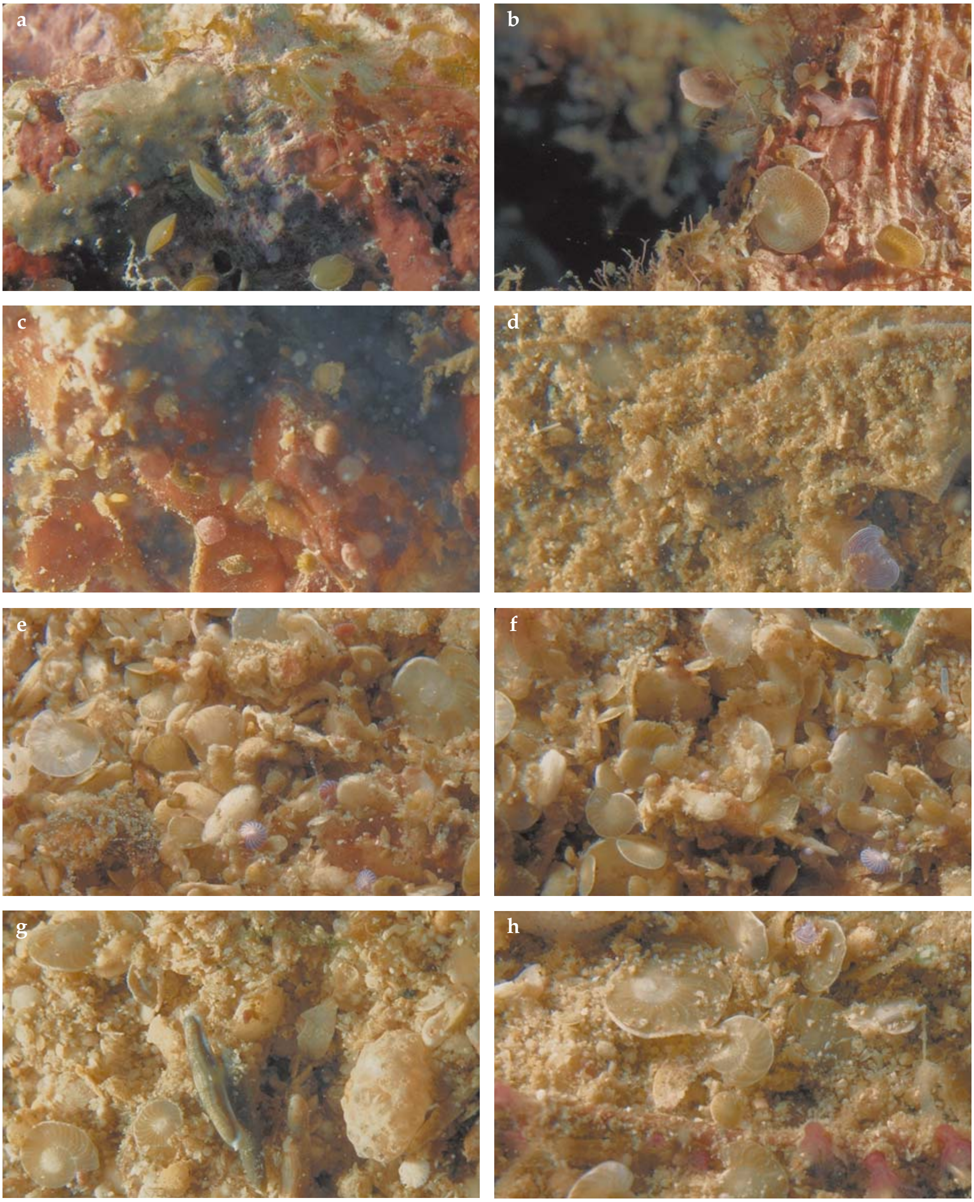


Fig. 2.20a: *Amphistegina radiata* on coral rubble covered by coraline algae (KKW6). b: *Heterostegina depressa*, *Baculogypsinoides spinosus* (background *Amphistegina lessonii* and *Calcarina spengleri)* on dead coral fragment covered by (coralline) algae (KKW18). c: *Elphidium craticulatum* on coral rubble covered by red algae (BBW6). d: Soft sediment assemblage with *Operculina ammonoides* and *Dendritina ambigua* (PLW30). e: Soft sediment assemblage with *Dendritina ambigua, Alveolinella quoyii, Operculina ammonoides* and *Amphistegina papillosa* (SW27). f: Soft sediment assemblage with *Operculina ammonoides* and *Parasorites orbitolitoides* (SE21). g: Soft sediment assemblage with *Alveolinella quoyii* and *Operculina ammonoides* (SW24). h: *Amphisorus hemprichii* attached to a large boulder of dead coral (LKW6).

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

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

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

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

Conclusions

1. Next to already known parameters like substrate type, depth and hydrodynamic energy (Hottinger 1983; Hohenegger, 1994; Hohenegger *et al.*, 1999), another important parameter for the distribution of larger foraminifera is nutrient concentration. This latter parameter is influenced by the distance to the shore and terrestrial run off by rivers over the shelf area. *Calcarina hispida*, *Amphistegina lessonii*, *A. radiata* and *Elphidium craticulatum* can withstand these conditions better than the other species.
2. In tropical areas away from the equator, the climate is often monsoonal with a dry and a wet monsoon. Seasonal changes in fluvial discharge over the shelf influences nutrient concentration (increasing the concentration of organic particles) and inorganic particle concentration nearshore. This seasonal variation also affects the distribution of larger foraminifera over the Spermonde Shelf.
3. The very different set of environmental parameters from other areas were the distribution of living larger foraminifera have been studied, shows that some species are not as critical as others. *Neorotalia calcar*, *Calcarina spengleri* and *Peneroplis planatus* have been recorded at the Spermonde shelf at both different substrates and greater depth than in previous studies.

   The absence of habitats forces the species otherwise living in these habitats to occupy other habitats or to be absent.
4. In mesotrophic conditions, *Elphidium craticulatum* is an important faunal component.

3. Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia)

Willem Renema; Simon R. Troelstra, Institute for Earth Sciences, Free University of Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands.

Previously published as:
Renema, W. & Troelstra, S.R., 2001. Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia). *Palaeogeography, Palaeoclimatology, Palaeoecology* **175**: 125-146.

Introduction

The geographical distribution of symbiont-bearing larger foraminifera is limited by two parameters i.e., nutrient flux and water temperature (Langer & Hottinger, 2000). Larger foraminifera can maintain themselves only in oligotrophic environments because they are housing symbionts (Hallock, 1985). Symbiosis is advantageous in oligotrophic conditions where radiant energy is abundant, growth-limiting nutrients are scarce and concentrated in particulate organic matter, and much energy must be expended to capture this organic matter (Hallock, 1981c). The symbionts use the metabolic waste products of the host that feeds on particulate organic matter otherwise unavailable to the symbiont. Any carbon fixed in excess of the metabolic and growth requirements of the symbiont is potentially available to the host (Muller-Parker & d'Elia, 1997).

Larger foraminifera are restricted to warm water. Their occurrence is limited to a climatic belt bounded by the 15-20°C winter isotherm of the surface water (Murray, 1991; Langer & Hottinger, 2000). In the Mediterranean, Hollaus & Hottinger (1997) found that the occurrence of symbiont-bearing benthic foraminifera (*Amphistegina*) was truncated by the thermocline, while elphidiids (showing chloroplast husbandry) occurred until the maximum depth of the photic zone.

In a biogeographical study, Langer & Hottinger (2000) showed that the distribution of larger foraminifera is constrained by the effective temperature minima tolerated by individual taxa. Of the studied taxa *Operculina heterosteginoides*, *Alveolinella quoyii, Heterostegina operculinoides* and *Palaeonummulites venosus* have the lowest tolerance to low sea surface temperatures. Because of the thermal gradient, it is more likely that the minimum temperature is sufficient in high sea surface temperature areas. They occur in a climate belt limited by the 25°C winter isotherm (Langer & Hottinger, 2000). *Sorites orbiculus* and *Amphistegina* sp. show the widest temperature tolerance of the taxa studied by Langer & Hottinger, as their occurrence is limited by the 14°C isotherm of seawater in the coldest month of the year (Langer & Hottinger, 2000). Within their geographical range, larger foraminiferal density and distribution is determined by a set of environmental parameters, such as light intensity, hydrodynamics, water temperature, salinity, food availability, and substratum, which correlate with depth (Hottinger, 1983).

Hallock (1987, 1988) presented a model in which the community structure of symbiont-bearing benthic foraminifera 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 densities and fluvial influx of dissolved organic matter and suspended sediments. Besides suspension by water turbulence,

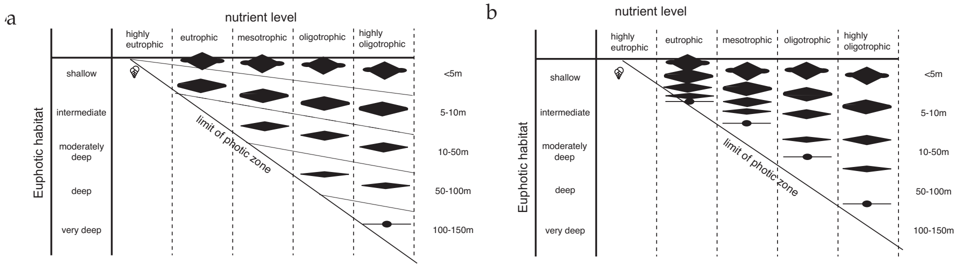


Fig. 3.1. Two possible ways larger foraminifera could react to decreasing transparency due to higher nutrient availability.

a: Schematic representation of Hallock's (1987) model. The species occurring in the deepest biotopes in oligotrophic conditions do not occur in more eutrophic conditions.

b: All species always occur in the same irradiation range (for example, the deepest species occurs always if irradaition is 1-10% of the surface irradiation).

increasing nutrient supply promotes an increase in densities of planktonic organisms and a decrease in transparency.

Furthermore, in eutrophic environments variability on a seasonal time scale is higher than in oligotrophic conditions (Hallock, 1987). Tropical climates away from the equator are often monsoonal, with high river discharge during the wet period. The latter causes several months with higher nutrient fluxes, higher particle concentration in the water column and higher turbidity resulting in a shallower euphotic zone.

Hallock's model predicts that species that are highly specialised to certain levels of light availability, can respond to some loss of water transparency by compressing their depth ranges. However, if water transparency is reduced too much, most will probably disappear, especially if less specialised species are available (Fig. 3.1a; Hallock, 1987).

However, Hohenegger (1995) and Hohenegger *et al.* (2000) presented a model in which the proportions of Nummulitidae were used in a function to estimate water depth at the sampling site (Fig. 3.1b). This model is based on the assumption that organisms tolerate a gradually increasing environmental parameter only within a certain range. In this model, species will occupy increasingly deeper habitats in response to the gradient (increasing transparency) if all other parameters remain the same. Thus, all species will occur in a narrower depth ranges with decreasing transparency. Hohenegger *et al.* (2000) show that an important parameter affecting (and often limiting) this shift into shallower habitats is the high hydrodynamic energy in the upper part of the water column.

The most oligotrophic conditions prevail in oceanic gyres. Many earlier studies have dealt with niche partition of larger foraminifera in areas where oceanic gyres wash ashore (Hottinger, 1983; Reiss & Hottinger, 1984; Hohenegger *et al.,* 1999). Under these conditions living larger foraminifera have been found down to 120 m (Reiss & Hottinger, 1984; Hallock, 1984; Hohenegger *et al.*, 2000).

Much less attention has been paid to the distribution of larger foraminifera in areas where rivers enter shallow tropical shelves (e.g., Troelstra *et al.*, 1996). Such areas display relatively high nutrient levels and a shallower euphotic zone, limiting the occurrence of larger foraminifera to shallow depths.

This study describes the distribution of larger foraminifera assemblages living around patch reefs on the Spermonde Shelf influenced by seasonally changing river discharge. Hallock's model (1987) was developed using hypothetical species. We use our data to test this model on a mesotrophic carbonate shelf setting.

Our data are also compared to the distribution of the larger foraminifera in more oligotrophic conditions within the same biogeographical province to further assess the influence of food availability and water transparency on the distribution of larger foraminifer communities.

The Spermonde Archipelago

The Spermonde Archipelago is an island group in the Makassar Strait west of Sulawesi. The islands lie to the west and northwest of Makassar (formerly Ujung Pandang), the capital of the Indonesian province Sulawesi Selatan (Fig. 2.1). The archipelago is situated on a broad carbonate platform and is separated from open marine settings by a discontinuous barrier reef on its western side.

The islands and shoals of the Spermonde Archipelago developed during the Holocene sealevel rise on top of Pleistocene topography (de Klerk, 1983) and are roughly situated on ridges parallel to the coast. The shelf depth increases gradually off shore to reach a maximum of 60 m just east of the barrier, then gradually shallows towards the barrier, which is about 15-20 m deep, with some islands and several shoals on it. In front of the barrier, depth increases rapidly to over 200 m in the Makassar Strait.

South of Makassar the river Jene Berang flows onto the Spermonde Shelf, carrying terrigenous sediments, which cause a shallowing of the euphotic zone. The Jene Berang also discharges nutrients and fresh water over the shelf, resulting in higher nutrient levels and lower salinity nearshore, compared to the rest of the shelf. The dominant current direction in the Makassar Strait and over the shelf is southward, so most of the terrigenuous input is deflected towards the south. Some smaller rivers north of Makassar have smaller discharge and have a limited effect on the distribution of nutrients over the shelf. During the wet season, the northwestern edge of the plume of the Jene Berang can reach as far as the island Samalona. South of the Jene Berang's mouth, no patch reefs occur for about 40 km. Maximum tidal amplitude in the study area is 1.2 m. Sea surface water temperature is 28.5°C, and decreases to about 26°C at 20 m depth (Storm, 1989). Salinity is about 33‰, except for the surface layer near the mouth of the Jene Berang, where it can be as low as 20‰ during periods of high river discharge.

Four ecological zones, based on marine plants and stony corals have been recognised in the Spermonde Archipelago (Moll, 1983; Hoeksema, 1990). These zones roughly parallel the isobaths on the shelf.

The nearshore zone is bordered by the 20 m isobath. This zone has the highest nutrient and clay/silt content (Erftemeier, 1993). Secchi depths around Lae Lae are 0.5-2.5 m during the wet season and 2.5-5 m during the dry season. The chlorophyll α concentration in the dry season was 2.9 ± 1.5 μg/l (Erftemeier, 1993). This zone shows the lowest diversity in stony corals (Hoeksema, 1990).

The Mid Shelf Zone is between 20 m and 30 m depth. Nutrient levels are similar to the third and fourth zone, as is the silt content. Chlorophyll α concentration in the dry season was 0.5 ± 0.2 μg/l (Erftemeier, 1993). Secchi depths vary from 1-5 m in the wet season to 10-17 m in the dry season.

The Outer Shelf Zone comprises the shelf deeper than 30 m except for the outer rim. In the third zone the secchi depth varies between 7.5-20 m in the wet season and 10-30 m in the dry season. Chlorophyl α concentration in the dry season was 1.0 ± 0.1 μg/l (Erftemeier, 1993). This zone is the most diverse zone based on stony corals (Hoeksema, 1990)

The outer rim zone is formed by the barrier itself. The secchi depth is similar to the outer shelf zone, but the hydrodynamic energy is higher. Chlorophyll α concentration in the dry season was 0.7 ± 0.1 μg/l (Erftemeier, 1993)

We used a similar division of the Spermonde Shelf roughly corresponding to the zones mentioned above (Fig. 3.2). The first zone, approximately limited by 20 m depth isobath, is further differentiated into two areas, the Northern Nearshore Zone (1b) and the Southern Nearshore Zone (1a). The parameters mentioned above are valid for the Southern Nearshore Zone.

Reef geometry and shelf depth are comparable in zone 1a and 1b, but in the latter the terrestrial influence is less. Transparency is higher and allows hermatypic corals to grow at depths down to 13 m, compared to only 7 m in zone 1a. Chlorophyll α concentration just off a reef in the Northern Nearshore Zone was 1.1 ± 0.1 μg/l (Erftemeijer, 1993).

The second zone (Mid Shelf) is similar to that of Moll (1983), but his zones 3 and 4 (Outer Shelf and Outer Rim) are combined in this study (Outer Shelf, zone 3+4, Fig. 3.1).

The reefs in the Spermonde Archipelago all are cay crowned reefs (Fig. 3.3, Umbgrove, 1929, 1930; Guilcher, 1988). The west side is exposed to oceanic swell during especially the rainy season and covered by coral. The east slope of the reef consists of carbonate sand (average grain size 0.5-0.25 mm) with isolated patches of coral growth. A rampart built of coral rubble borders the shallow reef flat to the west. The reef flat itself consists of barren carbonate sand (showing current/wave ripples) with some patchy corals, but hardly any sea grass.

The reef base consists of very coarse carbonate sand (average grain size 0.5-1 mm). At places there is rather diverse life, with solitary corals (both symbiont-bearing Fungiidae as non symbiont-bearing), sea pens and soft corals. Up to 70% of the sediment consists of empty foraminifera tests.

Methods

Fieldwork was carried out from August to November 1997 Fig. 2.2 shows the location of the investigated islands. The sampling sites were selected on the basis of maximum variation in parameters which may affect the distribution of larger foraminifera on the Spermonde shelf, such as distance to the coast and the river mouth and depth of the surrounding shelf. We sampled at 3 m depth intervals on both the west and east side of the islands by SCUBA diving. Due to restrictions in diving time and depth, the sample depths do not exceed 33 m.

In addition, bottom samples from the deeper parts of the shelf were taken with a van Veen grab. These samples were not suitable for quantitative analysis, but have been used to assess the presence and maximum depth of occurrence of living larger foraminifera. For each sample a circular surface area of 1000 cm^2 was collected. This could either be (calcareous) sand, coral rubble or (rarely) sea grass. On sand, macroalgae and sea grass substratum, it was possible to sample at every selected site. However, due to the dense coral cover on the seaward reef slope, the sampling was restricted to areas with coral rubble. On some outer shelf reefs (e.g., Bone Tambung and Kudinkareng Keke) it was very difficult to find suitable substrate for larger foraminifera on the seaward slope and samples have been taken as near as possible to the 3 m depth interval levels. The reef flats have been searched for foraminifera as well, but only around Langkai have larger foraminifera been found in water shallower than 2 m below low tide.

The samples were collected in bags, and taken to the laboratory, where the foraminifera were detached from the coral rubble and all samples were sun-dried. After sieving with a 0.5 mm sieve, the foraminifera that were alive when collected were separated from empty tests based by their symbiont colours.

Only the symbiont-coloured specimens were counted. Besides species belonging to the symbiont-bearing Nummulitidae, Amphisteginidae, Calcarinidae, Rotalidae, Peneroplidae, Soritidae and Alveolinellidae, *Elphidium craticulatum* was counted, because this well preserved tests show colouring. *Elphidium craticulatum* does not house symbionts but sequesters chloroplasts from algal food sources and utilises photosynthate produced by those chloroplasts (Reiss & Hottinger, 1984; Lee & Lanners, 1988; Lee & Anderson, 1991).

During the dives the most recognisable and conspicuous species were photographed. This adds information not only on how living species are positioned, but also on the presence of (rare) species which are underrepresented in the quantitative counts. Photographed species include *Operculina ammonoides*, *Dendritina ambigua, Amphistegina lessonii, Amphistegina radiata, Heterostegina depressa, Parasorites orbitolitoides, Amphisorus hemprichii* and *Calcarina spengleri*.

Species identifications follow Hohenegger (1994) and Hohenegger *et al.* (1999). For the generic subdivision we follow Loeblich & Tappan (1987). However, Hottinger *et al.* (1991) have shown that *Neorotalia* is not synonymous with *Pararotalia*. Additionally, Johann Hohenegger (pers. com.) identified some of the calcarinids. Our taxonomy differs somewhat from that by Troelstra *et al.*, (1996, see Chapter 2, above).

Cluster-analysis (squared Euclidean-distance, Ward's method) was carried out on a data matrix determined by samples and species densities (Figs. 3.2 and 3.3). A log transformation of the data was performed ($y = \log [y+1]$) in order to diminish extreme differences in abundance prior to analysis. The outcome of the cluster analysis was used for indicator species analysis by the method of Dufrêne & Legendre (1997), resulting in an indicator value for each species, ranging from 0-100. The indicator value for species x is calculated as a product of relative abundance in a cluster (average abundance of a given species in samples forming a cluster over the average abundance of the species in all samples) and the relative frequency of species x in a cluster (percentage of samples in a cluster in which species x is present). This value is calculated for each cluster, and the indicator value of a species is the maximum value calculated for any of the clusters. The Indicator value of a species is calculated using the following formulas:

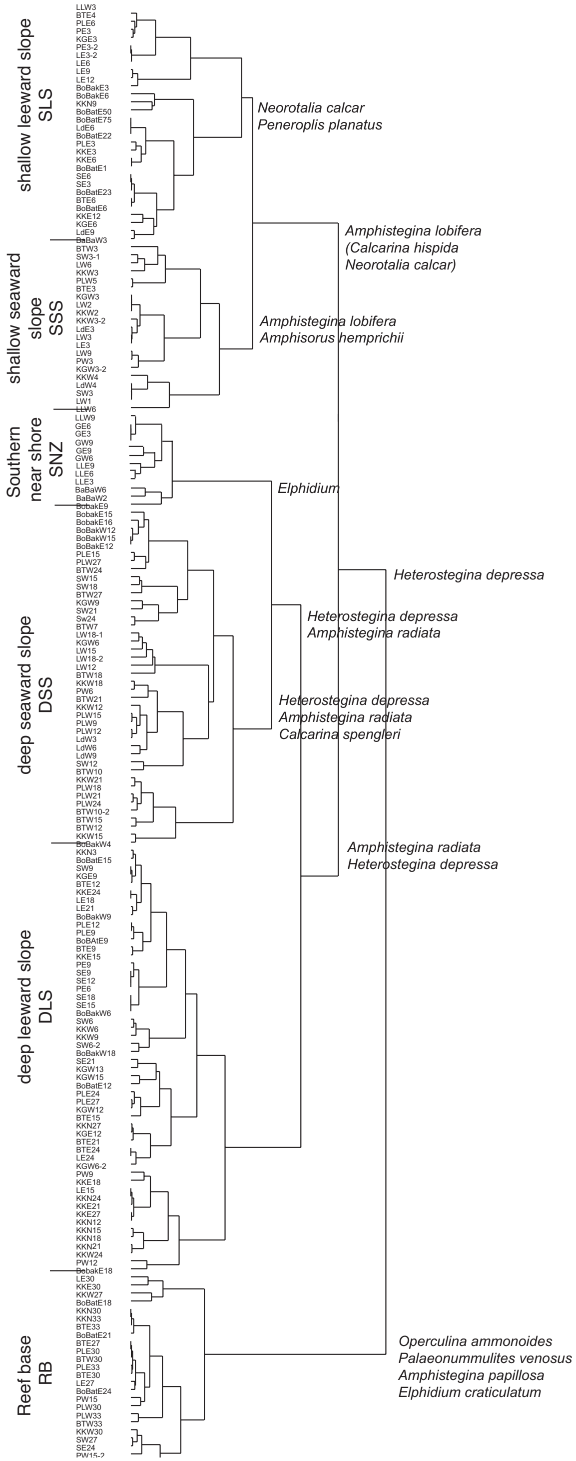


Fig. 3.2. Dendrogram resulting from a Q-mode cluster analysis using euclidian distance and ward's method of clustering for 182 samples taken in the Spermonde Archipelago. For the first 6 clusters the characteristic species as found in the indicator species analysis are shown.

Sample coding: the last number indicates the depth in metres at which the samples have been taken, the letter before the number indicates the side of the island at which the sample has been taken (E = east, W = west, N = north, S = south), the remaining letters are abbreviations of the island name: LL = Laelae, BT = Bone Tambung, PL = Pulau Lumulumu, P = Polewali, BoBak = Bone Bako, BoBAt = Bone Batang, BaBa = Barangbaringan, KG= Karanrang, L = Langkai, Ld = Lankadea, S = Samalona, KK = Kudinkareng Keke, G = Gusung

$A_{ij} = N_{ij}/N_i$
$B_{ij} = M_{ij}/M_j$
$IV_{ij} = A_{ij} \times B_{ij} \times 100$

In which

A_{ij} = mean abundance of species i in samples compared to all clusters
N_{ij} = mean number of individuals of species i across samples of cluster j
N_i = sum of the mean numbers of individuals of species i over all clusters
B_{ij} = relative frequency of occurrence of species i in cluster j
M_{ij} = number of samples in cluster j where species i is present
M_j = total number of samples in cluster j

Furthermore, a Montecarlo randomisation test is performed to test the significance of the observed indicator value.

Indicator value analysis was done first by assigning only 2 clusters with a cut-off level of 40, $p<0.05$. Species with an indicator value higher than 40 ($p<0.05$) are shown in the cluster diagram (Fig. 3.2) as typical for that cluster. Ultimately indicator species were determined for 6 clusters. Statistical calculations were done using PC-ORD version 4 (McCune & Mefford, 1999).

Results

The maximum depths at which larger foraminifera occur in the Spermonde area range from 6-9 m around coastal reefs to about 40 m around reefs in the Outer Shelf Zone (Tables 3.1; 3.3). The highest densities (up to 6 cm^{-2}) were found in reef base samples, followed by samples from the seaward oriented slope of the reefs (up to 3 cm^{-2}).

A very few living foraminifera have been found on the reef flats. The few samples that did contain foraminifera showed very low densities, confirming the results

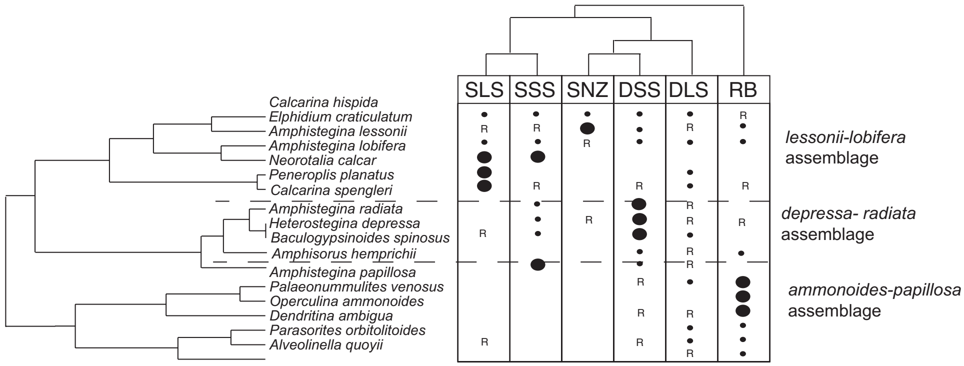


Fig. 3.3. A combined diagram of the results of a r and Q-mode clustering (for a complete version of the Q-mode dendrogram see Fig. 3.2). In the table the occurrence of species is given. Large dots represent species that are typical for an assemblage as shown by indicator value analysis (IV>40), small dots are species that occur regularly, but are not characteristic (5 < IV <40), and R species that are rare (IV<5). SLS: shallow leaward slope cluster, SSS: shallow seaward slope cluster: SNZ: southern nearshore zone cluster: DSS: deep seaward slope cluster, RB: reef base clustrer.

Table 3.1. Ecological parameters of the species of larger foraminifra found on the Spermonde shelf. For a more detailed discussion of these data see Chapter 2.
1) Hohenegger *et al.*, 1999, 2) Hohenegger, 1994, 3) Hallock, 1984, 4) Troelstra *et al.*, 1996, 5) Röttger & Krüger, 1990, 6) Hohenegger, 1996, 7) Hottinger, 1977a, 8) Vénec-Peyré, 1991.
* value in brackets was found in grab sample.

Species	Symbiont Type	Substrate Preference Spermonde	Substrate Preference Literature	Exposed to swell	Depth Spermonde	Depth published
Peneroplis planatus	Red algae	No preference	solid 1)	Not exposed	0-20 m, max at 3-12 m	0-30 m 1) 1-5 m 3)
Dendritina zhengae	Red algae	sand	sand 1)	No preference	3-30 m	10-50 m 1), 2)
Parasorites orbitolitoides	Chlorophyte	sand	sand 1)	No preference	6-24 m	10-70 m 2)
Amphisorus hemprichii	Dinoflagellate	solid	solid 1),2),4)	Exposed	0-20 m	0-40 m 1)
Amphistegina lessonii	Diatom	No preference		No preference	0-33 (40) m*	0-90 m 1), 3) 0-30 m 3) 5-35 m 8)
Amphistegina lobifera	Diatom	No preference		No preference	0-12 m	0-30 m 3) 0-20 m 2)
Amphistegina radiata	Diatom	solid	solid 1), 4) sand 3)	Exposed	0-33 m	0-60 m 2) 0->30 m 4)
Neorotalia calcar	Diatom	No preference	solid 1),2),3)	No preference	0-18 (30) m*	0-10 m 2) 0-5 m 3) 0-12 (21) m 4)
Calcarina gaudichaudi	Diatom	solid	solid 1)	Exposed	0-33 m	0-5 m 3),5) 0-20 m 1),2)
Calcarina hispida	Diatom	No preference	solid 1)	No preference	0-33 m	0-70 m 1), 2)
Baculogypsinoides spinosus	Diatom	No preference	solid 1), 2)	Exposed	6-30 m	20-80 m 1),2),6)
Elphidium craticulatum		No preference		No preference	0-33 m	
Heterostegina depressa	Diatom	solid	solid 1),4),7),8)	Exposed	0-33 m	0-100 m 3) 0-80 m 1)
Operculina ammonoides	Diatom	sand		No preference	9-33 m	27-60 m 6) 20-30 m 3) 6-20 m 4)
Palaeonummulites venosus	Diatom	sand	sand 1)	No preference	15-33 (40) m	30-80 m 1),2)

Table 3.2. Some ecological parameters of clusters defined in Fig. 3.2. Observed and expected number of samples (between brackets) per categories in the groups found in the cluster analysis. Observed number of samples that deviate substantially from expected are printed in bolt. The last column shows the average depth of the samples in the cluster, together with their standard deviation.

cluster	East facing	West facing	Southern Near Shore	Northern Near shore	mid shelf	Outer shelf	Average depth (m)
Reef base	15 (11.8)	9 (12.2)	0 (2.0)	2 (3.5)	6 (6)	16 (12.8)	26.6±5.6
Shallow seeward slope	**3 (10.4)**	18 (10.6)	1 (1.7)	5 (3.3)	2 (5.1)	13 (10.8)	3.3±4.0
Deep seeward slope	**5 (20.8)**	**37 (21.2)**	0 (3.5)	6 (6.7)	11 (10.2)	25 (21.7)	14.7±7.1
Shallow leeward slope	**27 (13.8)**	**1 (14.2)**	1 (2.3)	6 (4.6)	10 (7.0)	12 (14.9)	4.9±5.2
Deep leeward slope	30 (22.7)	16 (23.4)	0 (4.3)	10 (8.4)	15 (12.8)	28 (27.4)	14.5±8.2
Southern near shore	3 (3.5)	4 (3.5)	**13 (1.1)**	0 (2.1)	0 (3.1)	**0 (6.7)**	6.1±2.8
Total	83	85	15	29	44	94	

Table 3.3. Indicator values of 18 species of larger foraminifera in six assemblages as recognised in Fig. 3.3. The first six columns show the indicator value of the species for the six assemblages. The max group column shows the assemblage with the highest indicator value for each species, species with p<0.05 are printed in bold. The randomised indicator value and standard error of randomised indicator value shows the value obtained after 1000 runs with the samples randomly divided into 6 groups with the same number of cases in each group. The p-value shows the proportion of randomised trials with indicator value equal to or exceeding the observed indicator value.

number of cases	29	22	12	42	53	24				**standard**	
Species	**SLS**	**SSS**	**SNZ**	**DSS**	**DLS**	**RB**	**max group**	**IV**	**randomized IV**	**error of randomized IV value**	**p**
Calcarina hispida	24	7	14	8	12	3	**SLS**	24.2	17.8	3.07	0.0340
Calcarina gaudichaudii	0	21	0	46	4	0	**DSS**	46.3	14.0	3.54	0.0010
Neorotalia calcar	67	0	0	0	7	0	**SLS**	66.5	13.8	4.66	0.0010
Baculogypsinoides spinosus	0	0	0	15	2	11	**DSS**	15.1	8.9	3.35	0.0580
Amphistegina lessonii	24	18	2	15	22	18	**SLS**	24.4	20.2	1.90	0.0290
A. lobifera	41	49	0	0	0	0	**SSS**	49.0	12.6	3.00	0.0010
A. papillosa	0	0	0	2	7	52	**RB**	51.9	11.5	3.76	0.0010
A. radiata	0	21	2	51	4	4	**DSS**	50.8	16.5	3.33	0.0010
Operculina ammonoides	0	0	0	3	5	88	**RB**	88.3	16.6	3.87	0.0010
Heterostegina depressa	2	12	0	59	10	2	**DSS**	59.1	16.9	3.35	0.0010
Palaeonummulites venosus	0	0	0	0	0	73	**RB**	73.5	8.6	3.67	0.0010
Elphidium craticulatum	2	4	53	8	4	18	**SNZ**	53.3	18.8	3.23	0.0010
Peneroplis planatus	47	2	0	2	24	4	**SLS**	46.9	16.6	3.55	0.0010
Dendritina ambigua	0	0	0	0	9	23	**RB**	23.4	7.9	3.21	0.0020
Alveolinella quoyii	0	0	0	0	2	21	**RB**	21.1	6.5	3.22	0.0080
Laevipeneroplis proteus	2	4	0	0	0	0	SSS	4.4	3.6	1.99	0.2870
Amphisorus hemprichii	0	45	0	13	4	0	**SSS**	44.5	11.1	3.54	0.0010
Parasorites orbitolitoides	0	0	0	3	9	29	**RB**	29.4	10.3	3.44	0.0030

obtained by visual inspection. An exception is the western part of the reef flat of Langkai where high densities of larger foraminifera were found. Here, they occurred living attached to coral rubble at 0.5 m and deeper below the low tide level. The substratum on the other reef flats consisted either of clean sands showing wave ripples or patches of, usually living, corals. Neither substrate was favourable for larger foraminifera occupation.

On the reef flat of Langkai two samples were taken from *Enhalus* meadows, however no epiphytic foraminifera were found. In total, the research area yielded 20 larger symbiont-bearing species and *Elphidium craticulatum*. Of these, *Peneroplis pertusus* and *Laevipeneroplis proteus* were found in only a very few samples. *Laevipeneroplis proteus* was found on the reef flat around Langkai, where it occurred abundantly on sandy patches between the corals. *P. pertusus* occurred in very low numbers in two samples on sandy substrate.

The distribution of the most important species has been summarised in Table 3.1, and is discussed in more detail in chapter 2. All species exhibit an increasing lower depth limit offshore. In the Southern Nearshore Zone, living larger foraminifera have only been found on the top of the reef slope, the reef base was devoid of larger foraminifera. In the three other zones, the reef base showed the highest density (up to 6 cm^{-2}).

The Q-mode cluster analysis shows a grouping into 6 clusters (Fig. 3.2). The results of the indicator value analysis provides additional information on the ecological difference between the clusters. Based on the reef geometry, the samples can roughly be divided into three groups: shallow reef slope, deep reef slope and reef base. Samples collected both at the shallow parts of the reef slope and the deep reef slope can be differentiated into subclusters with samples taken at the seaward oriented reef slope and samples collected at the leeward oriented reef slope. A third subcluster is recognised within the deep slope group, comprising only samples that show a co-occurrence of *E. craticulatum, A. radiata* and *C. hispida*. For these six clusters, some environmental parameters (slope orientation, position on the shelf, and depth) characterising these clusters are summarised in Table 3.2. This confirms the pattern described above.

Based on the cluster analysis, no differences can be observed between the Northern Nearshore, Mid Shelf and Outer Shelf zones. Five clusters occur around the reefs sampled in these areas. The depth at which they occur increases gradually though, especially for the reef base and deep seaward slope cluster. In the Southern Nearshore Zone, the reef base assemblage is absent, and the reef slope is occupied by the Southern Nearshore Zone cluster. The shallow seaward slope cluster is found at 2-3 m water depth in this zone.

The indicator values of the species in each of the six clusters are shown in table 3.3. Note that there are no species indicative of the deep leeward slope assemblage. In the reef base cluster, three species have very high indicator value, and another three species have moderately high indicator values, but have hardly been found in samples in other clusters.

The R-mode cluster analysis indicates three assemblages (Fig. 3.3). Generally speaking, these are the *ammonoides- papillosa* assemblage, characteristic for the reef base-, the *depressa- radiata* assemblage, predominantly occurring on the exposed reef slope- and the *lessonii-lobifera* assemblage, predominantly on the leeward reef slope.

Most sample clusters contain species from at least two assemblages (Fig. 3.3). The clusters can not be expressed as simple mixing of two assemblages, since they usually do not contain all species from each assemblage, indicating gradual transitions between the assemblages. For example, the shallow seaward slope cluster contains species from the *lessonii-lobifera* assemblage and the *depressa-radiata* assemblage, but *Peneroplis planatus, Neorotalia calcar* and *Baculogypsinoides spinosus* are absent. In the following part we summarise the distribution of the species over the Spermonde Shelf.

Amphisteginidae

Two species groups can be recognised in this family, the *A. lessonii* group and the *A. radiata* group. The amphisteginids occurring in the Spermonde Archipelago occupy similar niches as in other areas (Table 3.1). *Amphistegina lobifera* Larsen has its highest densities in samples taken at 3-6 m, but is found in much lower densities on the reef flat. The depth range hardly increases going off shore. *A. lessonii* is the most common larger foraminifer, occurring in all samples collected by SCUBA diving. The highest densities were found on the reef slopes and less at the reef base.

A third species in this group, *A. bicirculata* Larsen , was not found in the Spermonde Archipelago. Elsewhere (Red Sea; Hansen & Buchardt, 1977, Hawaii; Hallock, 1984, and Okinawa; Hohenegger, 1994, 2000) this amphisteginid species occupies deep habitats.

Amphistegina radiata (Fichtel & Moll) is found predominantly on the west slope of the reefs, were it co-occurs with *A. lessonii* attached to coral rubble. *A. papillosa* Said is found to live below the zone with coral cover in reef base samples, irrespective of exposure.

Nummulitidae

Operculina ammonoides (Gronovius) is the most abundant foraminifera in the reef base assemblage in the Spermonde Archipelago. It is found on rather coarse sediments, in densities exceeding 3cm^{-2}. The maximum depth at which it has been found alive is 45 m (in a grab sample, 33 m was the largest depth for samples that have been counted) in the Outer Shelf Zone. This species was only present in samples taken at the reef base, which lies between 12-15 m in the Northern Nearshore Zone, 21-27 m in the Mid Shelf Zone and between 30-33 m on the Outer Shelf Zone (Fig. 2.18). It did not occur in the Southern Nearshore Zone.

Palaeonummulites venosus (Fichtel & Moll) is mainly found together with *O. ammonoides*. It only occurs in samples taken at the reef base, usually in the deepest samples. It has not been found in the Northern Nearshore Zone.

The other nummulitid in the Spermonde Archipelago is *Heterostegina depressa* d'Orbigny. This species is found at the exposed reef slopes in all four zones. It is rare in the Southern Nearshore Zone, where it is only found at the highest part of the slope. In the other three zones, *H. depressa* is found all over the exposed slope.

Operculina discoidalis (Cushman) has been recorded from Okinawa and Palau (Hohenegger, 1996; Hohenegger *et al.*, 2000), but not in the Spermonde Archipelago. *O. discoidalis* is found at similar depths to *Operculina ammonoides*, but is typical for muddy substrates in very calm water (Hohenegger *et al.*, 2000), a habitat which is not present in the Spermonde within the photic zone.

Operculina complanata (Defrance) and *O. heterosteginoides* Hofker are very rare in some grab samples from 35-45 m in the Outer Shelf Zone, and are more common in Okinawa (Hohenegger *et al.*, 2000).

Palaeonummulites cummingii (Carpenter), *Cycloclypeus carpenteri* Brady, and *H. operculinoides* Hofker have not been found in the Spermonde. Elsewhere, all three reach their highest density in samples taken at larger depth than *P. venosus* (Hohenegger *et al.*, 2000; Hohenegger, 2000).

Calcarinidae

Studies dealing with the habitat use of calcarinids usually show that they live attached to algae and are well adapted to high hydrodynamic energy levels (Hohenegger *et al.*, 1999). The calcarinid species of the seaward reef flat cluster of Palau (Hallock, 1984) and the upper slope at Okinawa (Hohenegger, 1994; Hohenegger *et al.*, 1999) are also present in our samples (except for *Baculogypsina sphaerulata* (Parker & Jones) and *Calcarina defrancii* d'Orbigny). *Calcarina hispida* Brady (Fig. 2.13) and *Neorotalia calcar* (d'Orbigny) show their highest abundance in samples in the leeward upper slope cluster, while *Calcarina spengleri* (Gmelin) (Fig. 2.14) has its highest abundance in samples in the lower seaward slope cluster. Here *C. spengleri* lives attached to coral rubble covered by red algae. *Neorotalia calcar* and *C. hispida* are abundant in samples taken on sandy substrate, where they live on top of the sediment, forming dense patches. *C. hispida* also occurred abundantly in the Southern Nearshore Zone. At the leeward slope, this was the most common larger foraminifera next to *Amphistegina lessonii*. Since it prefers quiet water *C. hispida* is most abundant on the upper slope, but avoids the reef edge and the reef crest (Hohenegger, 1994, 1996, 2000) in Okinawa. These three species occupy different habitats than observed in Okinawa and Hawaii (Hallock, 1984; Hohenegger, 1994), where *C. spengleri* and *N. calcar* occurred predominantly on the reef flat. Only the deepest living calcarinid, *Baculogypsinoides spinosus* Yabe & Hanzawa, is observed in habitats similar to Okinawa (Hohenegger, 1994; Hohenegger *et al.*, 1999), but this species occurs at shallower depth in the Spermonde Archipelago (maximum at 27 m in the Outer Shelf Zone, compared to the maximum at 55 m in Okinawa).

Peneroplidae

Peneroplis planatus (Fichtel & Moll) is the most abundant peneroplid. It is the characteristic species for the upper leeward slope assemblage. Here it occurs on sandy substrates. It has its maximum occurrence in the shallowest samples, but is found down to 30 m in the Outer Shelf Zone. The maximum depth is similar to that in Okinawa (Hohenegger *et al.*, 1999), where the highest density is also reached in the shallowest samples. *P. planatus* is said to avoid soft substrates (Hohenegger *et al.*, 1999). At Okinawa, this species lives attached to 'fine algal mats' where it finds shelter against high turbulence.

Dendritina ambigua (Fichtel & Moll) is the other regularly occurring peneroplid. It is found in reef base samples, together with *O. ammonoides* and *P. venosus. D. zenghae* Ujiíe, *Peneroplis pertusus* Forskål and *Laevipeneroplis proteus* (d'Orbigny) were found in only a few samples. Hallock (1999) argued that the high Mg calcite tests of porcelaneous foraminifera might account for part of the distributional limitations.

Soritidae

On the Spermonde Shelf, *Amphisorus hemprichii* Ehrenberg is found living attached to large boulders of coral rubble at the highest energy sites, as well as at more sheltered places.

Marginopora vertebralis (Quoy & Gaimard) is the largest soritid, living in very shallow water in the frontal and central region of the reef moat and on the upper reef slope in high hydrodynamic settings (Hohenegger, 1994). *Amphisorus hemprichii* was found in the same areas, but in more sheltered places (Hohenegger, 1994). We found *Sorites orbiculus* Forskål in only a few samples on solid substrate. *Parasorites orbitolitoides* (Hofker), the only regularly occurring larger foraminifer in the Spermonde housing chloroplast symbionts, is encountered at the reef base in all but the Southern Nearshore Zone. In Okinawa it is living in sheltered sandy places (Hohenegger, 2000).

Alveolinidae

We found only one species of alveolinid, *Alveolinella qouyii* (d'Orbigny) at the Spermonde. This species lives in very low densities at the reef base laying on top of coarse sand. It was often seen during diving, but it hardly occurred in collected samples. This is a species of solid, well structured habitats outside the Spermonde (Lipps & Severin, 1986; Hohenegger 1994, Hohenegger *et al.,* 2000). Here they find shelter against high hydrodynamic energy in shallow water. Hohenegger (1994) and Hohenegger *et al.* (1999) found this species also in a wider habitat range at Okinawa.

Elphidium craticulatum (Fichtel & Moll)

This species shows a similar distribution to *Operculina ammoinoides*, except for its occurrence in the Southern Nearshore Zone (Fig. 2.16). Here *Elphidium craticulatum* occurs abundantly on the reef slopes, while *O. ammonoides* is not present. In the other three zones, *E. craticulatum* reaches its highest density in the deepest samples.

Discussion

The species richness of larger foraminifera in the Spermonde region is much lower than in the Hawaii, Palau and especially Okinawa carbonate environments. About seven lamellar-perforate and three porcelaneous species are absent, while several of the other species are very rare.

The reefs in the Northern Nearshore, Mid Shelf and Outer Shelf Zones all show a very similar larger foraminiferal fauna. Samples taken around the reefs group in one reef base cluster and four reef slope clusters. The depth at which the cluster samples are found gradually increases in an off shore direction, associated with the increasing depth of the photic zone.

The southern nearshore cluster is the only cluster with a limited distribution over the shelf. The samples in this cluster have been taken where in the other zones the reef base and both deep slope clusters are found. Terrestrial input affects the Southern Nearshore area very directly and therefore only those species with a high tolerance to a seasonally varying environment occur.

In both deep and shallow water the largest species are absent. Large size is especially advantageous in stable, oligotrophic conditions. Seasonal variation in climate conditions affects the environment in which larger foraminifera are living. Symbiont-host systems are vulnerable to periodically low light levels, since the metabolic rate is higher than in asymbiotic foraminifera. Seasonally high nutrient fluxes cause a period of several months each year in which the conditions are unfavourable for symbiont-bearing foraminifera, although during the rest of the year the conditions may well be suitable.

A long generation time is advantageous to a foraminifer when the survival rate is strongly size dependent (Hallock, 1985). In this situation large parents have high fecundity with relatively large agamonts that have a higher chance of survival. The generation time of *Cycloclypeus carpenteri* is 11-13 months (Krüger *et al.*, 1996), that of *Marginopora vertebralis* 1-2 years (Ross, 1972), while the generation time of *Amphisorus hemprichii* is only 4 months (Zohary *et al.*, 1980) and that of *Heterostegina depressa* and *Amphistegina* 4-12 months (Röttger, 1974; Hallock, 1981c; Hallock *et al.,* 1986). For long living species the suitable substrate should be continuously present during their full live span (Hottinger, 1990). In the Spermonde Archipelago habitat disruption occurs by periods of high hydrodynamic energy during the rainy season, by strong oceanic swell and storms (Storm, 1989). During these periods, coral rubble on the ramparts and seaward reef slope is moved. Locally, the reef slopes become unstable and avalanches

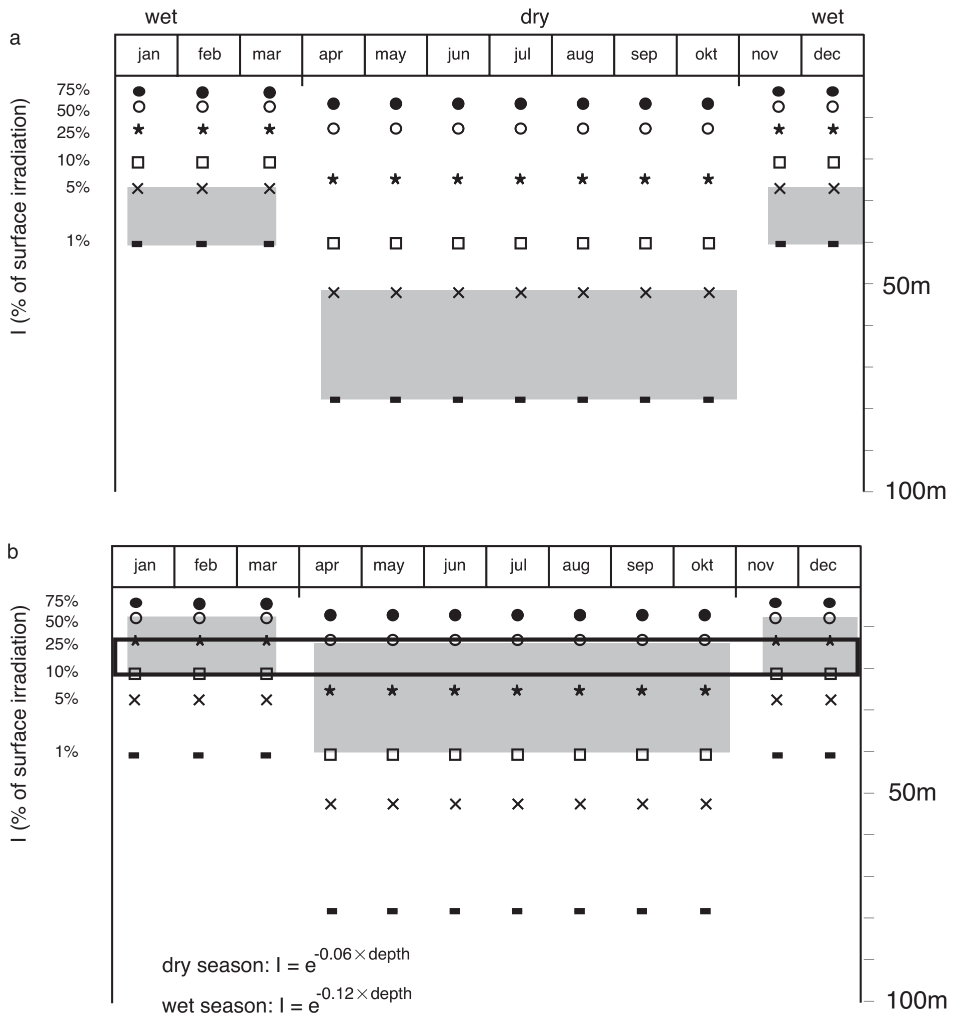


Fig. 3.4. Schematical representation of the irradiation levels (I) in the Spermonde Archipelago. During the fair weather season transparency is twice as high as during the rainy seeason. For convenience it is assummed that the transition from fair to rainy weather season and vice versa is abrupt. The shaded area indicates the depth with suitable irradiation levels.
a: A species that lives at larger depth and tolerates I = 1-5% surface irradiation
b: A species that lives at shallower depth and tolerates I = 10-50% surface irradiation

of reef debris (5-20 m wide) are caused. Larger foraminifera with long life cycles will not reproduce in this environment.

Another environmental parameter that varies year round is the water transparency. The limited extent of the euphotic zone during the wet season is less favourable for the deep living species. A simple model can explain why species that can survive in low irradiation levels are more susceptible to seasonal variation than shallow living species. In this model the first assumption is that all species have the same response function to irradiation level. For example, a shallow living species has a range of 10-50% of the surface irradiation level, a deep living species 1-5%. The only figures available are those provided by Hohenegger *et al.* (2000). These figures show that deep living species like *Operculina heterosteginoides* and *Heterostegina operculinoides* have similar ranges to the shallower living species such as *Operculina ammonoides* or *Heterostegina depressa.* The second assumption is that populations are not able to move into deeper/shallower habitats seasonally.

Larger foraminifera can only maintain their large cell mass because of the energy provided by their symbionts. During longer periods of adverse conditions, maintaining symbionts will not be profitable anymore. Thus, larger foraminifera will only be able to live in places where the conditions will be favourable yearlong. In seasonal conditions, transparency is reduced during part of the year. The hypothetical depth at which the foraminifer species can live thus becomes shallower (Fig. 3.4a, b). A species can only survive at a locality, otherwise favourable, when the irradiation level is sufficient yearlong. This condition is more likely to be met for shallow living species than for deep living species (Fig. 3.4a).

In the Spermonde Archipelago the difference between the transparency in the fair weather and rainy weather season decreases with increasing distance off shore. This increases the chance that yearlong profitable irradiation levels are present for deeper living species (Fig. 3.4b).

The Spermonde Archipelago has a very shallow photic zone limiting the depth at which symbiont-bearing foraminifera can live. They are absent in coastal waters and gradually appear in deeper waters offshore. On reefs in the Southern Nearshore Zone such as Gusung, Lae Lae and Barang Beringan, larger foraminifera have only been found on the reef slope and reef crest down to 9 m. The reef base and shelf around these islands are devoid of living larger foraminifera. In this zone *E. craticulatum* is an important faunal component on the lower and upper reef slope. In the northern nearshore strip, high densities of larger foraminifera occur both on the reef slope and the reef base which is only 15 m deep here. The deepest living larger foraminifera in the Outer Shelf Zone have been found in a grab-sample from 40 m depth. In deeper samples no living larger foraminifera were observed. This pattern compares with the change in the secchi depth over the shelf and shows that light is the most important parameter in limiting the occurrence of larger foraminifera on the shelf.

Hallock (1984) performed a comparative study on samples from Palau and Hawaii. She found that for the Palau samples, depth was the most important property affecting the position in a cluster of a species. Her study revealed four clusters, a cluster characteristic of seaward reef flats, one for more protected shoals, one for shallow slopes (5-20 m) and an assemblage containing typical deeper dwelling species. On Oahu (Hawaii) the seaward reef flat cluster was absent. The samples were divided into a shallow and a deep cluster (Hallock, 1984).

Our observations from Spermonde are a combination of the Palau and Hawaii patterns. We found that depth related parameters such as light and hydrodynamic energy are the most important variable, but a reef flat cluster is absent. Furthermore the deep and shallow reef slope clusters can be divided into seaward and leeward components.

Our data show that depth of occurrence is dependent on light intensity. Both species and assemblages occur in deeper water when transparency is higher. Fauna composition is only affected in areas with direct fluvial influence where seasonal variation in nutrients, transparency and salinity directly influence the occurrence of larger foraminifera. Under these variable conditions, the Reef Base cluster is not present at all, and the reef slope is inhabited by a characteristic assemblage for this region.

In the Northern Nearshore, Mid Shelf and Outer Shelf Zones, annual variation in nutrient level and salinity has not been recorded. Transparency increases going offshore, and is lower in the wet season than in the dry season (Erftemeijer, 1993; Verheij, 1993).

Hallock's (1987, 1988) trophic resource continuum model has been designed to explain diversity differences, both in time and between regions. In this model the diversity of larger foraminifera is related to nutrient levels (Fig. 3.1a). On a regional scale, faunas in oligotrophic areas show the largest maximum depth of occurrence and highest diversity. In less oligotrophic conditions light penetration is limited by higher plankton concentrations in the water column. The maximum depth at which larger foraminifera are found is thus less. As predicted by Hallock (1987), in areas with mesotrophic conditions and seasonal variation, such as the Spermonde Archipelago, the habitat for deep living species is not available. We noticed that in the deepest samples, near the bottom of the photic zone the density of *Elphidium* increases. This species is less sensitive to periods of adverse conditions since it does not keep symbionts but retains chloroplasts out of digested algae (chloroplast husbandry, Lopez, 1979). This implies that foraminifera take up and retain free undamaged chloroplasts from their food under natural conditions which show active photosynthesis for at least several days. The foraminifera utilise products of the photosynthesis by their chloroplasts (Lopez, 1979). There is a continuous turnover of the chloroplasts, with a turnover time varying from days to weeks (Lopez, 1979; Lee & Anderson, 1991). When there is no light available the foraminifer can digest chloroplasts and does not have to provide metabolic energy to the symbionts. A similar pattern was observed by Hollaus & Hottinger (1997) near Crete. Here *E. craticulatum* replaced *A. lessonii* below the thermocline, again showing that *E. craticulatum* is less vulnerable to conditions that are not favourable for larger foraminifera.

Conclusion

Variations in nutrient concentration do not directly affect the distribution of all larger foraminifera, and only a limited number of species of larger foraminifera are able to live in an area with high seasonal variations in nutrients and salinity. In the mesotrophic, seasonally variable Spermonde Archipelago, the largest species with the longest life-cycles are absent.

Seasonal variation in transparency of the water in the Northern Nearshore, Mid Shelf and Outer Shelf Zones limits the maximum depth of occurrence of larger foraminifera to depths above the deepest part of the photic zone in the fair weather season.

All species were living in deeper water further from shore than nearshore, rendering it impossible to estimate the depth at which a sample is taken by looking at its living foraminifera content alone. The same assemblage (for example *Operculina ammonoides, Amphistegina papillosa* and *Parasorites orbitolitoides*) can be found at 14 m on the reef base of nearshore islands, and at for example 40 m around offshore islands. If you find these three species in a fossil sample, you can not see whether it was deposited at 14 or 40 m, unless you find other indications of depositional environment.

The larger foraminiferal fauna of the Spermonde Archipelago is characterised by a relatively low diversity and a shallow lower depth limit. Apart from a near coastal zone, we could not distinguish the zonation based on Scleractinia (Moll, 1983) and marine plants (Verheij, 1993). The most important parameters determining larger foraminiferal distribution are light intensity, fluvial influence, hydrodynamic energy, and related parameters like reef geometry.

Because of specific features such as exposure to oceanic swell, bathymetry, and fluvial influence, not all habitats observed in Okinawa and Palau are present. However, not all species typical for these habitats are absent from the Spermonde Archipelago. Some, like *Neoratalia calcar* and *Peneroplis planatus*, have been found in habitats characterised by other parameters. Thus, the habitat preferences of these species are broader than previous studies have shown.

As a consequence of assigning the maximum depth of occurrence to nutrient level, the Hallock model predicts that species that live in the deepest habitats under oligotrophic conditions are the first to disappear when nutrient concentration increases. Shallower living species will occur at shallower depth and exhibit the smallest depth variation. Generally speaking, these predictions are met in the mesotrophic Spermonde Archipelago. However, differences are seen between various families of larger foraminifera.

The distribution of members of the families Nummulitidae and Amphisteginidae most closely match the predictions of this model. Large, deep living taxa have not been found in the Spermonde, while shallow living taxa occur hardly deeper in the Outer Shelf than Northern Nearshore Zone. A tolerant species like *Operculina ammonoides* is found in the Northern Nearshore, while *Palaeonummulites venosus* is found only in the Outer Shelf Zone.

The calcarinid species, except for *Baculogypsinoides spinosus* do not react to the environmental parameters as predicted by the model. Some of the shallowest living species are absent, while the highest density of other species have been found in deeper water than in more oligotrophic areas like Okinawa and Japan. This shows that *C. spengleri* and *N. calcar* are more eurytopic than *Baculogypsina sphaerulata* and *Calcarina defrancii*.

Of the Peneroplidae, *Peneroplis planatus* shows a pattern similar to *N. calcar* and *C. spengleri*. Because the habitat it prefers at Okinawa is not present, *P. planatus* is found in a different habitat in the Spermonde Archipelago. The maximum depth at which *P. planatus* is found, however, is similar to that at Okinawa (Hohenegger, 1994).

The soritids do not form an exception to Hallock's model. The only difference is that the largest species is absent, and *Amphisorus hemprichii* is found at all hydrodynamic energy levels, while at Okinawa *A. hemprichii* is not found at the most exposed sites where *M. vertebralis* is found.

Alveolinella quoyi shows a broad habitat spectrum at Okinawa, and is found in the Spermonde Archipelago only in the deepest part of the range it occupies at Okinawa.

4. Thanatofacies of larger benthic foraminifera on the Spermonde Shelf (Southwest Sulawesi, Indonesia)

Introduction

In modern day tropical marine environments larger foraminifera are important carbonate producers (Hallock, 1981b; Scoffin & Tudhope, 1985; Yamano *et al.*, 2000). On the Pater Noster platform at the west side of Makassar Strait the sediment mass consists for more than 33% of larger foraminifera (Boichard *et al.*, 1985). Calcarinids were found only in samples near two shallow areas, while *Operculina* occurred in the deeper parts. *Alveolinella* and *Heterostegina* were present near islands as well, but had their maximum further away from the islands (Boichard *et al.*, 1985).

A sedimentological study of the Great Barrier Reef showed that over the whole area larger foraminifera were the most important sand producers (Scoffin & Tudhope, 1985; Tudhope & Scoffin, 1988). Benthic foraminifera sands dominated the bulk of the shelf area. Seven facies along a transect from the inner shelf to outer shelf were recognised. The most important foraminifer contributing to the sediment was *Operculina* sp. (Tudhope & Scoffin, 1988).

Yamano *et al.* (2000) found that larger benthic foraminifera were the single most important contributor to the sediment production that maintain the sand cay reefs. They found high production of foraminifera associated with algae on the reef flat of the island they investigated. The most important producers were *Calcarina hispida, Baculogypsina sphaerulata* and *Amphistegina lessonii*.

Symbiont-bearing larger foraminifera live within the photic zone, both on reefs and on carbonate platforms. The most important environmental parameters influencing the distribution of living larger foraminifera on modern day reefs are temperature, light intensity, substrate type and nutrient availability, all interrelated with depth (Hottinger, 1977a, b; Hallock, 1981b; Hohenegger, 1994; Hohenegger *et al.*, 1999, 2000). Larger foraminifera only occur in warm water with a minimum temperature higher than 16°C in the coldest month (Murray, 1991; Langer & Hottinger, 2000). Different types of symbiont, shell structure and shell morphology determine the preferred depth at which larger foraminifera species occur. Generally speaking, light transparency of the shell is less in imperforate compared to lamellar perforate foraminifera, restricting the former to shallower habitats.

In order to increase the surface-to-volume ratio deep living larger foraminifera have flatter shells than shallow living larger foraminifera (e.g., Hallock, 1981c; Hallock *et al.*, 1991b). Microstructures on the test serve to increase strength and to focus light to get maximum profit from their symbionts (Hallock *et al.*, 1991b; Hottinger,1997). Species that live in shallow water have to deal with higher hydrodynamic energy and illumination levels. These species are more robust, or are capable of strongly attaching to the substrate.

Another important parameter is substrate type. The main types of substrate are sea grasses or macroalgae, solid substrates and sandy substrate (Hohenegger, 1994). Foraminifera live attached to solid substrates to find shelter in high energy environments. Shallow living foraminifera can move their symbionts in response to light intensity. In this way they can regulate the light intensity to which the symbionts are exposed. In order to do so they need a dark substrate, such as coral rubble covered by coralline algae or sea grass (Hottinger, 1997). Larger foraminifera attach to solid substrate by means of a sheath of protoplasm (for example *Amphisorus*) or by their pseudopodia (like *Amphistegina* or calcarinids). When they die, they detach from the substrate because of the decay of the protoplasm and can easily be transported.

Larger benthic foraminifera can make up to 80% of tropical Cenozoic carbonates, and are often important contributors to marly sediments as well. Foraminifera are widely used for stratigraphical reasons. However, the use of larger benthics as palaeoenvironmental indicators is limited. In palaeoenvironmental reconstructions, larger foraminifera are often associated with bioherms, usually with barrier or fringing reef settings (Hottinger, 1983; van Gorsel, 1988). Larger foraminifera are used to discriminate between (deep and shallow) fore reef and back reef settings. For example, abundant occurrences of imperforate foraminifera (including alveolinids) are interpreted as typical for back reef settings, while the predominant occurrence of large flat discocyclinids, lepidocyclinids or *Cycloclypeus* are indicators for deep fore reef settings (Hottinger, 1997).

The most common use is as indicator for depositional depth. Turnover events changed the composition of larger benthic foraminifera communities during the Cenozoic. In each of these periods, species did specialise to live in restricted parts of the euphotic zone. For example *Discocyclina* (during the Eocene) and *Lepidocyclina* and *Cycloclypeus* (during the Oligocene and Miocene) live in the deepest parts of the photic zone. In an overview of the use of shallow benthic foraminifera for depth estimations, Hottinger (1997) concludes that within each unit of evolutionary community maturation the depth zonation of larger foraminifera species should be considered separately. Before using larger foraminifera in palaeoenvironmental reconstructions, it is necessary to know whether the dead assemblage is a good representation of the living fauna. Are the empty shells of the species only found where they lived, or can they be found all over the area?

In this study the distribution of empty shells of larger foraminifera in 208 samples taken in three transects over the Spermonde Shelf has been compared with the distribution of living larger foraminifera, in order to improve their use as palaeoenvironmental indicators.

Area

The Spermonde Archipelago (Fig. 4.1) is located on a shallow carbonate platform off SW Sulawesi (Indonesia) in the Makassar Strait. Water depth increases gradually going offshore until the platform reaches its maximum depth of 60 m on the Outer Shelf (Fig. 4.2). The shelf edge is not marked by continuous reef growth. The rim is about 20 m deep over most of its length, but some reefs occur on the shelf edge (e.g., Langkai). To the south, the research area is bordered by the outflow of a river (the Jene Berang) which discharges sand and silt on the Spermonde Shelf.

After the last Pleistocene sealevel lowstand, the platform was flooded and sand-cay type reefs formed on top of an ancient relief (de Klerk, 1983). Island-topped reefs occur on shore-line parallel ridges. Between 0-15 km off the mainland shore, most reefs are island topped, while beyond this most reefs are submerged.

The Western (exposed) slope of a typical reef in the Spermonde Archipelago has a

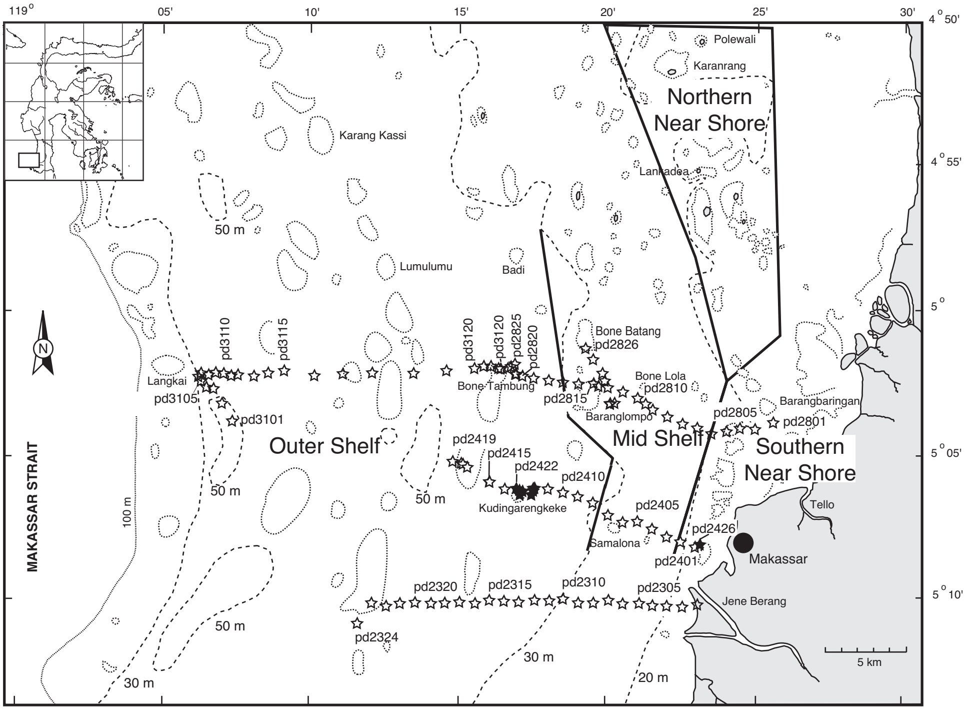


Fig. 4.1. Map of the study area, SW Sulawesi, Indonesia. A-A' cross section of fig. 4.2.

dense coral cover (Fig. 4.3). The deepest part of the western slope is not covered by corals, but by debris and very coarse sand. The coral cover reaches a shallower depth going towards the South or North of the island, and is not present on the Eastern slope (Fig. 4.3). The Eastern (leeward) slope consists entirely of carbonate sand, with some sea grass (*Halophilus)* patches. These patches never reach large sizes nor high densities. Around the reefs the slope gradient decreases and grades into the reef base.

The main current through the Makassar Strait (and over the Spermonde Shelf) is flows southward, providing a relatively well mixed and constant environment all over the shelf. Transparency is minimal during the SW monsoon, but nutrient levels are rather stable. Previous studies have shown that the Spermonde Archipelago can be divided into four biozones (Moll, 1983; Hoeksema, 1990). The first zone extends from the mainland shore to the 20 m isobath, the second from the 20 m to the 30 m isobath. The third and fourth zones comprise the Outer Shelf (depth larger than 30 m) and the barrier, respectively. In chapters 2 and 3 the nearshore zone was divided into two. Zone 1A (Southern Nearshore zone) is the area shallower than 20 m and near the mainland shore, while zone 1B (Northern Nearshore zone) is found within the same depth interval, but at more than 4 km from the shore. In zone 1A variability in nutrient and chlorophyll a concentration is higher than elsewhere on the shelf where nutrient and chlorophyll a concentration are two to three times higher during the SW monsoon than during the NW monsoon (Verheij, 1993). In the other zones, these concentrations are more constant year-round.

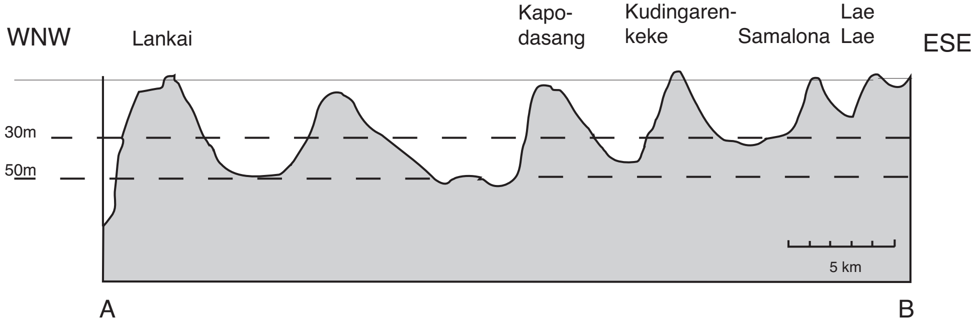


Fig. 4.2. Cross section over the Spermonde Shelf, showing the bathymetry

The carbonate content of the sediment varies from 0.1% near the mouth of the Jene Berang to about 45% off Laelae. Further from the coast the carbonate content is between 70 and 95%. The non carbonate component near the Jene Berang consists mainly of very fine quartz sand to clay. All over the shelf a small silliciclastic silt to clay fraction is found.

The climate is dominated by a SW-NE monsoonal system. The SW monsoon blows from November until April, when oceanic swell and storms cause high hydrodynamic energy on the west side of the reefs. During the SW monsoon the discharge of the Jene Berang is high, and its plume can extend over 6 km to just South of Samalona.

Sand cay reefs are typical for areas with a high hydrodynamic energy (Guilcher, 1988). On the exposed side the reef slope is covered by coral growth. During storms (carbonate) sand is swept over the islands, changing the reef cay into a more elongated shape during the SW monsoon. In the fair weather season the roundish shape is restored again (de Klerk, 1983). Overall, large volumes of sediment are move over as well as around the island.

In the Spermonde Archipelago 20 species of living larger foraminifera have been found. Of these, four species have been found predominantly on soft substrates at the reef base. *Operculina ammonoides, Palaeonummulites venosus, Dendritina ambigua* and *Parasorites orbitolitoides* live on sand and especially *O. ammonoides* can reach high densities (up to 4 cm^{-2}).

Some other species show a preference for solid substrates at the exposed slope of the reefs. *Amphisorus hemprichii* occurs mainly on the upper part of the exposed reef slope. *Heterostegina depressa, Calcarina spengleri* and *Amphistegina radiata* can be found at all depths on coral rubble. *Baculogypsinoides spinosus* lives on the lowest part of the exposed slope, at coral rubble in between or just below the deepest zone of coral cover.

Other species did not show a preference for substrate type and were found living on both the exposed and leeward slopes of the reefs. *Calcarina hispida* and *Amphistegina lessonii* occur in most samples taken on the reef slopes. Life *A. lessonii* is found in samples taken at the reef base as well, but in very low density.

Neorotalia calcar and *Peneroplis planatus* occur predominantly on the leeward reef slope on soft substrate.The last species that ought to be mentioned is *Elphidium craticulatum*. This species does not house symbionts but sequesters chloroplasts from algal food sources and utilises their photosynthates (Lopez, 1979; Lee & Anderson, 1991;

Table 4.1. Species of living larger foraminifera as found in six assemblages on the Spermonde Shelf by Renema and Troelstra (chapter 3). X: species is characteristic for the assemblage, - species has been found, but is not characteristic for the assemblage.

Species	Shallow Exposed cluster	Shallow Leeward cluster	Deep Exposed cluster	Deep Leeward cluster	Reef base cluster	Near Shore cluster
Calcarina hispida	-	-	-	-	-	-
C. spengleri	-		X	-		
Neorotalia calcar		X		-		
Amphistegina lessonii	-	-	-	-	-	-
A. lobifera	X	X				
A. papillosa			-	-	X	
A. radiata	-		X	-	-	-
Operculina ammonoides			-	-	X	
Heterostegina depressa	-	-	X	-	-	
Palaeonummulites venosus					X	
Elphidium craticulatum	-	-	-	-	-	X
Peneroplis planatus	-	X		-	-	
Dendritina ambigua				-	-	
Alveolinella quoyii				-	-	
Laevipeneroplis proteus	-	-				
Amphisorus hemprichii	X		-	-		
Parasorites orbitolitoides			-	-	-	

Lee & Lanners, 1988). Chloroplast retention is less sensitive to adverse conditions since symbiosis is not hampered but symbionts can not reproduce in these conditions (Hollaus & Hottinger, 1997). *E. craticulatum* lives in highest densities in the nearshore area and in the deepest parts of the other areas of the shelf. These are also the areas nearest to the depths at which no symbiont housing foraminifera have been found.

Based on the abundance of living larger foraminifera, the samples can be divided into six clusters (Chapter 3, above): reef base, deep exposed slope, shallow exposed slope, deep leeward slope, shallow leeward slope and nearshore cluster (Table 4.1). The most important environmental parameters determining the composition of these six clusters were depth related parameters like light intensity and exposure to hydrodynamic energy.

Most clusters have been found all over the Spermonde Archipelago. No difference could be detected between the zones 1B, 2 and 3+4, while zone 1A had a very different fauna composition (Chapter 3, above) with the absence of the reef base cluster, and a limited number of species occurring on the reef slope (samples clustering in the nearshore cluster). The average depth of the samples in the clusters increases going off shore and a very gradual transition from zone 1B into 2 and 3+4 was found.

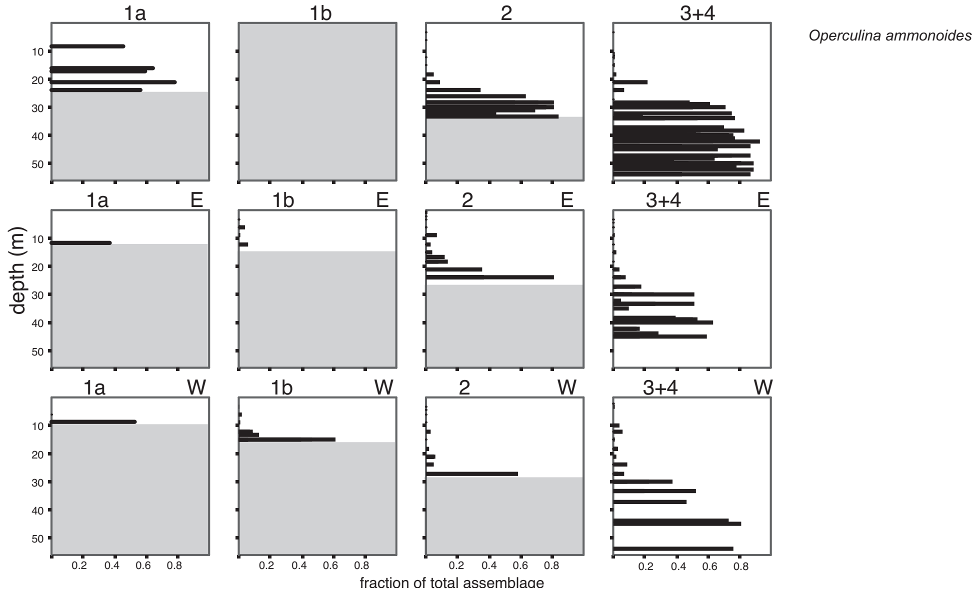
Methods

Fieldwork was carried out in August-November 1997. Around reefs 120 samples were taken at 3 m depth intervals at both the west (exposed) and the east (leeward) sides to collect dead and living specimens. Additionally, 88 samples for dead assemblages were collected with a van Veen grab along three transects over the Spermonde Shelf (Fig. 4.1). The transects have been chosen to represent a section directly off the river mouth and two at an increasing distance from the river.

The reefs around which samples have been taken are shown in Figure 4.1. Samples from the east slope of the islands all contained empty foraminiferal tests. Coral rubble samples on the west side of the reefs often only contained living foraminifera, hardly any empty tests were found in these high energy areas. Data on foraminifera from the shallow west sides of reefs are derived from sand pockets occasionally present between the high coral cover. Below the coral cover (deepest 6-9 m of the west slopes) empty tests of foraminifera were abundant.

All samples have been sieved over a 0.5 mm sieve and from a split all dead foraminifera have been counted. Juveniles of most species, but especially of the smaller amphisteginids, calcarinids and *Elphidium* are thus not included in the counts. The used split was chosen so that each sample contained 250-320 foraminifera. From the same samples taken around the reefs all living foraminifera have been picked and counted as well (Chapters 2 and 3, above).

After sorting, identifying and counting a log transformation was performed on the data matrix to eliminate large differences in abundance between species. With the resulting data-matrix several analyses were performed. First a cluster analysis was done, using Sorensens distance measure and flexible b (β = -0.75) method of clustering.



Figs. 4.3-4.21. Occurrence of empty larger foraminifera tests (>0.5 mm) in four zones over the Spermonde Shelf. 1A: Southern Nearshore Zone, 1B: Northern Nearshore Zone, 2: Mid Shelf Zone, 3+4 Outer Shelf Zone. Shaded area has not been sampled. E: leeward slope, W: exposed slope, no indication means that the sample is taken too far from an island to indicate slope direction.
Note the deepening of the reef base in offshore direction. Percentages are percentages of total fauna. Note differences in scale between figures.

The results were used for Indicator Value analysis (Dufrêne & Legendre, 1997). The second analysis performed was non-metrical multi-dimensional scaling (NMS), also using Sorensens distance measure. All calculations were done using PC-ORD (McCune & Mefford, 1999).

Results

Sixty foraminifera species were recognised, of which 19 larger benthic foraminifera. This study deals only with larger benthic foraminifera and the small benthic species *Elphidium craticulatum*. Most species have a wide distribution and often occur in samples all over the shelf. The most common species, *Elphidium craticulatum* and *Amphistegina lessonii* are present in 90% of the samples. The rarest species, *Laevipeneroplis proteus* and *Operculina heterosteginoides* were found in 1% and 5% of the samples respectively.

Up to 80% of the dry sediment mass consists of larger foraminifera. Samples in the nearshore areas had a low larger foraminifera content, and those tests present are poorly preserved, often showing dark coloration within the test. Samples taken on the reef slope also contain a lower amount of larger foraminifera, on average 10-25% of the dry sediment mass. On the west side, coarse fragments of coral rubble are important contributors to the sediment, while on the east slope coral remains are usually much smaller sized. On the east slope of Langkai, *Halimeda* remains are abundant as well.

The preservation state of *Operculina* increases going offshore in transect I, and the type of test damage changed from deposition of dark minerals to breakage/abrasion. No dark shells were found beyond PD2312 in transect I and PD2815 in transect III, both roughly corresponding with the transition of zone 2 into zone 3+4. Some of the deepest samples taken in zone 3+4 have a very low foraminifera content as well. Preservation is very good in those samples though.

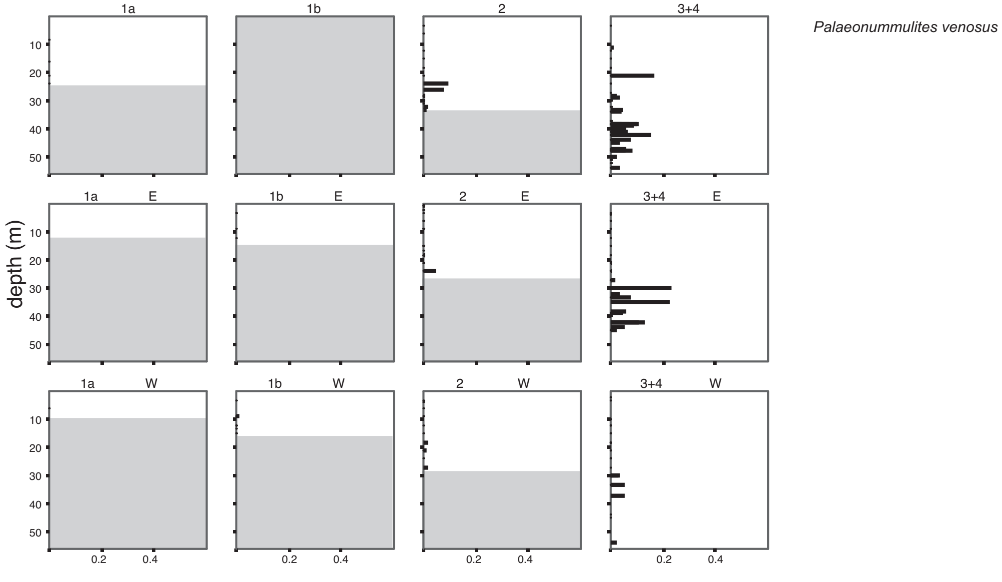


Fig. 4.4.

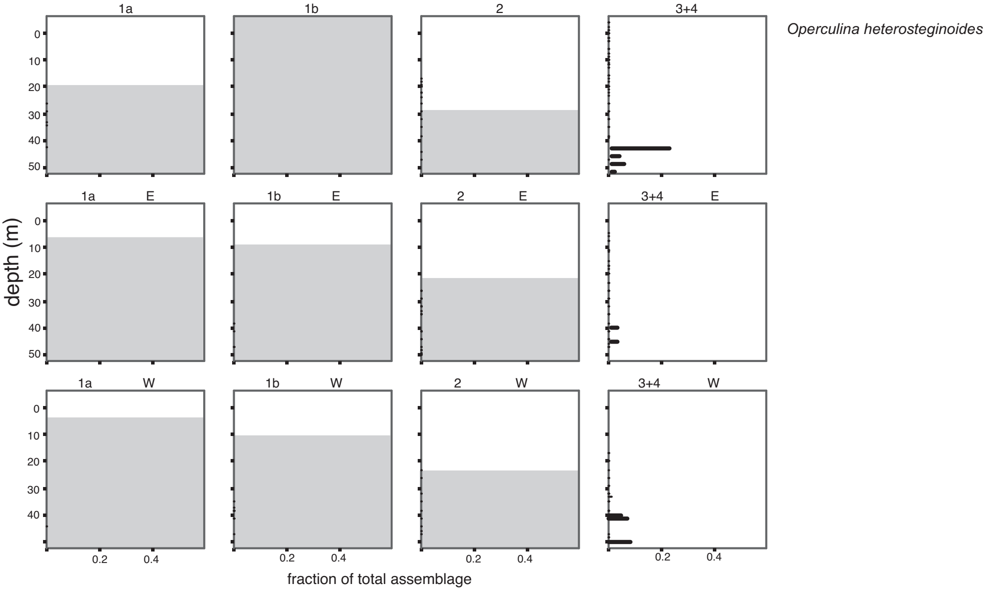

1a
1b
2
3+4
Operculina heterosteginoides
1a E
1b E
2 E
3+4 E
1a W
1b W
2 W
3+4 W
depth (m)
0
10
20
30
40
50
0.2
0.4
fraction of total assemblage

Fig. 4.5.

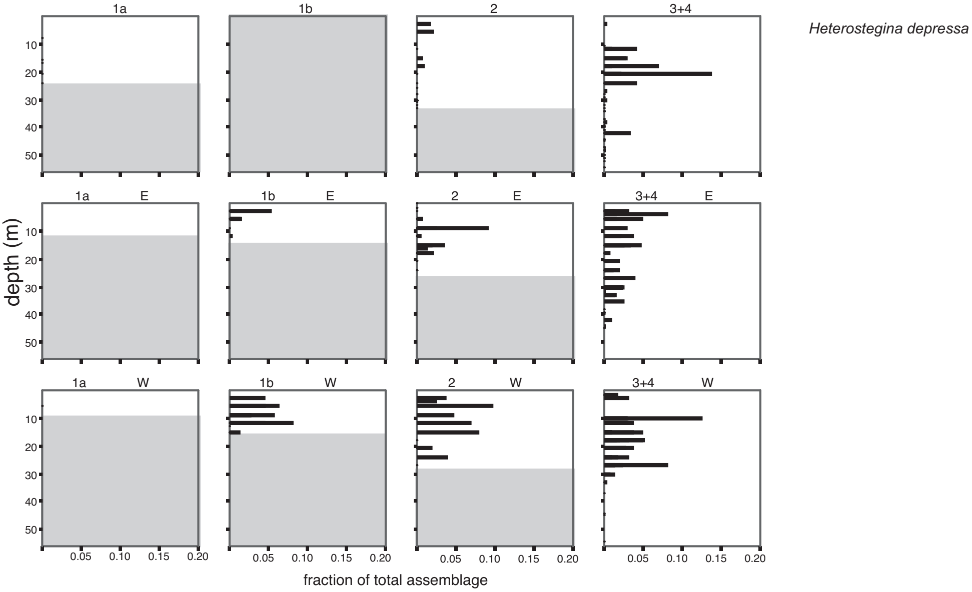

1a
1b
2
3+4
Heterostegina depressa
1a E
1b E
2 E
3+4 E
1a W
1b W
2 W
3+4 W
depth (m)
10
20
30
40
50
0.05
0.10
0.15
0.20
fraction of total assemblage

Fig. 4.6.

Nummulitidae

Operculina ammonoides (Gronovius) is the most abundant species in both samples taken from the reef base and the basin floor (>60-90%, Fig. 4.3). It is found in only a small percentage of samples taken on the reef slopes and then it occurs in low densities (<5% of the total assemblage). In the Southern and Northern Nearshore zone they occur in high abundance from about 10 m down, while in the Mid Shelf and Outer Shelf zones the increase in density of *O. ammonoides* is down from 20 m and 30 m.

Living *O. ammonoides* has been found at the reef bases all over the shelf except in the Southern Nearshore zone, with a maximum depth of 40 m in the Outer Shelf zone (Chapters 2 and 3, above).

Palaeonummulites venosus (Fichtel & Moll) has a similar distribution over the Spermonde Shelf (Fig. 4.4), but occurs in lower abundance than *O. ammonoides* (Fig. 4.3). It has only been found in the Mid Shelf and Outer Shelf zone. In the Outer Shelf zone it has a maximum abundance at about 30-35 m depth. Both below and above this depth the abundance decreases.

Living *P. venosus* occurs preferentially at the reef bases in the Mid Shelf and Outer Shelf zones. Its maximum abundance was found at similar depths as *O. ammonoides*, but it is found less in shallower samples.

The rarest nummulitid is *Operculina heterosteginoides* Hofker, which is found only in low abundance in some grab samples in the Outer Shelf zone, usually at more than 40 m (Fig. 4.5). In one sample it makes up more than 20% of the total assemblage. This species has not been found alive. Preservation state is generally well.

In contrast to the above nummulitids, *Heterostegina depressa* d'Orbigny is found mainly in samples taken from 30 m and shallower (Fig. 4.6). It does not occur in the Southern Nearshore zone, and the maximum depth at which it has been found

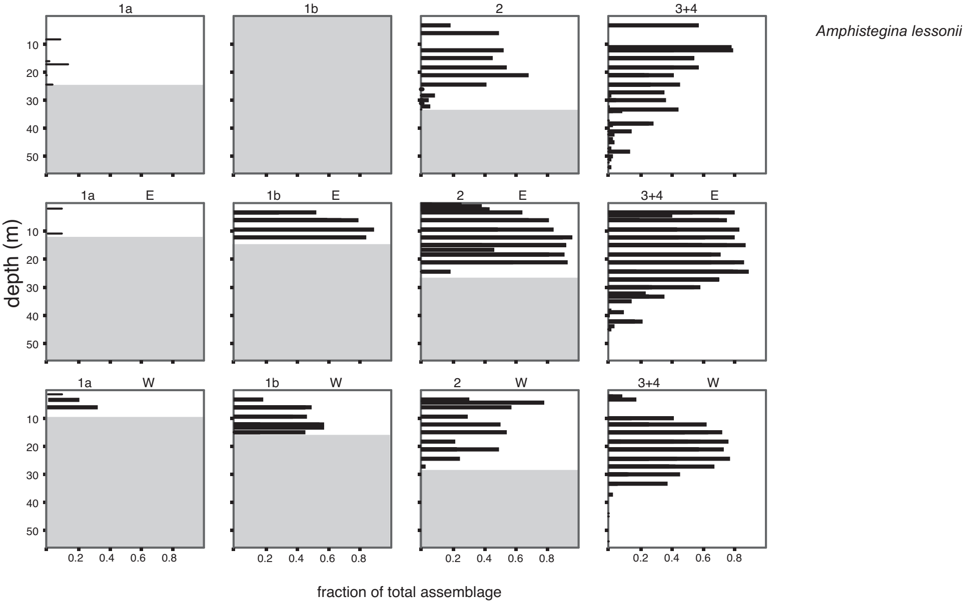


Fig. 4.7.

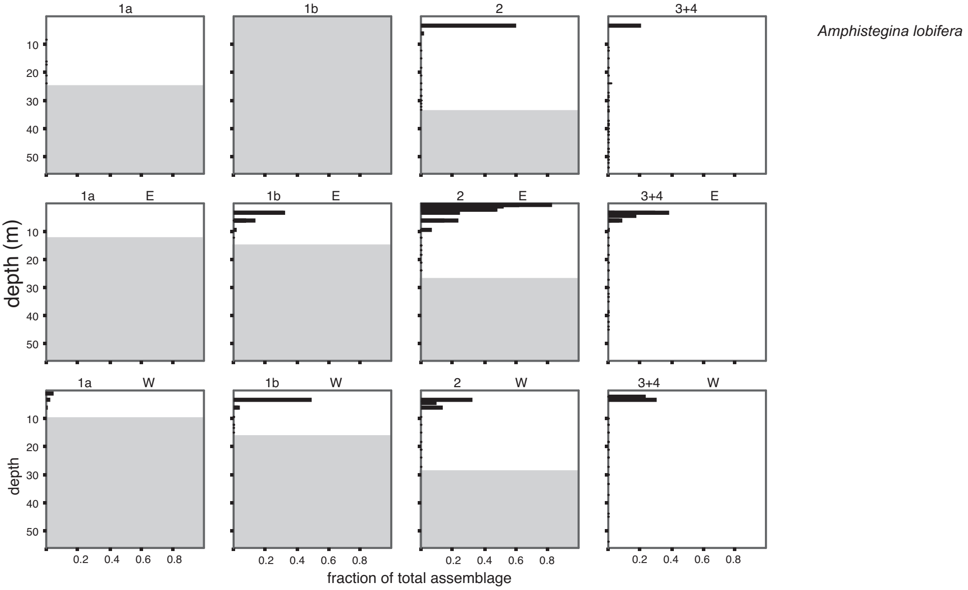

1a
1b
2
3+4
Amphistegina lobifera
1a E
1b E
2 E
3+4 E
1a W
1b W
2 W
3+4 W
depth (m)
depth
10
20
30
40
50
0.2
0.4
0.6
0.8
fraction of total assemblage

Fig. 4.8.

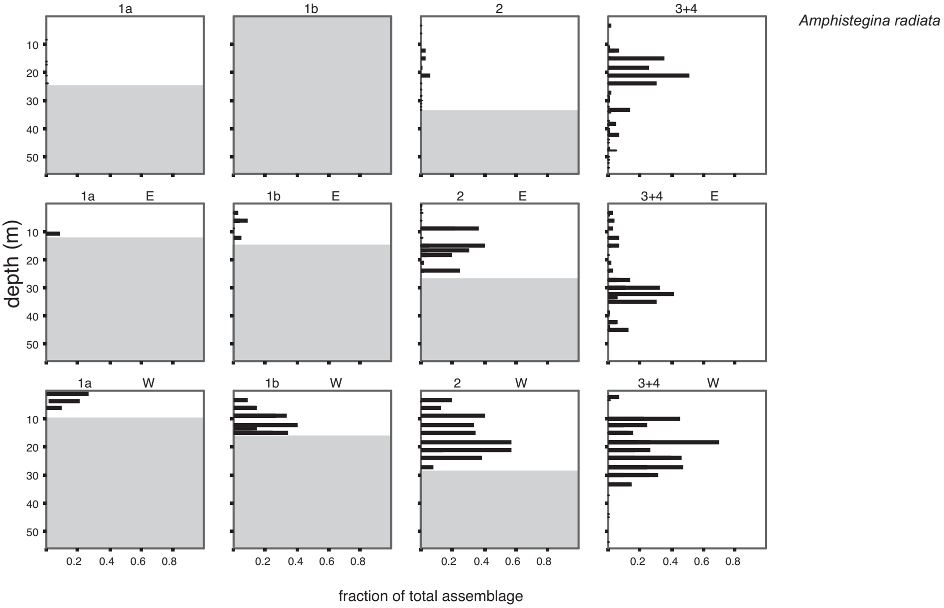

1a
1b
2
3+4
Amphistegina radiata
1a E
1b E
2 E
3+4 E
1a W
1b W
2 W
3+4 W
depth (m)
10
20
30
40
50
0.2
0.4
0.6
0.8
fraction of total assemblage

Fig. 4.9.

increases from 15 m to 25 m to 35 m in respectively the Northern Nearshore, Mid Shelf and Outer Shelf zones. The abundance is slightly (but not significantly) higher on the exposed slope than on the leeward slope.

In the living fauna *H. depressa* has a significant preference for the seaward slopes and solid substrates. It has been found in all zones, except for the Southern Nearshore Zone (Chapters 2 and 3, above).

Amphisteginidae

Amphistegina lessonii d'Orbigny is the most abundant larger foraminifera on the Spermonde Shelf. In the dead assemblage it is found in all samples on the exposed and leeward slopes of the reefs (Fig. 4.7). It is rare in samples taken at greater depth. Its abundance does not differ between the exposed and leeward slope. *A. lessonii* is not as common in the Southern Nearshore zone, where it constitutes only up to 20% of the total fauna, whereas in the other zones it is often 40-70% of the total fauna.

In the living fauna *A. lessonii* occurs in most samples, but reaches highest densities on shallow soft substrates. It lives down to 9 m in the Southern Nearshore zone increasing to 30 m around Outer Shelf reefs (Chapters 2 and 3, above).

In samples taken at shallow depth *A. lobifera* Larsen accompanies *A. lessonii. A. lobifera* is found in all zones down to rather the same depth (9 m in the Southern Nearshore zone, 10 m in the Mid Shelf and Outer Shelf zones, Fig. 4.8).

Living *A. lobifera* does not show a preference for either substrate type or slope orientation of the reefs (Chapter 2, above). It was found at depths down to 12 m in the Outer Shelf zone and down to 6 m in the Southern Nearshore zone.

Amphistegina radiata (Fichtel & Moll) has a similar distribution as *Heterostegina depressa,* where it occurred mainly on the reef slopes, and has, contrary to *H. depressa*,

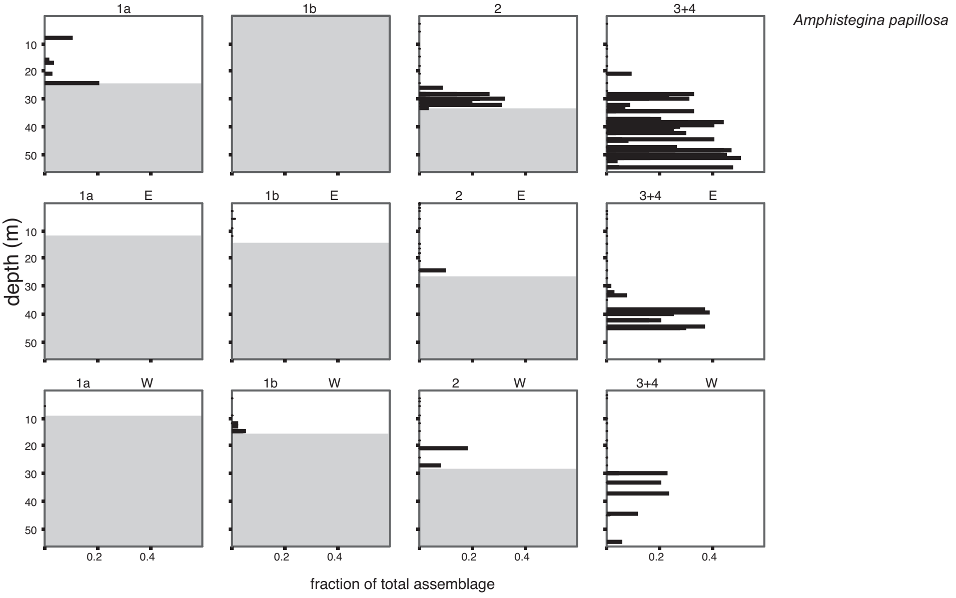


Fig. 4.10.

a preference for the exposed reef slope (Fig. 4.9). It is found down to 8 m in the Southern Nearshore Zone, increasing to 35 m at the exposed slope and 45 m at the leeward slope in the Outer Shelf zone. At the leeward slope, this species reaches its highest abundance at the lower part of the slope, while at the exposed slope abundance is about the same all over the slope.

Living *A. radiata* prefers exposed slopes and solid substrate (Chapter 2, above). It is living on and between coral rubble. It is found alive down to 6 m in the Southern Nearshore zone, increasing to 33 m in the Outer Shelf zone.

The fourth amphisteginid occurring on the Spermonde Shelf is *Amphistegina papillosa* Said, which occurred in the dead assemblage in the deepest samples (Fig. 4.10). Like *O. ammonoides* it is not found at the reef slopes. It occurs down from 10 m in the Northern Nearshore zone, 20 m in the Mid Shelf zone and 30 m in the Outer Shelf zone. In the Southern Nearshore zone it has only been found near the mouth of the Jene Berang, where the tests were very poorly preserved.

Living *A. papillosa* shows a preference for soft substrates at greater depth. It is not found alive in the Southern Nearshore zone, and lives at depths from 6-15 m in the Northern Nearshore (exposed side only), from 18-27 m in the Mid Shelf zone and from 24-33 m in the Outer Shelf zone.

Calcarinidae

Neorotalia calcar (d'Orbigny) is found mainly on the leeward reef slope. It is most abundant in the Outer Shelf zone but has not been found as empty tests in the Southern and Northern Nearshore Zones. The maximum depth at which it has been found is 20 m in the Mid Shelf and 35 m in the Outer Shelf Zone (Fig. 4.11).

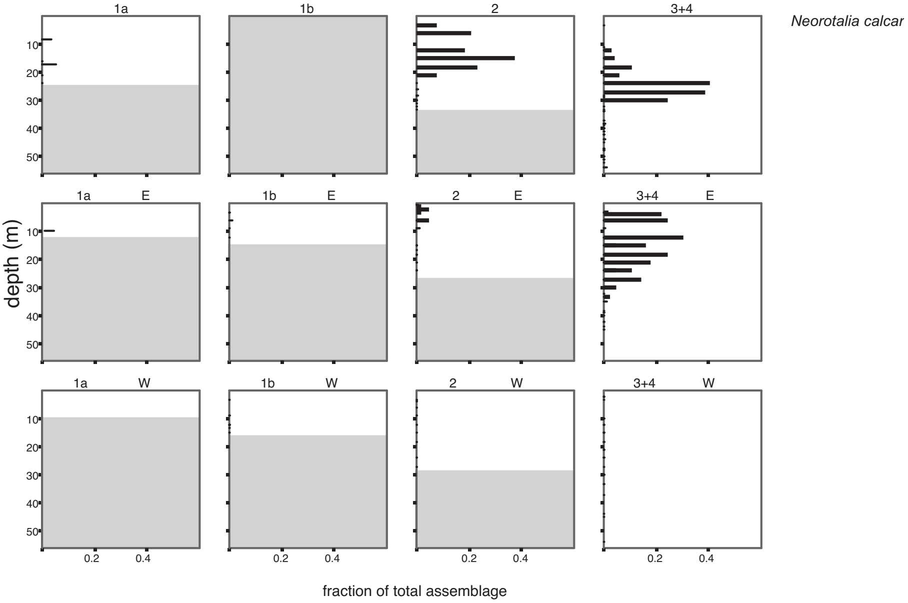


Fig. 4.11.

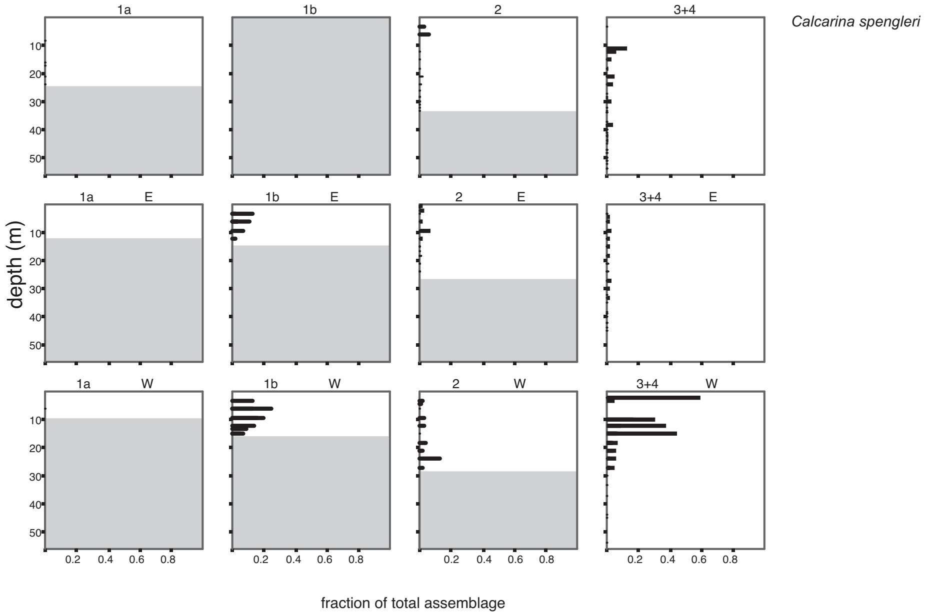


Fig. 4.12.

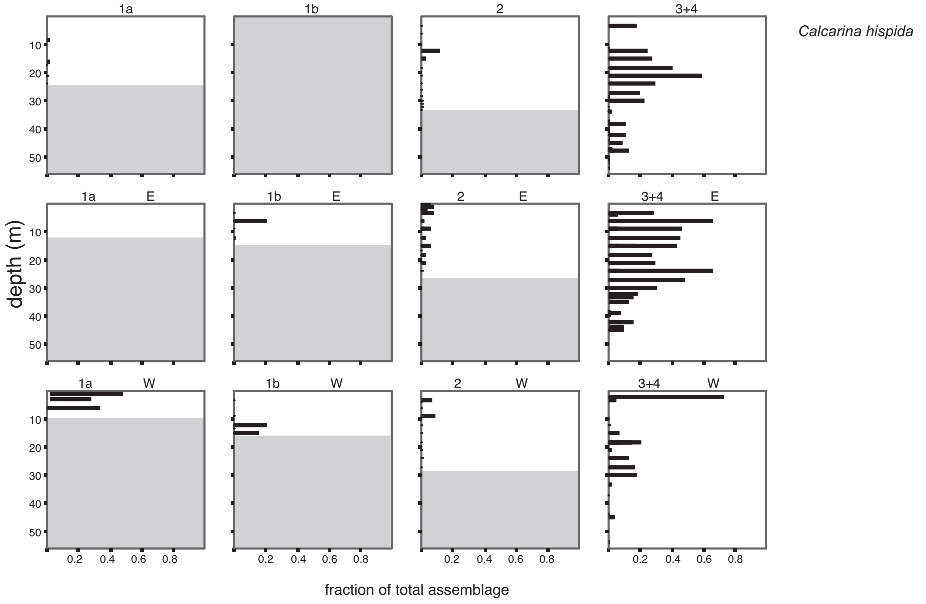


Fig. 4.13.

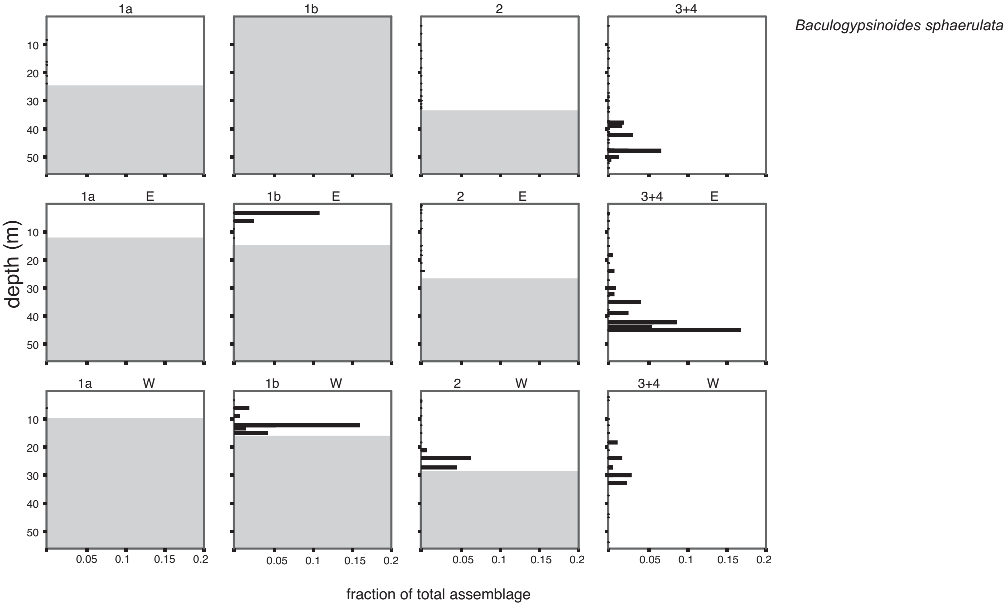


Fig. 4.14.

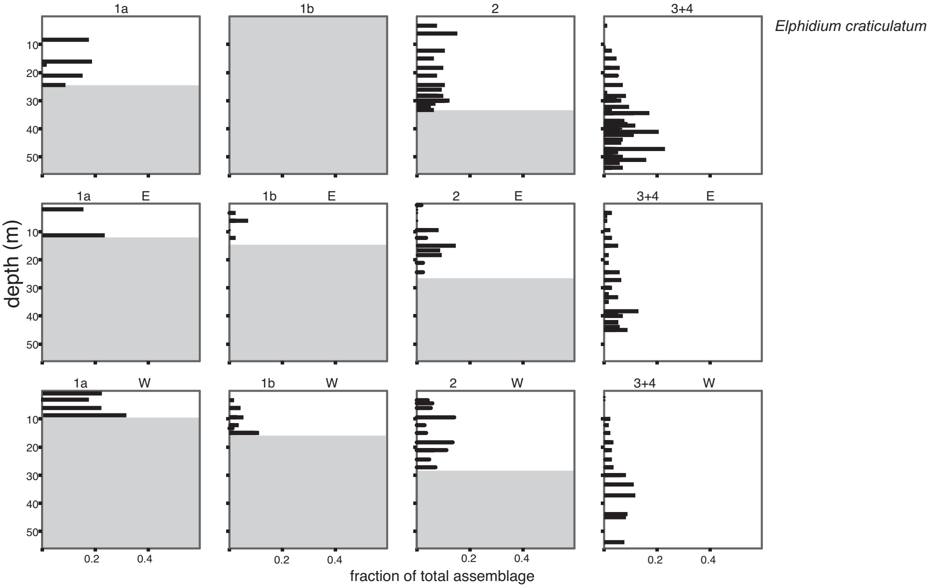


Fig. 4.15.

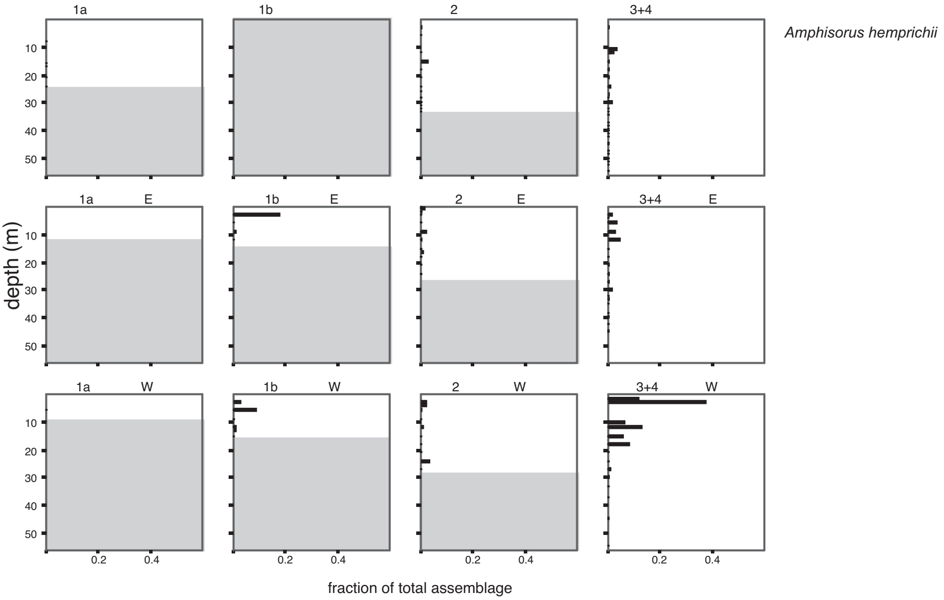


Fig. 4.16.

N. calcar has been found alive on the leeward slopes of reefs in the Northern Nearshore, Mid Shelf and Outer Shelf zones. In the Mid Shelf zone it is found on the exposed slope as well. *N. calcar* has a preference for soft substrates on the leeward slope of the reefs (Chapter 2, above).

The distribution of *Calcarina spengleri* (Gmelin) in the dead fauna is the reverse to that of *N. calcar*. It is found in the highest frequencies on the exposed slope of the reefs (Fig. 4.12) and occurs in low abundance (up to 10%) on the leeward slope. It is found down to 15 m in the Northern Nearshore Zone and down to 30 m at the exposed slope in the Outer Shelf Zone. The deepest record comes from a grab sample taken in the Outer Shelf Zone (39 m).

C. spengleri has been found living on the exposed slopes of the reefs. It has a preference for solid substrates (Chapter 2, above). The depth at which it has been found alive increases from 3 m in the Southern Nearshore zone, to 30 m in the Outer Shelf zone (Chapter 2, above).

Calcarina hispida is the second common species after *A. lessonii*. It occurs on both the leeward and exposed slopes, with slightly higher frequencies on the leeward slope than on the exposed slope (Fig. 4.13). The high abundance in samples taken at the exposed slope in the Southern Nearshore area deviates from this pattern.

Living *C. hispida* is found homogeneously over the Spermonde Shelf on the reef slopes. It occurs down to 33 m in the Outer Shelf zone, but only to about 6 m in the Southern Nearshore zone. Together with *A. radiata* and *Elphidium craticulatum* this species can stand the changes in nutrient level and salinity best (Chapter 3, above).

Baculogypsinoides spinosus Yabe & Hanzawa occurs on the lowest parts of the reef slopes, in all zones except for the Southern Nearshore zone (Fig. 4.14). It reaches its highest abundance at the exposed slope, but is also found on the leeward slope.

Alive, *B. spinosus* is found in highest density on the deepest part of the seaward slope, especially in the Outer Shelf, but also in the Mid Shelf and Northern Nearshore zone. The greatest depth at which it has been found alive was 30 m.

Rotalidae

Elphidium craticulatum (Fichtel & Moll) is found evenly all over the Shelf. In all reefs, it has the highest abundance at larger depth (Fig. 4.15). This species reaches its highest frequencies in the Southern Nearshore zone, where it makes up more than 20% of the total fauna in most samples. In the other zones, it comprises usually just over 10%.

In the living fauna *E. craticulatum* reaches its highest density in the southern Nearshore zone, and in samples taken at the reef base (Chapter 2, above). In the shallow samples (3-6 m respectively 3-21 m) *E. craticulatum* is rare.

Soritidae

The largest soritid in the Spermonde Archipelago is *Amphisorus hemprichii*. In the dead assemblage it is a rather rare species. It is either found in very low numbers (often broken individuals) in samples taken at either the leeward or exposed slope (Fig. 4.16). On the exposed slope samples taken in pockets between coral sometimes contain more abundant *A. hemprichii*. The deepest samples in which it was found were taken at 20 m depth.

It has a preference for solid substrate and the exposed slope of the reefs (Chapter 2, above). In the Mid Shelf zone it also occurred attached to sea grasses at the reef base of some reefs. The maximum depth at which *A. hemprichii* has been found attached to

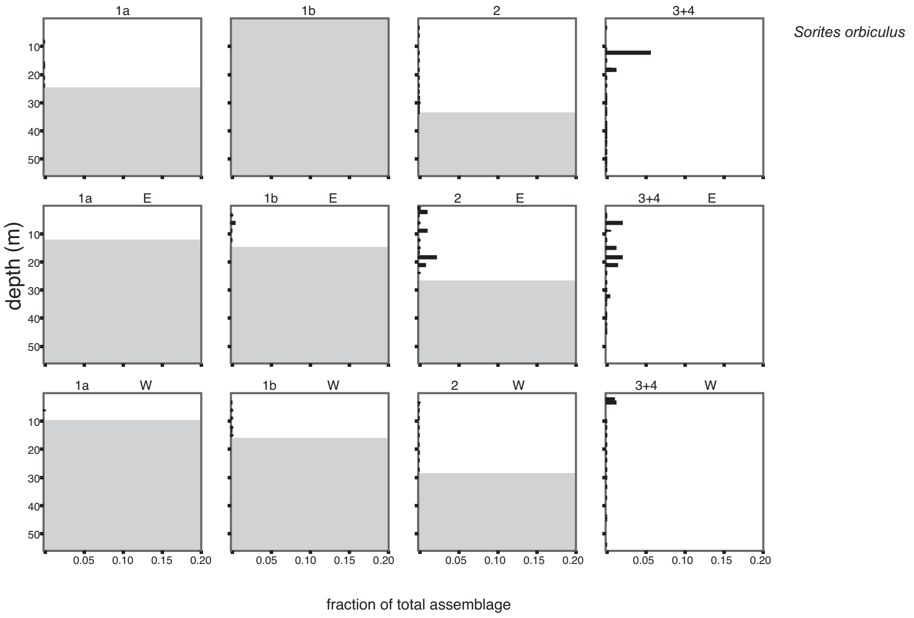


Fig. 4.17.

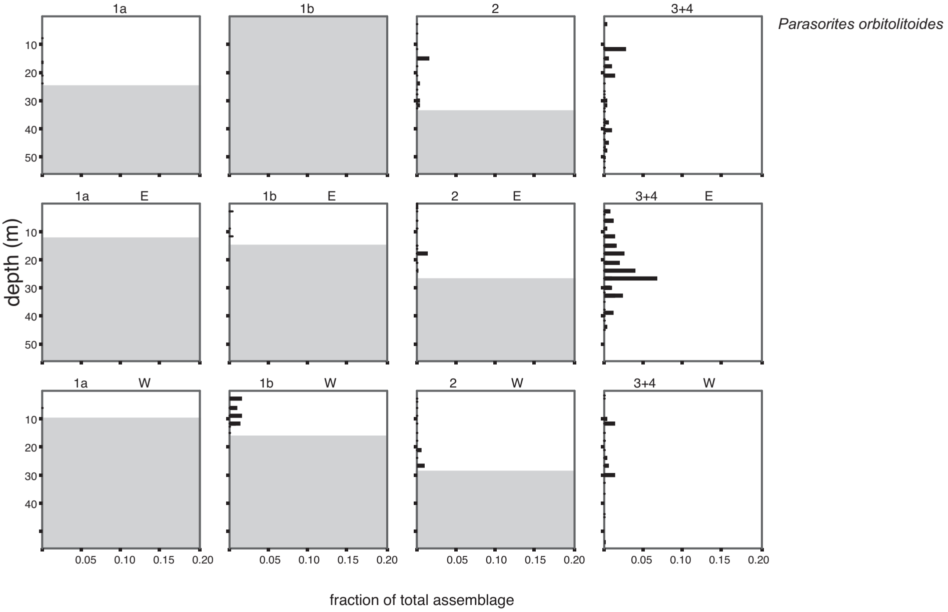


Fig. 4.18.

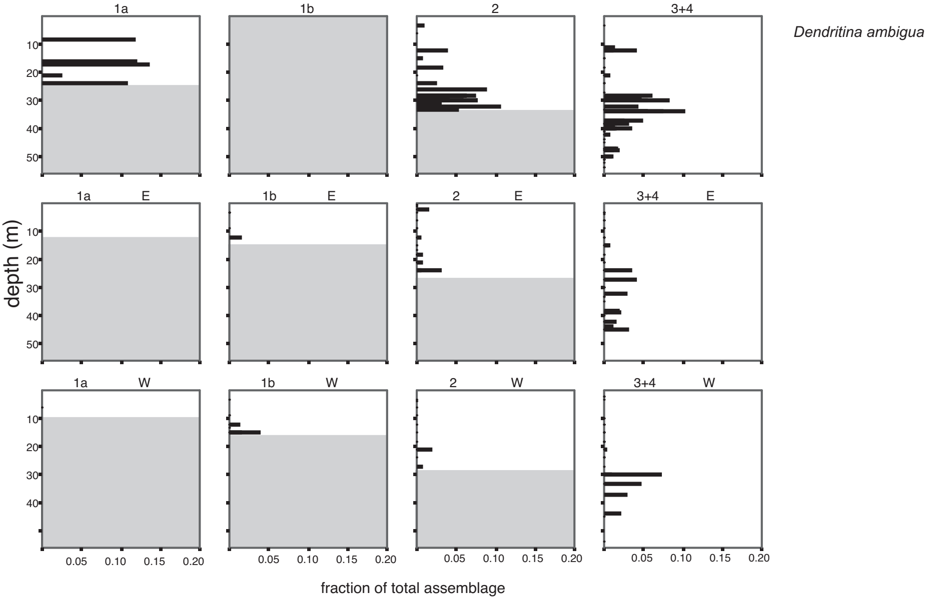


Fig. 4.19.

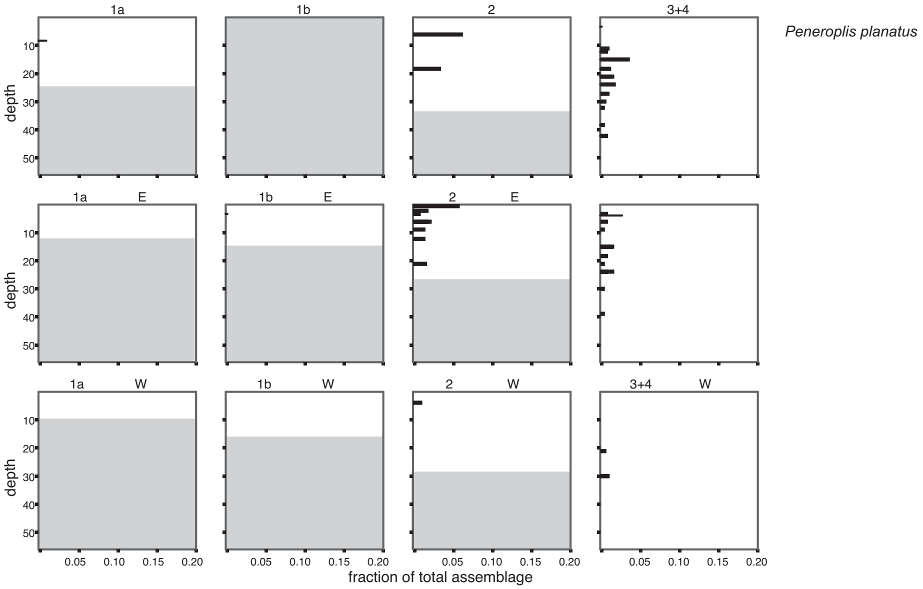


Fig. 4.20.

coral rubble is 6 m in the Mid Shelf and increases to 18 m in the Outer Shelf zone. It was not found in the Southern Nearshore Zone.

Sorites orbiculus (Forskål) is rare in samples taken on the upper reef slopes in the Northern Nearshore, Mid Shelf and Outer Shelf Zones (Fig. 4.17). It occurs for more than 5% in one sample only.

In the living fauna this species was rare as well. It did not show a preference for slope orientation or substrate type (Chapter 2, above).

Parasorites orbitolitoides (Hofker) occurs regularly in low numbers in samples taken at both the exposed and leeward slopes (Fig. 4.18), being more abundant in the latter. It was not found in the Southern Nearshore zone, and the maximum depth at which it has been found increases from 12 m in the Northern Nearshore to 40 m in the Outer Shelf zone.

Living *P. orbitolitoides* was observed on reef slopes all over the Spermonde Shelf. Densities were generally low, though. Highest densities were reached in samples taken at the reef base.

Peneroplidae

Dendritina ambigua (Fichtel & Moll) was mainly found in samples taken at larger depth. It hardly occurred in samples taken at the reef slopes (Fig. 4.19). *D. ambigua* reached its highest abundance in the Mid Shelf zone at about 25-30 m and in the Outer Shelf zone from 30-40 m. *D. ambigua* was found in all four zones. Preservation state of the test of *D. ambigua* often was poor. Especially at greater depth in the Southern Nearshore Zone, the chamber walls were dissolved leaving only the centre of the shell and the septa.

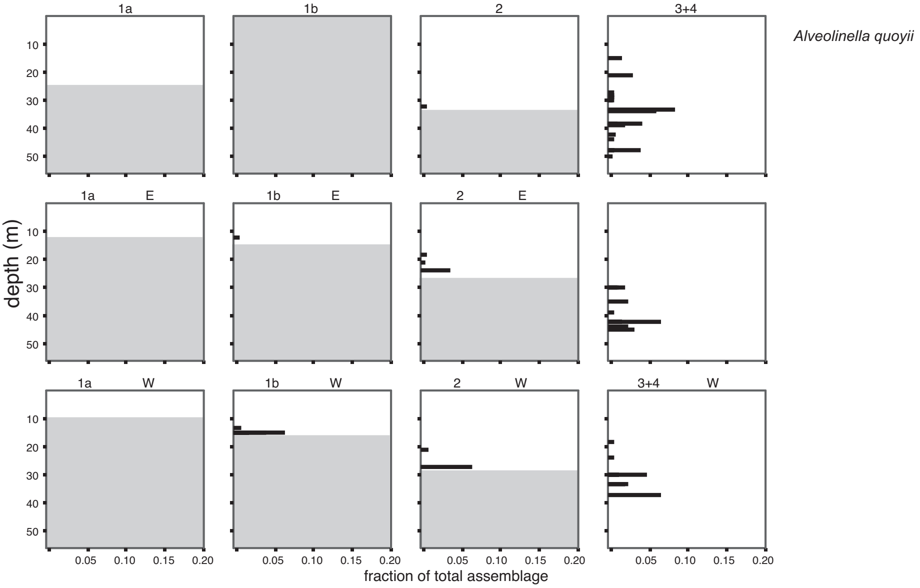


Fig. 4.21.

Living *D. ambigua* was found at the reef bases in the Northern Nearshore, Mid Shelf and Outer Shelf reefs. It was living preferentially on soft substrate, but did not show a preference for slope orientation.

In the dead assemblage *Peneroplis planatus* (Fichtel & Moll) is only found at reefs in the Mid Shelf and Outer Shelf Zone (Fig. 4.20). It is extremely rare on the exposed slopes. On the leeward slopes its highest density 5%. The maximum depth at which it has been found is just over 20 m in the Mid Shelf Zone and just over 40 m in the Outer Shelf Zone.

P. planatus was not found living in the Southern Nearshore Zone. In the other three zones it was found to have a preference for the leeward slopes of the reef, but did not show a preference for substrate type. It is found down to 30 m in the Outer Shelf Zone, generally the highest density was found in the upper part of the reef slope.

Alveolinellidae

The spindle shaped *Alveolinella quoyii* (d'Orbigny) occurs regularly, but in low frequency at greater depth at both the exposed and leeward slopes (Fig. 4.21). It was not found in the Southern Nearshore zone, and is found in samples taken at respectively 12-15 m and 19-27 m in the Northern Nearshore and Mid Shelf zone. The depth range is larger in the Outer Shelf zone, but it did not occur in the deepest samples.

In the living assemblage, *A. quoyii* was rare (Chapter 2, above). It was found in very low density at the reef base of reefs in the Mid Shelf and Outer Shelf area.

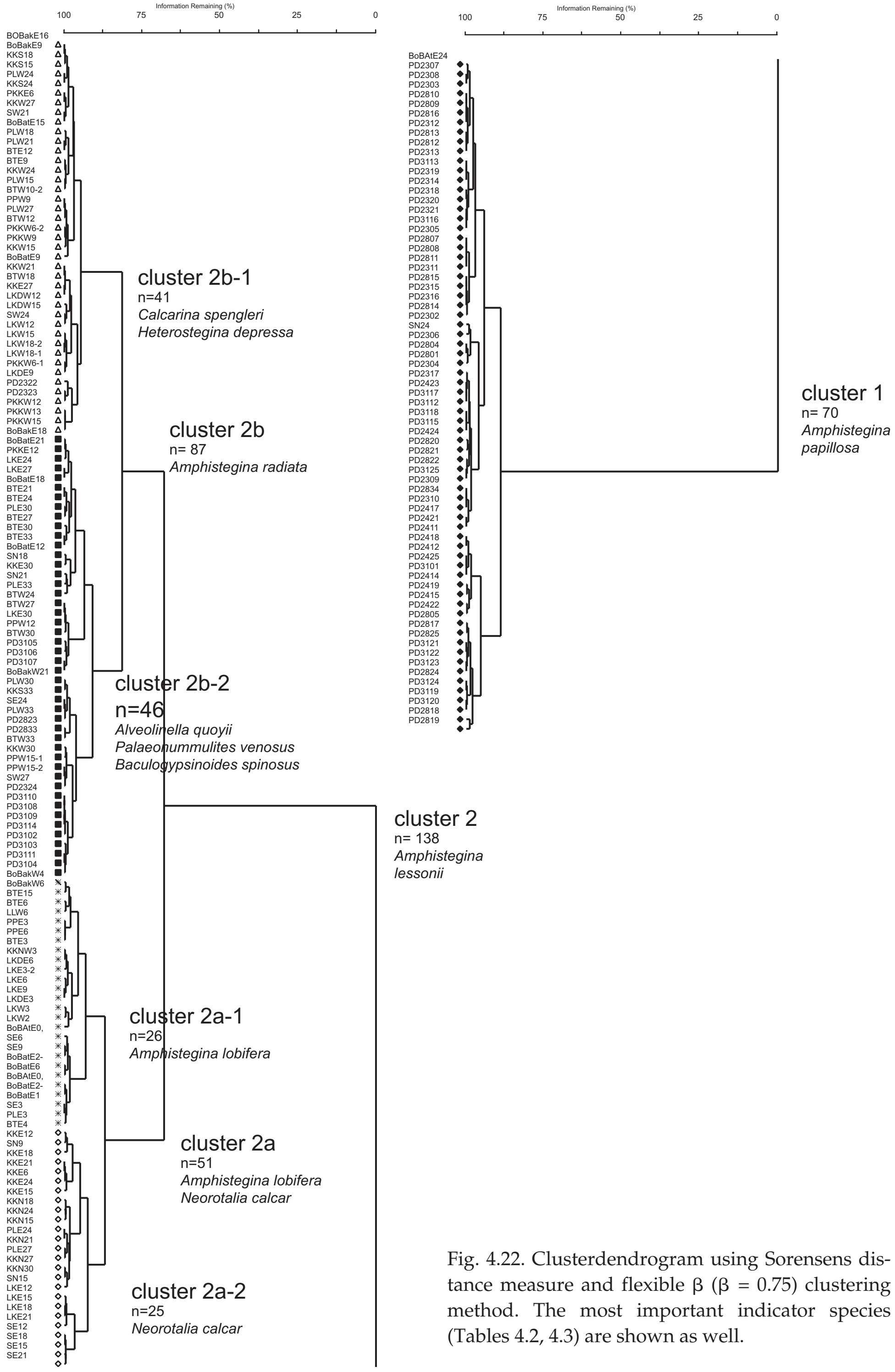


Fig. 4.22. Clusterdendrogram using Sorensens distance measure and flexible β (β = 0.75) clustering method. The most important indicator species (Tables 4.2, 4.3) are shown as well.

Assemblages

Cluster analysis in combination with indicator species analysis shows that a division into five clusters has the highest resolution and that all five clusters can be characterised by species with high indicator values. The cluster analysis (Fig. 4.22) separates at the first level between samples rich in *Amphistegina papillosa* (cluster 1) and those rich in *Amphistegina lessonii* (cluster 2). Two other species, *Elphidium craticulatum* and *Operculina heterosteginoides* have their highest indicator values in cluster 1 as well (Table 4.2). *O. heterosteginoides* is restricted to samples in cluster 1, but occurs in only a few samples, resulting in a low indicator value. *Elphidium* is found in 90% of the samples, but the highest numbers are found in samples from this cluster.

Cluster 2 can be divided into two sub-clusters, the second level sub-cluster 2a char-

Table 4.2. Indicator values of species and environmental parameters of samples characterised by a division of the dataset into three clusters in the dead assemblage. Indicator values for species characterising a cluster are printed in bold. Depth indicates the average depth at which the samples in the cluster are found, together with the standard deviation.
Leeward and exposed slope refer to samples taken in the vicinity of islands, on the leeward respectively the exposed sides. Samples taken in between islands are referred to as none. The table gives the observed number of samples in a category and in brackets the number that is expected in a random sample of the total data set is given.

Species	Cluster 1	Cluster 2a	Cluster 2b
Amphistegina lobifera	0	**52**	0
A. lessonii	7	44	45
A. radiata	0	8	**76**
A. papillosa	**73**	0	8
Operculina ammonoides	**65**	1	28
O. heterosteginoides	14	0	0
Palaeonummulites venosus	33	0	16
Heterostegina depressa	0	27	45
Calcarina spengleri	0	17	33
C. hispida	6	43	21
Neorotalia calcar	1	**45**	1
Baculogypsina spinosus	1	1	32
Elphidium craticulatum	49	11	30
Amphisorus hemprichii	0	22	20
Parasorites orbitolitoides	2	10	15
Sorites orbiculus	0	26	0
Alveolinella quoyii	3	0	28
Peneroplis planatus	1	**34**	3
Dendritina ambigua	**50**	0	8
Laevipeneroplis proteus	0	6	0
N	71	60	77
Depth	38 ± 10 m	13 ± 9 m	22 ± 11 m
Distance to nearest reef	1.93km	0.20km	0.596km
Leeward slope	**1** (24)	**37** (21)	28 (26)
Exposed slope	**5** (16)	6 (14)	**39** (18)
None	**64** (30)	8 (26)	20 (33)

Table 4.3. Indicator values of species and environmental parameters of samples characterised by a division of the dataset into five clusters in the dead assemblage. Indicator values for species characterising a cluster are printed in bold. Depth indicates the average depth at which the samples in the cluster are found, together with the standard deviation.
Leeward and exposed slope refer to samples taken in the vicinity of islands, on the leeward respectively the exposed sides. Samples taken in between islands are referred to as none. The table gives the observed number of samples in a category and in brackets the number that is expected in a random sample of the total data set is given.

Species	Cluster 1	Cluster 2a-1	Cluster 2a-2	Cluster 2b-1	Cluster 2b-2
Amphistegina lobifera	0	**83**	1	2	0
A. lessonii	4	23	25	25	21
A. radiata	0	3	8	42	34
A. papillosa	**58**	0	0	0	29
Operculina ammonoides	45	0	3	7	36
O. heterosteginoides	14	0	0	0	0
Palaeonummulites venosus	22	0	0	0	**42**
Heterostegina depressa	0	11	17	**38**	9
Calcarina spengleri	0	5	8	**49**	3
C. hispida	3	24	20	6	16
Neorotalia calcar	0	13	**30**	0	0
Baculogypsinoides spinosus	0	1	0	7	**36**
Elphidium craticulatum	31	5	10	16	26
Amphisorus hemprichii	0	28	5	20	2
Parasorites orbitolitoides	1	5	16	1	11
Sorites orbiculus	0	0	0	19	7
Alveolinella quoyii	2	0	0	1	**59**
Peneroplis planatus	1	18	17	1	1
Dendritina ambigua	34	0	1	1	24
Laevipeneroplis proteus	0	8	1	0	0
N	71	20	40	41	36
Depth	38 ± 10m	4 ± 3m	18 ± 7m	16 ± 7m	30 ± 10m
Distance to reef	1.9km	0.20km	0.20km	0.23km	1.0km
Leeward slope	**1** (24)	**17** (9)	20 (9)	10 (14)	19 (16)
Exposed slope	**5** (16)	0 (5)	6 (6)	**27** (9)	12 (10)
none	**64** (30)	8 (11)	**0 (11)**	**4** (18)	15 (20)

acterised by *Neorotalia calcar* and *Amphistegina lobifera* is separated from sub-cluster 2b characterised by *Amphistegina radiata* (Fig. 4.22, Table 4.2).

The *N. calcar* — *A. lobifera* sub-cluster (2a) can be further divided into two sub-clusters, one characterised by *A. lobifera* (cluster 2a-1) and another characterised by *N. calcar* (cluster 2a-2) respectively (Fig. 4.22, Table 4.3).

The *radiata*-cluster (2b) is divided into sub-cluster 2b-1 characterised by *Heterostegina depressa* together with *Calcarina spengleri* and sub-cluster 2b-2 characterised by *Alveolinella quoyii*, *Baculogypsinoides spinosus* and *Palaeonummulites venosus* (Table 4.3). In cluster 2b-2 *Operculina ammonoides* and *Amphistegina papillosa* also occur.

Comparison between observed parameters in the five clusters shows the environmental parameters determining the distribution of larger foraminifera over the Spermonde Shelf (Tables 4.2, 4.3).

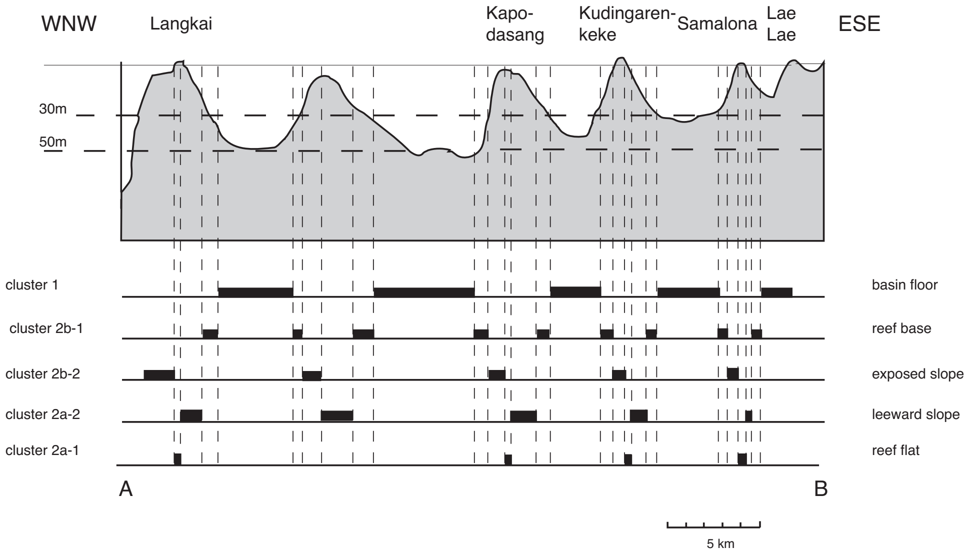


Fig. 4.23. Occurrence of the clusters over the transect over the Spermonde Shelf

Cluster 1 does not show a dominance of any reef side; it consists mainly of samples taken at a larger distance from islands, and has the highest average depth of the five clusters (Table 4.3). The environment where this cluster is collected will be indicated with basin floor (Fig. 4.23). In surface area, this is the largest area in the Spermonde Archipelago. The samples that group in cluster 1 are mainly samples taken in the three grab transects. Note that the depth at which this assemblage is found increases from 15-20 m in between Lae Lae and Samalona, to 45-50 m just east of Langkai.

Cluster 2a-1 is found on the leeward slope, but also almost as often as expected on the exposed side of the island. The average depth at which this cluster has been found is 5 m. This cluster is mainly found on the reef flat on both sides of the islands.

Cluster 2a-2 is mainly found in samples taken on the leeward sides of the reefs, in moderately shallow water. Samples grouping in this cluster are collected in the direct neighbourhood of islands. This cluster is characteristic for the leeward slope (Table 4.3).

Cluster 2b-1 is found almost three times more often than expected on the exposed (West) sides of the islands. The average depth is similar to cluster 2a-2, about 16 m. Most samples in this cluster have been taken on the exposed slope of the reefs, but some samples come from the leeward slope.

The number of samples taken on either the exposed or leeward sides of the reefs in cluster 2b-2 do not show much deviation of the expected value. The distance to the nearest island and the average sampling depth is higher than in the two slope clusters (2b-1 and 2a-2), but lower than in cluster 1. Cluster 2b-2 consists of samples taken in the reef base environment. The average depth of the samples is slightly shallower than that of cluster 1. The average distance to the nearest reef is much smaller than for cluster 1.

To obtain a data set that is directly comparable with that in the living assemblage

Table 4.4. Environmental parameter characteristics for the species of larger foraminifera as found on the Spermonde shelf in the living and dead fauna.

Species	**Depth Living**	**East/West Living**	**Substrate Living**	**Depth Dead**	**Exposure Dead**
Calcarina hispida	No preference				
C. spengleri	up to 27m in zone 3+4	West	Solid		West
Neorotalia calcar	Mainly on the higher part of the slope	East			East
Baculogypsinoides spinosus	Only in the deepest slope samples	West		reef base	
Amphistegina lobifera	Shallow	No preference		Shallow	No preference
A. lessonii	No preference			Around islands	
A. radiata	No depth preference	West	Solid		West
A. papillosa	Reef base	West	Soft	Deep	
Operculina ammonoides	Reef base		Soft	Deep	
O. heterosteginoides	Not found			Deep	
Heterostegina depressa		West	Solid		West
Palaeonummulites venosus	Deep		Soft	Deep	
Elphidium craticulatum	Near shore and deep samples	West		Deep	
Peneroplis planatus	Highest density in upper slope samples	East			East
Dendritina ambigua	Reef base		Soft	Deep	
Alveolinella quoyii	Reef base		Soft	Deep	
Laevipeneroplis proteus					
Amphisorus hemprichii	Upper slope	West	Solid	Shallow and slope	West
Parasorites orbitolitoides			Soft		

(in which the grab samples were not used), another cluster analysis was performed without the grab samples. The results of this analysis had a higher heterogeneity, as shown by MRPP (Multi-Response Permutation Procedures, A=0.22 for four clusters, the chance of obtaining a similar or higher A, p<0.000). In this analysis for A=1 all items in each cluster are identical, for A=0 the heterogeneity within the groups is as large as would be expected by chance. The MRPP result for the complete data set was much higher (A=0.45, p<0.000). Values resulting from indicator value analysis show that the four clusters in the reduced database are the same as those in the total data set.

The main environmental parameter characterising the clusters is depth, followed by exposure. Within the leeward and exposed slope clusters no differentiation can be made, but a shallow cluster with no preference for exposure is present.

Similarity and differences with the living larger foraminifera fauna

The distribution of living larger foraminifera over the Spermonde Shelf is discussed in Chapters 2 and 3. In the next part the biocoenosis is compared with the thanatocoenosis.

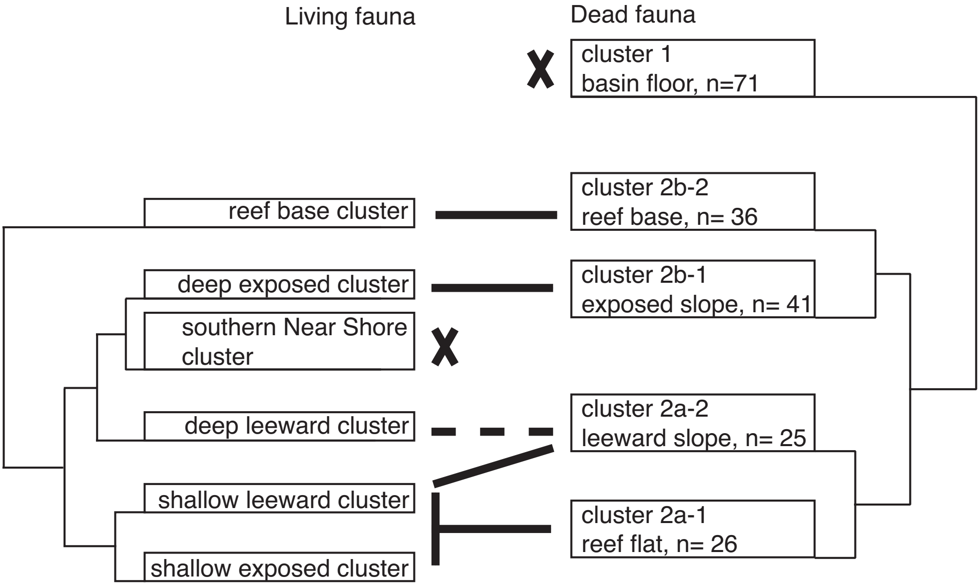


Fig. 4.24. Comparison of the cluster dendrograms of clusters found in the living and dead faunas

Twenty species of living larger foraminifera were found on the Spermonde Archipelago (Chapters 2 and 3, above). Two of them, the rare *Peneroplis pertusus* and *Dendritina zenghae* were not found in the dead fauna. *Operculina heterosteginoides* was found in several samples taken at the deepest places in the area between Kudingarengkeke and Langkai, but was not found in the living fauna. Although *Elphidium craticulatum* is not a larger symbiont-bearing foraminifera, it is a characteristic species in the living fauna and has been used during the analyses for both the living and the dead fauna.

Unlike more areas with very gradual transitions in the most important environmental parameters, the occurrence of species is partly determined by the presence or absence of essential elements in the habitat for a species. If there is no solid substrate in an area, for example *Calcarina spengleri* will have a hard time colonising the area. The transition between the assemblages co-occurs with transitions in environmental parameters. The reef base assemblage (in the living fauna) occurs around reefs on places where the steepness of the reef slope decreases and below the storm wave base. The exposed slope assemblage occurs in areas with solid substrate. Only the Southern Nearshore zone assemblage is an exception, since it is found in areas where further off shore the exposed slopes assemblages would be present.

Some of the species occurring in the reef base assemblage are more abundant in the thanatofacies than in the biofacies. *Operculina ammonoides* was not found alive in the Southern Nearshore zone, but occurs there in the dead fauna. The preservation state of the shells in those samples is worse than that of samples taken in the other three zones. Many shells are corroded and part of them are filled with glauconite.

The rank order of the 19 species occurring in both data-sets differed significantly (Kendall's coefficient of rank correlation, $\tau=1.23$ $p<0.05$). *Amphistegina lobifera* and *Pen-*

Table 4.5. Maximum observed depth of some species in both the living and dead assemblage.

Species	Max depth alive	Max depth empty
Heterostegina depressa	33m	48m
Operculina ammonoides	40m	54m
Palaeonummulites venosus	40m	54m
Neorotalia calcar	30m max 0-18m	54m
Calcarina spengleri	27m	44m
Baculogypsinoides spinosus	30m	50m
Peneroplis planatus	20m max 3-12m	51m
Amphistegina radiata	33m	48m
A. lobifera	12m	34m
A. lessonii	40m	54m

eroplis planatus occur less in the dead assemblage than in the living assemblage, while *Dendritina ambigua* and *Amphistegina papillosa* are more common in the thanatocoenosis than in the biocoenosis. This is probably because the dead data set contains relatively more samples taken at depth (two shallow living species are under-represented, while two deep dwelling species are over-represented).

In the dead fauna only five clusters can be recognised, compared with six in the living fauna (Fig. 4.24). Three of these clusters compare well with those found in the living assemblages. The shallow leeward and shallow exposed slope clusters in the living fauna, compare best with the cluster 2a-1 (*A. lobifera*) in the thanatocoenosis. *Neorotalia calcar*, characteristic for the shallow leeward slope assemblage in the living fauna, is in the dead assemblage characteristic for samples found lower on the leeward slope (cluster 2a-2). In the living fauna the latter samples occur in the deep leeward cluster.

In the dead fauna samples taken nearshore and offshore cluster together in cluster 1 (characteristic species: *A. papillosa*). The environmental characteristics of this cluster are a high average depth of deposition and a large distance to the nearest island. This implies that, solely based on larger foraminifera content of samples from a palaeo-carbonate platform, it is not possible to discriminate between nearshore and off shore settings on the platform.

All foraminifera were found dead in deeper water than alive (Table 4.5). Species occurring predominantly in the reef base and basin floor assemblages have hardly been found on the reef slopes or reef flat. Thus most of the sediment involved in changing the shape of the reefs during the monsoonal cycle is derived from the reefs and their slopes, not from the area surrounding the reefs.

Transport down slope was not the only transport of foraminifera shells in the system however. Some of the samples taken on the leeward slope actually cluster together with samples taken on the exposed sides of the reefs (Table 4.2). Most of these are rather shallow samples. No samples taken on the exposed side of the islands were found in the leeward slope cluster (Table 4.2). This indicates that at least part of the shells produced on the exposed side of the island end up at the leeward slope, as is expected following the main sediment transport around the islands. The reef base assemblage only rarely contains shells of species that have been found predominantly on the exposed slope.

Post-mortem processes affecting larger foraminifera

In order to understand the relation between the biocoenosis and the thanatocoenosis of foraminifera the post mortem fate of a foram shell has to be known. The thanatocoenosis is the result of the processes accounting for the production and loss of shells in the system. Comprehensive models have been published showing all processes that affect the translation of the biocoenosis into the thanatocoenosis for molluscs (Kidwell, 1991; Kidwell & Flessa, 1996) (Fig. 4.25).

Life processes affecting the incongruence between the living and dead assemblages are differences in production rate between species (Murray, 1991). In the ideal dead assemblage, the proportion of all species is the same as in the living assemblage. However, due to differences in production rate between species, the dead assemblage differs from the living assemblage. Long living species will tend to produce fewer tests than short living species. This can not be quantified in this study, since all samples were taken at one moment.

Major post mortem sources of bias for foram assemblages are out of habitat transport, selective destruction of species at the accumulation site and mixing with non-contemporaneous material.

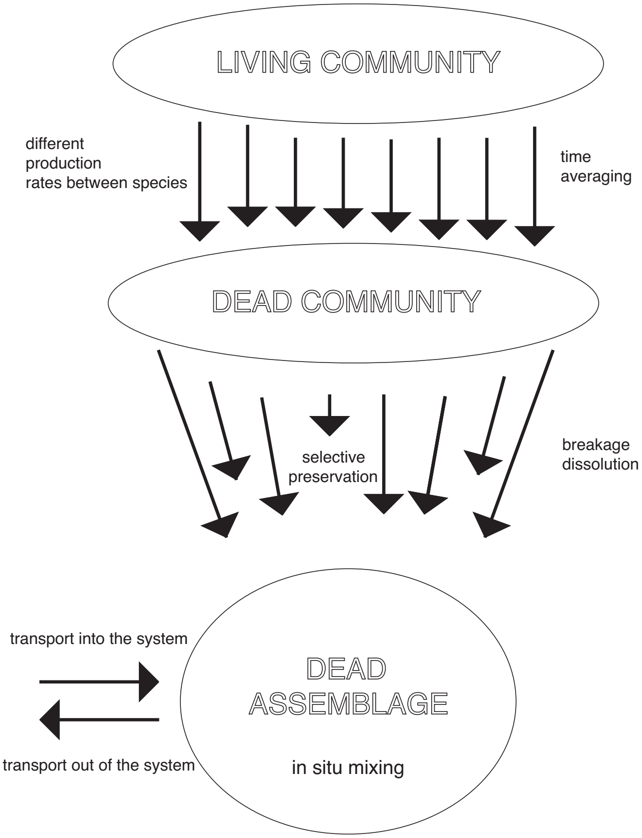


Fig. 4.25. Taphonomic processes affecting the translation of the living community into the dead assemblage (modified after Kidwell & Flessa, 1996)

Larger foraminifera are relatively small and light organisms that are prone to transport (Martin, 1999). Maiklem (1968) studied the settling of bioclastic carbonate grains, including larger foraminifera. He found that round particles with the same mass (for example calcarinids) settle in a smooth path directly to the bottom. Plate like grains, like for example soritids, zig-zagged back and forth while settling, showing a much longer settling time than spheres. Furthermore, platy forms have a lower drag coefficient than spheres and especially cylindrical shapes (Alexander, 1983; Hohenegger & Yordanova, 2001). A weaker current is needed to carry away particles with a lower drag coefficient, given that all other conditions are similar. This implies that soritids have a higher transport potential than calcarinids. This process includes both removal and addition of tests to assemblages. Hohenegger & Yordanova (2001) found that three factors influence the depth transport of larger foraminifera tests; 1) traction caused by storms and off shore currents, 2) slope steepness, and 3) differences in test buoyancy between species. Due to the depth position of living populations, the combination of these three factors leads to varying displacement intensities and mixing of empty tests (Hohenegger & Yordanova, 2001). The reef geometry on the Spermonde Shelf is quite different from the study area of Hohenegger & Yordanova (2001), where the distribution of larger foraminifera species could be described in terms of coenoclines on, steep or gentle, reef slopes (e.g., Hohenegger, 2000). The foraminifera occur along a gradient and the maximum density of each species differs along this gradient. Individual species showed marked differences between the maximum density in the living individuals and the empty tests. All species were transported down slope, but the solid substrate preferring *Baculogypsinoides spinosus* showed a smaller difference than *Alveolinella quoyi, Amphisorus hemprichii* or *Heterostegina depressa*. *Palaeonummulites venosus* was found dead at approximately the same depth as alive, especially on the gentle slope. The deeper living *Cycloclypeus carpenteri* was transported over a much larger distance. In the Spermonde Archipelago most species have been found at similar places dead or alive, apart from the species preferring solid substrate which were either transported down slope or swept over the reef towards the leeward side of the reefs.

The overall similarity between the distribution patterns found in living and dead larger foraminifera shows that out of habitat transport of tests is a minor component in determining the empty test found in an area. On the exposed slope only a small fraction is derived from the exposed slope, usually not more than 3-5%. The reef base and basin floor assemblages are found around all reefs, and the dead reef base assemblage is characterised by some shallower living species and the rare occurrence of species living on the reef slopes (*Baculogypsinoides spinosus*). On the other hand, typical reef base species are very rare on the reef slope. Thus, the reefs all maintain themselves by autochthonous production of carbonate by corals and foraminifera.

The reef slope assemblages show that transport occurs on the reefs. Samples taken on coral rubble hardly contain any empty tests. Cluster 2b-1, characterised by *Calcarina spengleri* and *Heterostegina depressa* contains samples taken on the exposed slope as well as samples taken on the leeward slope, indicating transport of shells from the exposed to the leeward side of the island. No samples taken on the leeward slope group into cluster 2b-1, the exposed slope cluster.

Destruction of shells includes both abrasion and dissolution of tests. Laboratory studies did not show much difference in resistance to abrasion in 12 taxa of reef dwelling foraminifera, except for *Planorbulina*, a very fragile species (Kotler *et al.*, 1989). These results were obtained after a 1000 hour laboratory experiment. Wetmore & Plotnick (1992) did experiments to quantify the crushing strength of some species of larger foraminifera, but did not find a difference between species. The variation in crushing strength was higher between populations found in exposed than in sheltered areas. Kotler *et al.* (1989) concluded that once produced, foraminiferal tests can persist for a long time in pure carbonate environments, based on the marked abrasion and surface degradation seen on larger foraminifera on the sediment surface. However, Martin (1999) showed that there was a similar range in the ^{14}C ages of foraminifera with highly abraded tests and in fresh-looking foraminifera.

Apart from abrasion and breakage, dissolution is another way of removing foraminifera from the assemblage. The dissolution potential is higher for prismatic shells than for hyaline shells. This effect is amplified since shells with prismatic carbonate often incorporate more organic tissue in the shell (Kidwell & Flessa, 1996). Imperforate foraminifera have their shells built with prismatic carbonate grains. Especially of the deep dwelling foraminifera the opaque tests of this group have a lower transparency and to cope with the low light intensity at depth, they have to decrease the test thickness. In the Spermonde Archipelago, most *Dendritina* and *Peneroplis* have dissolved chamber walls. Further dissolution will make them not recognisable.

Sediment accumulation rates are generally much lower than biological generation rates, so most assemblages are time averaged to some extent (Kidwell & Flessa, 1996). Generalised, sediment mixing can occur in two ways: 1) bioturbation and 2) wave action and sediment reworking during storms. Kidwell & Flessa (1996) suggest that assemblages from reefs and carbonate platforms are time averaged over a hundreds-to-thousands years range. This is confirmed by ^{14}C data on larger foraminifera from such a setting gathered by Martin (1999), who found a 2000 year age range for foraminifera shells. The occurrence of tests filled with glauconite might indicate that these tests are derived from older, reworked sediment. These tests are found either nearshore, or in deeper parts of the shelf near steeper slopes. This would explain the high abundance of species found alive predominantly in the reef base assemblage in the dead assemblage in the Southern Nearshore zone.

Despite all processes that change the living assemblage during the process of burial, studies performed so far showed a high fidelity between living and death assemblages in molluscs (Kidwell & Flessa, 1996). 80-95% of the individuals in the dead assemblage was documented to live in the same habitat. Exotic species generally account for few individuals, even if they make up a large part of the species list. Most exotics are derived from immediately adjacent environments (Kidwell & Flessa, 1996). In 12 out of 14 environments rank order did not differ significantly between the living and death assemblage for molluscs. Other marine organisms with more fragile tests show lower fidelity (Kidwell & Flessa, 1996).

Larger foraminifera as indicators for environmental parameters

In both the living and dead faunas depth-related parameters are important in determining the fauna composition. However, it is not possible to distinguish between samples taken at 15 m just west of the Jene Berang and a sample taken at 40 m just west of Bone Tambung. The presence of *Operculina heterosteginoides* in samples taken at large depth around Kudingarengkeke distinguishes these samples, but this species is not found at similar depths around Bone Tambung, and only in one very deep sample East of Langkai. In cluster 1, samples containing this species were not collected at a significantly greater depth than samples without this species (Welch approximate t-test, t=1.2, P>0.05).

Hottinger (1997) evaluated the use of, mainly larger, foraminifera for palaeoenvironmental analysis as depth-indicators. Most, if not all of the studies on recent larger foraminifera were performed in areas low in nutrients and with a very deep lower limit of the photic zone. For example, Hottinger (1997) divided the photic zone into three compartments, reaching down to 120 (140) m depth. In shallow nearshore carbonate platforms with rivers discharging terrigeneous sediment, the euphotic zone may extent for only a few metres to 50 m, or the extent can vary following seasonal changes in sediment input by the river. Some of the species indicated by Hottinger (1997) to be indicative of a water depth of 80-120 (140) m were found at less than 40 m in the Spermonde Archipelago.

Water depth influences the fauna composition indirectly, since light penetration through the water column diminishes with depth. Hohenegger *et al.* (2000) could fit the distribution of several species of Nummulitidae to the same function, but with different values for transparency of the water column.

Comparison with other areas shows that most species found in the Spermonde occur in shallower water than in previously published studies (Chapter 3, above). In palaeoenvironmental studies it is needed to evaluate the setting of the area where the samples have been collected.

Larger foraminifera can reach large sizes in response to long, stable conditions poor in nutrients. The permanent scarceness of nutrients as decisive limiting factor enforces the constant recycling of organic matter produced by the organisms by symbionts (Hottinger, 1997). In areas with seasonally changing food supply, the depth of the photic zone changes accordingly. Symbiont housing species that are found in the photic zone can not survive long periods without light, because they not only have to provide energy for their own metabolism, but also for their symbionts (Hallock, 1988). Deep living species are more vulnerable for seasonal changes in transparency because of the logarithmic decrease in light intensity. The window in which suitable light intensities occur for deep living species moves in a way that there is no depth range in which year round suitable occur. For shallow living species there is a larger chance that this will be a depth range with favourable conditions all year (Chapter 3, above).

Imperforates, and especially the smaller forms, are better capable of dealing with high water temperatures and salinity (Hallock, 2000). In carbonate settings these conditions are often related to a lagoonal setting. In the Spermonde Shelf *Amphisorus* and *Peneroplis* occur, both dead and alive, only in areas with a normal marine setting.

Empty shells are found down to large depths, but highest densities occur in sediments collected at less than 20 m depth. *Alveolinella* and *Dendritina* occur in the quoyii assemblage, an assemblage found at rather large water depth in the direct proximity of reefs. These two groups, easily distinguished on morphological characters, can be used as indicators for the proximity of reefs in a carbonate platform setting.

Fossil settings

What do these data teach us about the habitat use of larger foraminifera in, say, the Miocene or Eocene? During the Cenozoic several faunal turnovers have taken place (e.g Adams, 1984; Adams *et al.*, 1990; Hottinger, 1997). During these turnovers, the fauna composition changed markedly. During the Eocene, orthophragminids, nummulitids and alveolinids dominated the larger foraminifera faunas, while during the Miocene *Cycloclypeus*, lepidocyclinids and miogypsinids were important groups. Some of the extant genera have a long fossil record. The first *Operculina* occurs in the Thanetian or Ypresian (Hottinger, 1977b; Serra-Kiel *et al.*, 1998), *Heterostegina* is found from the Lutetian onwards. All orthophragminids, lepidocyclinids and miogypsinids are extinct however.

In both the Paleogene and Neogene faunas the species living on the shelf floor make up most of the fossil assemblages. In the Eocene *Nummulites, Assilina* and orthophragminids can make up large packets of limestones, while taxa typical of living on solid substrates occur much more localised. The same holds for the Neogene. In the Spermonde Archipelago, most of the shelf is occupied by the basin floor, followed by the reef base. The reef related habitats make up about 10% of the total surface area. The foraminifera content is much lower in the reef sediments compared with the reef base and basin floor sediments.

Most depth estimations are done by analogues with extant relatives. Hottinger (1997) evaluates several morphological adaptations in foraminifera shells in order to use them as depth indicators. Both inter- and intra-specific variations occur that are related to variations in depth. Species and populations tend to have a lower volume/surface ratio with depth. Hallock (1988) relates the trophic level with differentiation in larger foraminifera. During periods of low oceanic recycling, few nutrients are added to the surface ocean and (as a response) the photic zone extends into deeper water. Foraminifera diversify along the light gradient and during periods of lowest trophic gradient larger foraminifera diversity (both taxonomic as morphologic) is highest (Hallock, 1988). This model is further extended to regional scale as well (Hallock, 1988).

The Spermonde Archipelago is richer in nutrients and has a shallower photic zone than most previously studied areas. Living larger foraminifera occur to 45 m (Chapters 2, 3, above), compared to 100 m or more in Okinawa (Hohenegger *et al.*, 2000). Several of the deepest living species in Okinawa do not occur in the Spermonde where the species shift their occurrence to shallower water (Chapter 3, above). The Nummulitidae behave according to this model, but for example the Calcarinidae do not. In the thanatocoenosis *Assilina* and *Nummulites* occur all over the shelf, except on the reefs, but *Operculina heterosteginoides* occurs only in basin floor samples.

In the dead tests, this is reflected in the depth of cluster1 from 15-30 m nearshore to 40-55 m near the barrier. Apart from the shifting depth distribution, most empty tests of species are found in deeper water than the living specimens. The occurrence of a species or a community can not be used to estimate the depth during the time of deposition but rather is indicative of being deposited in a certain part of the light gradient in the water column.

Conclusions

The thanatocoenosis is a good reflection of the species living in the area. The relative frequency has shifted towards species living in the reef base assemblage. Empty tests of all species living on the exposed slope are found on both the exposed and leeward slope, but no empty tests of species living exclusively on the leeward slope are found on the exposed slope.

The five groups recognised in the thanatocoenosis correspond with four of those recognised in the biocoenosis. The samples taken in the nearshore assemblage cannot be differentiated from samples taken at larger depth further offshore. The shallowest assemblages in the living fauna, can not be differentiated into a leeward and exposed cluster in the dead assemblage. Cluster 1 (basin floor) has no equivalent in the living fauna.

For living larger foraminifera, light is the most important parameter determining the distribution of their tests over the shelf, followed by hydrodynamic energy (exposure). This is directly reflected in the dead fauna.

In carbonate platform settings the presence of *Alveolinella* and *Dendritina* indicates a near reef setting, if *Peneroplis* and soritids are present, the samples have been taken in reef slope conditions. *Amphistegina lobifera* is only found in reef flat situations.

Absolute depth of deposition is difficult to estimate, based solely on larger foraminifera species, but their relative depth can be estimated from their position in the light and energy gradients.

5. Larger foraminifera from Cabilao Island (Bohol, Philippines)

Introduction

Transparency, nutrient availability, hydrodynamic energy and substrate type determine the distribution of larger foraminifera over reef and shelf areas (Hottinger, 1983; Hallock, 1984; Hohenegger, 1994; Chapter 3, above). In a study on the distribution of larger benthic foraminifera over the Spermonde Shelf (SW Sulawesi), Renema & Troelstra (Chapter 3, above) showed that stability of the ecosystem is another important parameter.

In areas nearest to the shore no larger foraminifera occurred at the reef base, while at increasing distance from the shore the reef base was inhabited by a rich and diverse assemblage. The reef base assemblage and its characteristic species occurred at increasing depth going off shore in the Spermonde Archipelago (Chapter 3, above), whilst the long-living species were absent in nearshore areas.

Due to seasonal changes in water transparency combined with the logarithmic decrease of light intensity in the water column, there is no depth at which, for deep-living species, the light conditions are suitable the year round (Chapter 3, above). The distribution of species living at the reef base, and especially that of nummulitids preferring soft substrate, matches this model in the Spermonde Archipelago, but also other long living species are affected.

Not all species of larger foraminifera respond in the same way to changes and differences in environmental parameters. Calcarinids (except *Baculogypsinoides spinosus*) did not occur in highest density on the reef flat in the Spermonde, as they did at Okinawa (Hohenegger 1994, 2000; Hohenegger *et al.*, 1999), but on the reef slope, either on the exposed (*Calcarina spengleri*) or on the leeward side (*Neorotalia calcar*), whilst *Calcarina hispida* did occur on both sides of the reefs. On the reef flat of sand cay type reefs of the Spermonde Archipelago a lot of moving, clean sands were present and no macroalgae or sea grass meadows were found, whilst at Okinawa, high densities of the before mentioned species were found living in between the algae on the reef flat (Hohenegger 1994, 2000; Hohenegger *et al.*, 1999).

In the present study I compare the distribution of shallow living larger foraminifera around Cabilao and Sandigan Island with the distribution around reefs in the Spermonde Archipelago. The main objective was to look for variability in habitat use in response to varying environmental parameters.

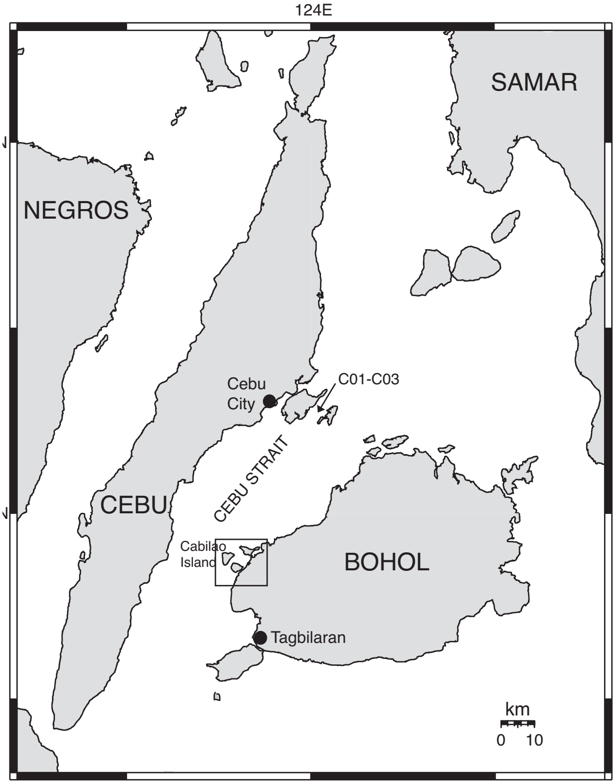


Fig. 5.1. Map of the central Visayas (Central Filippines), showing the geographic position of the research area. Inset refers to Fig. 5.2.

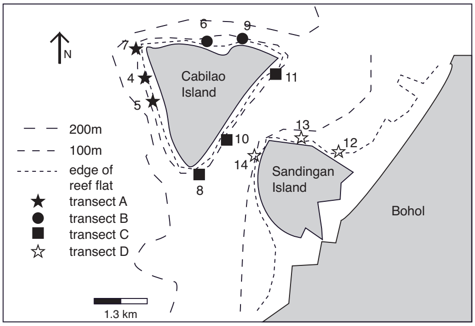


Fig. 5.2. Map of the research area (inset of Fig. 5.1). Sampling stations are numbered and symbols show the transects in which they group together. Sites 1, 2 and 3 are positioned outside the area shown on this map.

Research area

The research area is located just west of Bohol in the Cebu Strait (fig. 5.1). Eleven dive-sites were sampled along three composite transects at each side of the triangular island Cabilao and one transect just off Sandingan Island, which in fact is a peninsula off the mainland coast of Bohol (fig. 5.2). Each composite transect comprises two or three dive-sites.

The North (transect B, fig. 5.3) and West side (transect A, fig. 5.4) of Cabilao consist of a reef flat and a steep reef slope. The reef flat is dominated by large macroalgae on a rocky substrate with hardly any carbonate sand in between (inner reef flat, figs. 5.3, 5.4) but has a zone lacking vegetation that consists of patches of corals with crevices with patches of clean, moving sands, often showing wave ripples in between (outer reef flat, figs. 5.3, 5.4). The inner reef flat usually starts at 1.5-2 m depth. The deepest part of the

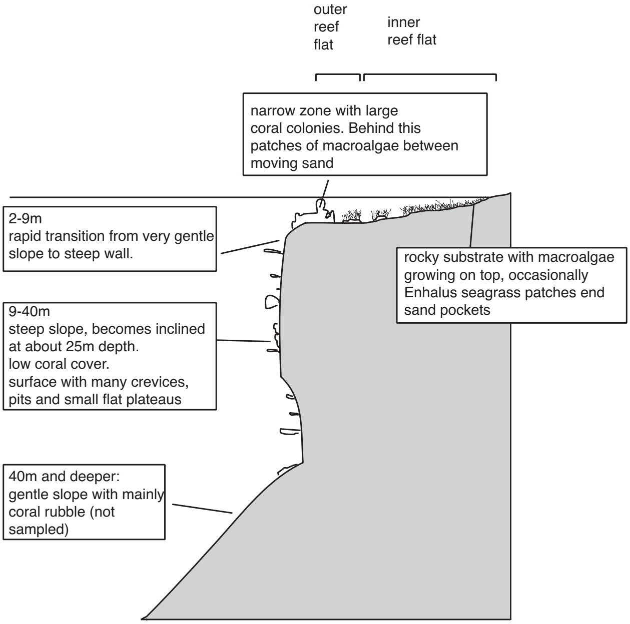


Fig. 5.3. Sketch of the vertical reef profile showing the biotopes in transect B.

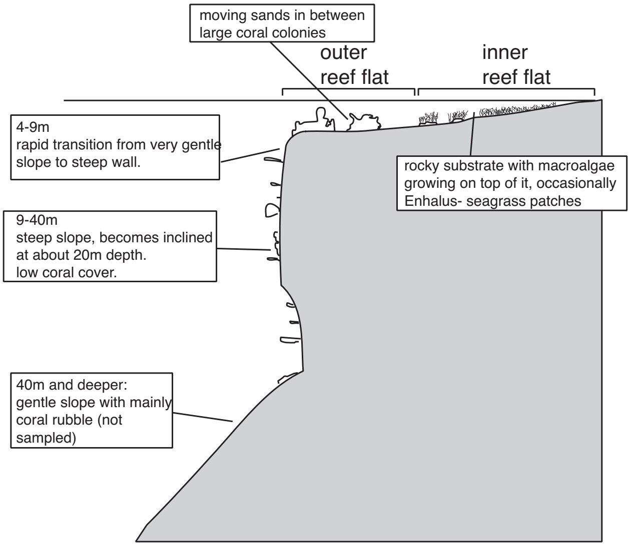


Fig. 5.4. Sketch of the vertical reef profile showing the biotopes in transect A.

outer reef flat usually is about 3-4 m deep. In the more exposed transect A, the outer reef flat is broader than in transect B. From 4 m down there is a very steep, almost vertical reef slope, covered by sponges, algae and corals, showing many crevices and small ridges on which coral rubble and sand accumulate. The upper part of the slope and the transition from reef slope into outer reef flat is densely grown by corals.

At about 20 m depth the reef slope is inclined and at around 30-40 m depth the slope becomes more gentle, with sand patches and localised coral colonies, though still remaining rather steep. At this depth, coral rubble covered by coralline algae accumulate, providing abundant suitable habitat for larger foraminifera.

The southeastern slope of Cabilao Island (transect C) and the northern slope off Sandingan Island (transect D, Fig. 5.5) are more gentle, consisting of a shallow part covered by corals (6-9 m), and a deeper part of the slope with coral rubble, sand patches and local coral colonies. The reef flats consist of moving sand and coral patches all the way towards the island, and is slightly deeper than the reef flat of transect B and A. At none of the visited localities in section D a reef flat comparable to that in sections A and B is present. At the deeper part of the reef flat, sea grass (*Halophilus*) are growing.

Methods

During SCUBA diving, samples were taken at least at intervals of 3 m depth, and sometimes in between these depths if suitable sampling sites were present. Samples were coded with C followed by the number of the dive site and the depth at which it was taken (for example C05-7.5 stands for a sample taken at station 5 at 7.5 m depth). At some stations several samples were taken from several substrate types.

A sample of all suitable substrates represents a surface area of 100 cm^2. In some cases a larger surface area was sampled because of the nature of the substrate, but

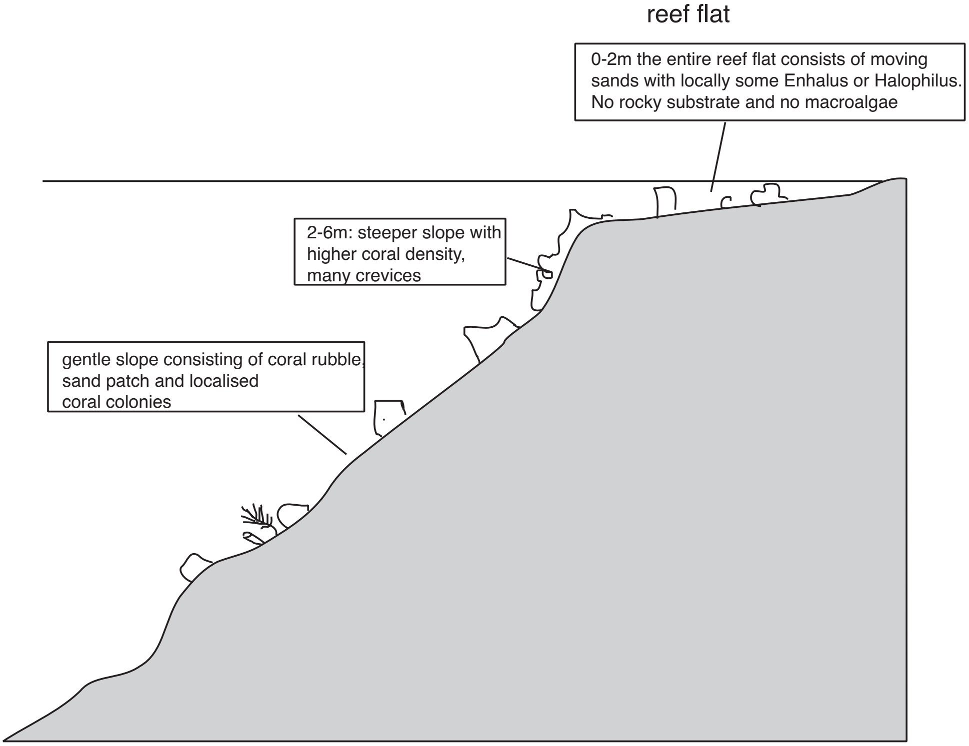


Fig. 5.5. Sketch of the vertical reef profile showing the biotopes in transects C and D.

then the surface area was noted. The samples were sun dried. Foraminifera were washed from the substrate and subsequently sieved over a 0.5 mm mesh size. From the reside, specimens living at the time of sampling, recognised by their symbiont colour, were sorted and identified up to species level.

The data-base of 68 samples and densities of 16 taxa were converted using a logarithmical transformation (y= log (density$_{\text{species x}}$+ 1).With the resulting database subsequently cluster analysis (Sorensens distance measure and Flexible β (β=-0.75)) and indicator analysis (Dufrêne & Legendre, 1997) was performed. Additionally a DCA (detrended principal component analysis) was run. All statistical analyses were run using PC-ORD (McCune & Mefford, 1999).

Distribution of larger foraminifera over the Cabilao reef

Among all samples, the highest density, over 13 specimens cm^{-2}, of larger foraminifera was found on the inner reef flat (Fig. 5.6). The outer reef flat and upper part of the reef slope were almost barren with larger foraminifera, while lower on the slope the density was maximally 4 cm^{-2}, and gradually decreasing from 8 m downwards in transects A and B. The more gently sloped transects C and D showed a maxi-

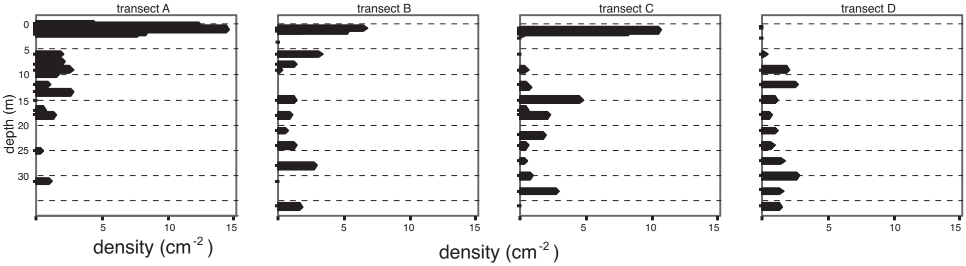


Fig. 5.6. Total density of larger foraminifera along four transects around Cabilao (Bohol, Filippines). Samples are marked by a dot on the scale bar.

mum on the reef slope, apart from one station in transect C which had a reef flat comparable to those in transects A and B.

In total 18 species of larger benthic foraminifera have been found, one of which was separated into two morphotypes. Five species were very rare, three of these were found in less than five samples and have not been included in the analysis. These were *Dendritina ambigua*, *Peneroplis pertusus* and *Palaeonummulites venosus*. *Elphidium craticulatum* was also present in too few samples to be included in the analysis.

Below, all species and densities of species encountered are given. Species definitions are as in chapter 2 and Hohenegger (1994), in which all of the mentioned have been figured. Some additional plates are provided for the Calcarinidae.

Family Peneroplidae
Genus *Peneroplis*
Peneroplis pertusus (Forskål, 1775)

Peneroplis pertusus was recorded in five samples, but always with only one specimen per sample. The deepest record is from 36 m, the shallowest from 0.5 m.

Peneroplis planatus (Fichtel & Moll, 1798) (Fig. 5.7)

Peneroplis planatus is the most abundant imperforate foraminifer in our samples next to *A. hemprichii*. The maximum density of *P. planatus* is almost 1.0 cm^{-2}. It reaches its highest density on the reef flat, but is also found (in much lower density) on the upper part of the reef slope, extending down to 30 m. Like *C. hispida*, *P. planatus* lives hidden between the macroalgae on the inner reef flat and was not seen on the leaves of the algae.

Genus *Dendritina*
Dendritina ambigua (Fichtel & Moll, 1798)

Dendritina ambigua was found in only two samples, both at 18 m on a small ridge on the steep reef slopes in transects A and C. On these ridges foraminifera lay on flat surfaces which are usually covered with coralline algae.

Figs. 5.7-5.22. Density of larger foraminifera (specimen cm^{-2}) along four transects around Cabilao (Bohol, Philippines. Samples marked by dot on vertical scale line. Note scale difference in horizontal scale. A sample represents 100 cm^2.

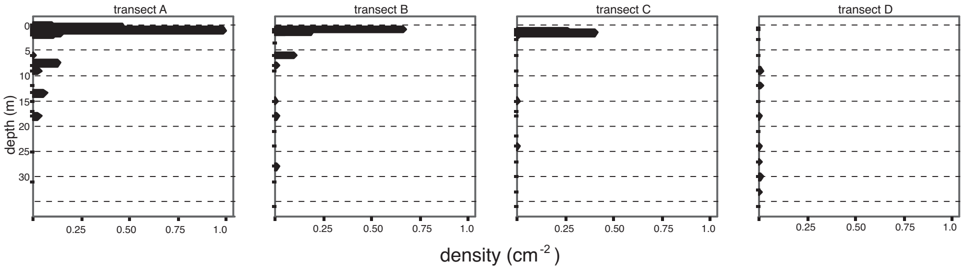


Fig. 5.7: *Peneroplis planatus*.

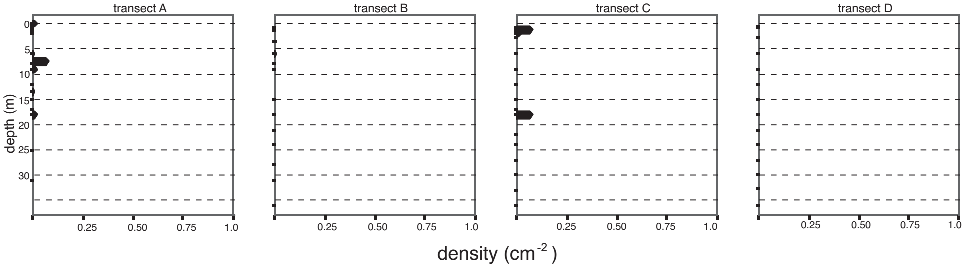


Fig. 5.8: *Laevipeneroplis proteus*.

Genus *Laevipeneroplis*
Laevipeneroplis proteus (d'Orbigny, 1839) (Fig. 5.8)

A rare species recorded in 10 samples and living attached to macroalgae. It was found mainly in the upper 10 m, but also in two samples at 18 m.

Family Soritidae
Genus *Parasorites*
Parasorites orbitolitoides (Hofker, 1930) (Fig. 5.9)

This is a rare species around Cebu. *P. orbitolitoides* was found in only seven samples. In one sample a density of 0.18 cm^{-2} was found, while the six other samples contained only 1-3 individuals. All specimens found were living attached to coral rubble, most of them in very shallow water.

Genus *Sorites*
Sorites orbiculus (Forskål, 1775) (Fig. 5.10)

Another rare species but recorded in more samples than *P. orbitolitoides*. No clear pattern can be distinguished in the records of this species. Most specimens were attached to coral rubble, but also to thalli of macroalgae. They have been found at depths ranging from 0.5-24 m, but always in extremely low density.

Genus *Amphisorus*

Amphisorus hemprichii Ehrenberg, 1839 (Fig. 5.11)

The highest densities have been found on the reef flats of transects A, B and C, where it was recorded in the inner reef flat only, living attached to macroalgae and sea grasses (*Halophilus*). However, *A. hemprichii* is not restricted to the reef flat, and can be found down to 20 m, found attached to coral rubble covered by coralline algae, but densities higher than 1.0 cm^{-2} are restricted to the upper 10 m of the water column.

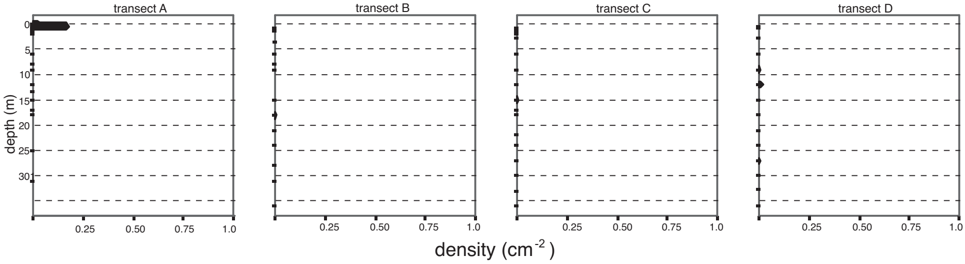


Fig. 5.9: *Parasorites orbitolitoides.*

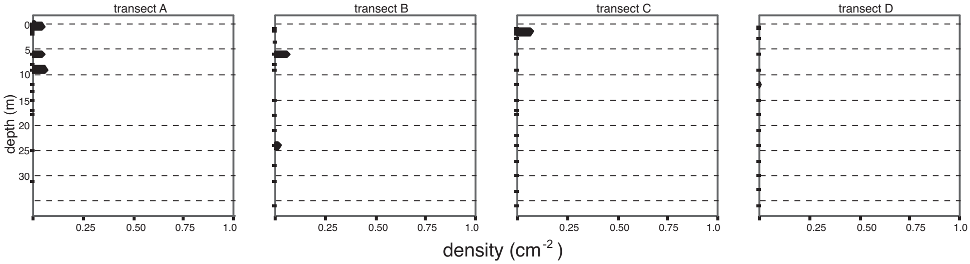


Fig. 5.10: *Sorites orbiculus.*

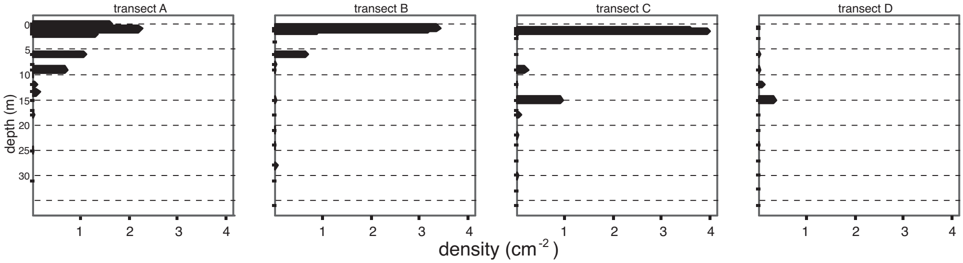


Fig. 5.11: *Amphisorus hemprichii.*

Family Amphisteginidae
Genus *Amphistegina*
Amphistegina lessonii d'Orbigny, 1826 (Fig. 5.12)

Amphistegina lessonii is the only species present in all samples in which larger foraminifera have been found. Its density is also rather constant in all samples, varying between 0.1-1.5 cm^{-2}. Highest densities have been found in areas covered by algae. Especially on the steep reef slopes, A. lessonii is found on ridges and in small cavities where rubble accumulates on which algae can grow.

Amphistegina lobifera Larsen, 1976 (Fig. 5.13)

This is a species that mainly occurs in very shallow samples taken on the inner and outer reef flat. In the latter it is found on coral patches, but not in the clean moving sands between these patches. The highest density of this species is just over 1.0 cm^{-2}.

Amphistegina radiata Fichtel & Moll, 1798 (Fig. 5.14)

Amphistegina radiata is hardly found on the reef flat, but is found in most samples on the reef slope. Its occurrence is rather patchy, high densities have been found below protruding pieces of coral rubble and on ridges. It is often found in cryptic places not directly exposed to light. On more gentle reef slopes in transects C and D the distribution was more evenly spread over the entire slope, and the highest density was reached at 25-30 m depth, whilst low densities were found on soft substrate.

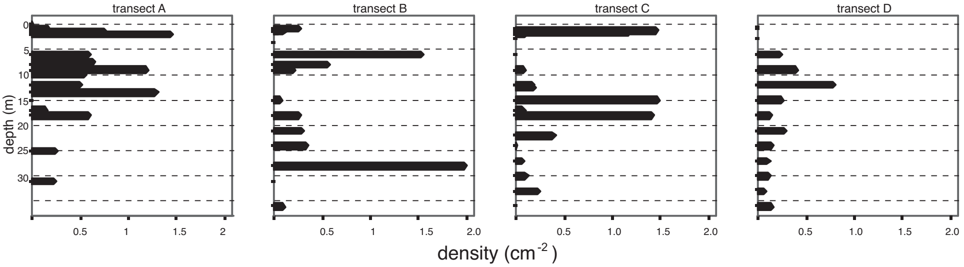


Fig. 5.12: *Amphistegina lessonii.*

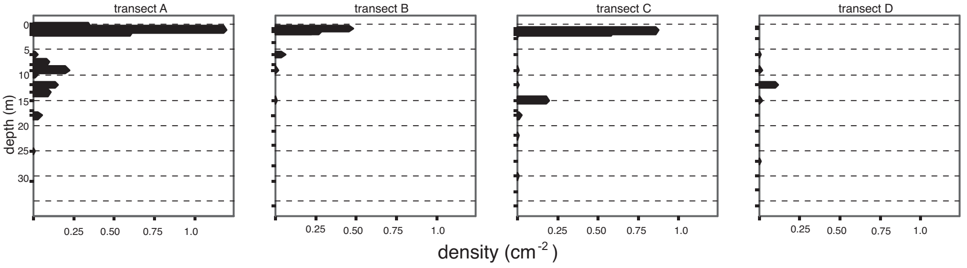


Fig. 5.13: *Amphistegina lobifera.*

Family Calcarinidae

Genus *Neorotalia*

Neorotalia calcar (d'Orbigny, 1839) (Fig. 5.15)

N. calcar has a distribution very similar to *Calcarina hispida*, but the density in which *N. calcar* has been found is much lower. The highest density in which *N. calcar* has been found is 0.5 cm^{-2}.

Genus *Calcarina*

The taxonomy of the genus *Calcarina* is not yet satisfactory resolved. Most species are very variable and often two or more (ecopheno)types can be recognised within a species.

The two types of *C. hispida* have been described as two forms by Hohenegger *et al.* (1999) and subsequently as two species by Hohenegger (2000). I will follow the latter concept, with the long spined, less hispid species being referred to as *C. mayori*, while the shorter spined and more hispid species is referred to as *C. hispida*.

Morphological variation is more gradual in *C. spengleri*, but almost the same differentiation can be made in specimens from Cabilao. *C. spengleri* sensu lato can be recognised by the parallel striae on the spines and the absence of very short hispid spines. Within *C. spengleri* s.l., spine morphology and the presence of tubercles on the central part of the shell can be used to distinguish the two types, *C. spengleri* sensu stricto *and C. spengleri* type A. Of the two morphotypes *C. spengleri* s.s. has more robust spines and

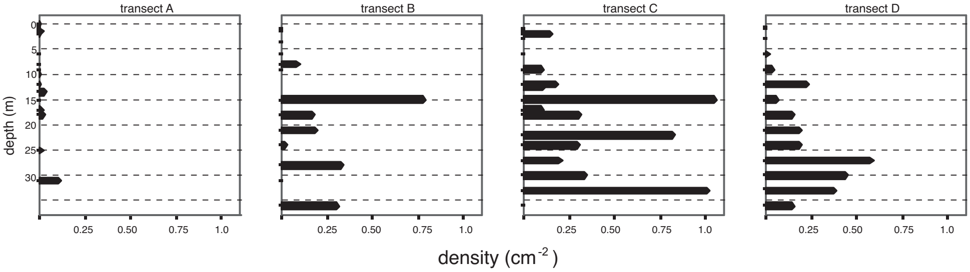


Fig. 5.14: *Amphistegina radiata*.

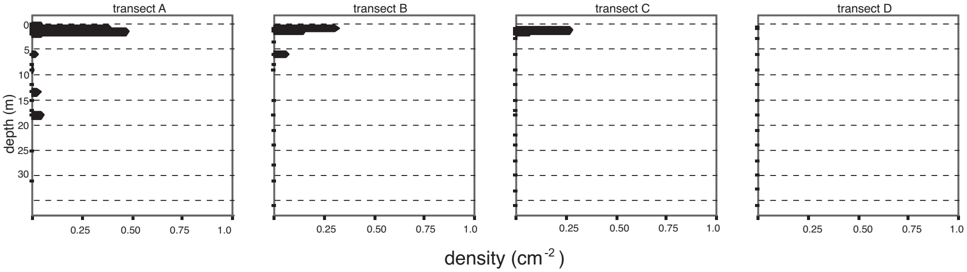


Fig. 5.15: *Neorotalia calcar*.

the transition of the spines into the central part of the test is gradual, while it has hardly any tubercles on the test. In *C. spengleri* type A the spines are more clump shaped and do not grade into the central part of the test, which has large tubercles roughly placed in a spiral. Although transitional forms are not known from Cabilao and surroundings, in the Spermonde Archipelago all specimens of *C. spengleri* show mixed characters and thus these forms are interpreted as morphotypes rather than species.

Calcarina hispida Brady, 1876 (Fig. 5.16; Pl. 5, figs. 7-8)

This species was predominantly found on the inner reef flat, its density regularly exceeding 1.0 cm^{-2}, and could get as high as 3.8 cm^{-2}. On the reef flat it was found hidden deeply between thalli of macroalgae near the sediment surface. Its occurrence extends down to the upper reef slope on the west side of Cabilao. It was not found on the gentle reef slope of Sandingan (transect D). On the reef slope it was found on highly structured coral rubble covered by coralline algae.

Calcarina mayori Cushman, 1924 (Fig. 5.17; Pl. 5, figs. 5-6)

Calcarina mayori occurred in fewer samples than *C. hispida*. *C. mayori* was always found on the reef slope, never on the reef flat. It was most numerous on pieces of coral rubble. The two samples showing the highest density of *C. mayori*, C09-36 and C12-36, were taken on places with large pieces of rubble covered by algae. Most individuals were not attached to the algae but to a piece of rubble.

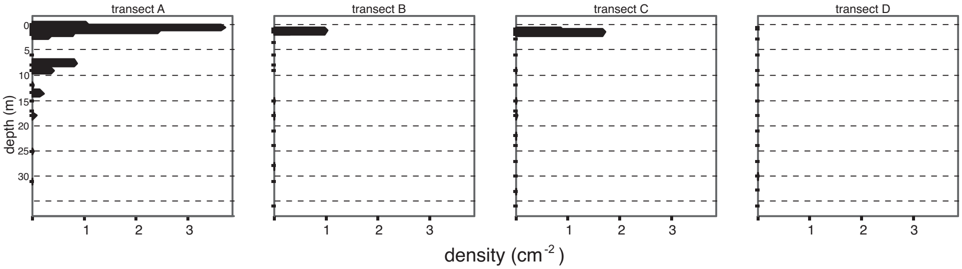


Fig. 5.16: *Calcarina hispida.*

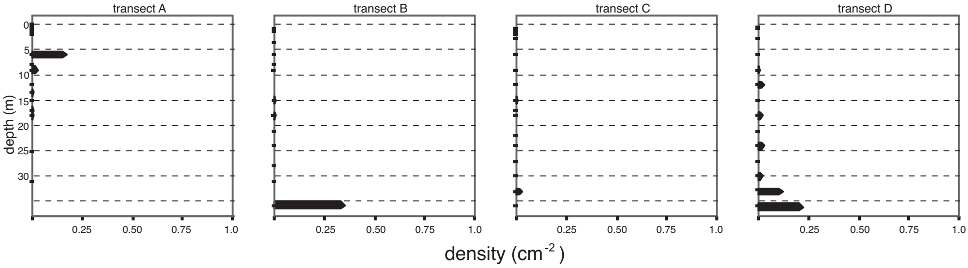


Fig. 5.17: *Calcarina mayori.*

Calcarina spengleri (Gmelin, 1791) sensu stricto (Fig. 5.18; Pl. 5, figs. 1-2)

This morphotype is only recorded in the inner reef flat in between large macroalgae. Contrary to *C. hispida* this species lives stacked up in between the well structured macroalgae, not necessarily near the sediment surface. It was not seen attached to the vertical, free moving macroalgae thalli. The highest densities have been found on the west side of Cabilao. In transect D no area with abundant macroalgae was present. The reef flat is entirely made up of instable sandy substrates and patches with coral growth without *C. spengleri*.

Calcarina spengleri (Gmelin, 1791) type A (Fig. 5.19; Pl. 5, figs. 3-4)

Just like *C. mayori*, this species is mainly found on the reef slope, were it occurs in many samples, but usually in low density (up to 1.0 cm^{-2}). In three samples it is found in higher density, two of these are located on the upper slope, one at 30 m depth. Specimens were usually found attached to coral rubble covered by coralline algae.

Genus *Baculogypsinoides*

Baculogypsinoides spinosus Yabe & Hanzawa, 1930 (Fig. 5.20)

This calcarinid species is predominantly found in the deepest samples. In transect D it occurred in all samples from 15 m downward, reaching its highest density at 33-36 m depth. The highest density is recorded at 28 m depth in transect B. *Baculogypsi-*

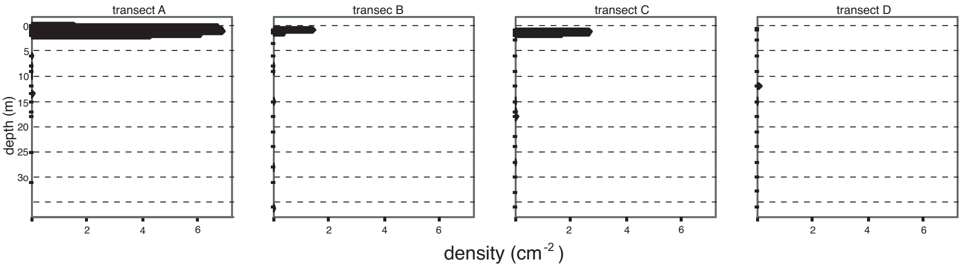


Fig. 5.18: *Calcarina spengleri* s.s.

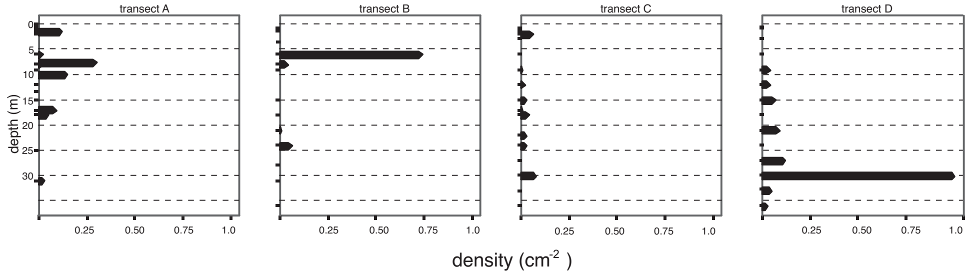


Fig. 5.19: *Calcarina spengleri* type A.

noides spinosus is always found below and between coral rubble, usually attached to the sides of large pieces of rubble covered by coralline algae.

Family Rotalidae
Genus *Elphidium*
Elphidium craticulatum (Fichtel & Moll, 1798)

This non-symbiont-bearing species is very rare, and recorded in only four samples, all except one in transect D. Densities are low.

Family Nummulitidae
Genus *Heterostegina*
Heterostegina depressa d'Orbigny, 1826 (Fig. 5.21)

Heterostegina depressa occurs mainly on the reef slopes. On the steep reef slopes of transects A and B it occurred abundantly attached to short algae on the surface of the reef wall, where it usually was the only living foraminifera. On these sites, they are directly exposed to light and currents. *Heterostegina depressa* was hardly found on the upper reef slope from 4-8 m. It reached its highest density at about 10-15 m depth, was found abundant down to the deepest sites visited. On the more gentle slopes of transects C and D, *H. depressa* was more abundant than in the other transects, and occurred on and between coral rubble, to which it is attached.

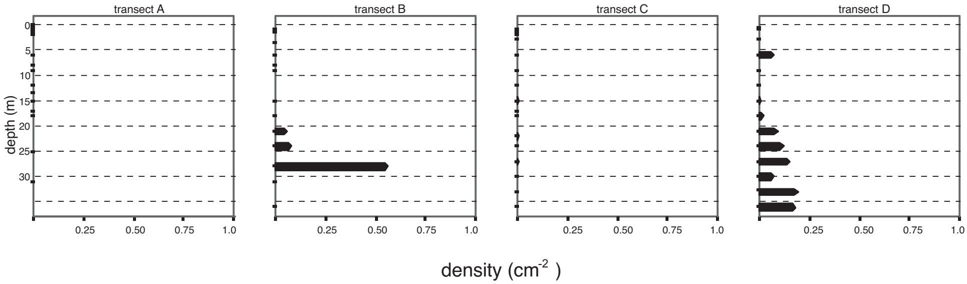


Fig. 5.20: *Baculogypsinoides spinosus.*

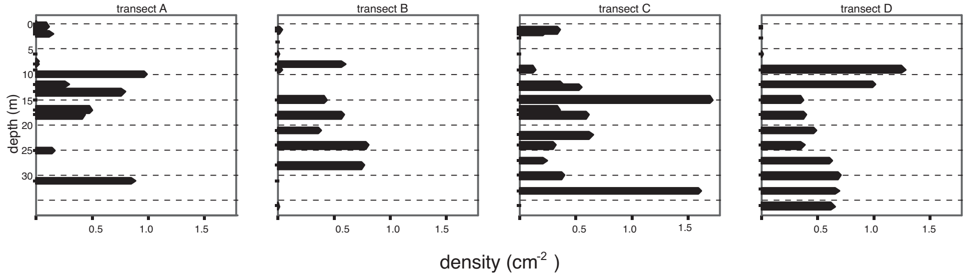


Fig. 5.21: *Heterostegina depressa.*

Genus Operculina

Operculina ammonoides (Gronovius, 1781) (Fig. 5.22)

This species has been found in almost half of the samples, but always in very low numbers. On the gentle slope of transect D it occurred in somewhat higher densities. On sand pockets in between coral rubble the highest density found is 0.4 cm^{-2}. *O. ammonoides* was also found on solid substrates.

Genus *Palaeonummulites*

Palaeoummulites venosus (Fichtel & Moll, 1798)

The only other nummulitid that has been found is a single specimen of *P. venosus* in C12-36 at 36 m depth. This is on the same gentle reef slope where most of the specimens of *O. ammonoides* has been found.

Assemblages

Q-mode cluster analysis shows a very strong division into two clusters (Fig. 5.23). Indicator analysis shows that cluster 1 is characterised by the occurrence of *Amphistegina radiata* and *Heterostegina depressa* (Table 5.1). In about a quarter of the samples these two are the only species found (sub-cluster 1b), while the remaining samples are divided into a sub-cluster with additionally species that otherwise have their highest indicator value in cluster 2 (sub-cluster 1-a) and a cluster with additionally *Baculogypsinoides spinosus* and *Operculina ammonoides* (sub-cluster 1-c, Table 5.1). The subdivision of this cluster, especially the differentiation between sub-clusters 1-a and 1-b, is very weak, omitting a few samples results in a different cluster arrangement.

Samples in cluster 2 are characterised by the occurrence of *Calcarina hispida, Neorotalia calcar* and *Peneroplis planatus*. Other frequently occurring species are *Amphisorus hemprichii* and *Amphistegina lobifera* and *Calcarina spengleri* s.s. (Fig. 5.23, Table 5.1).

Since especially the samples in cluster 1 show a gradual decrease in similarity, a DCA (detrended principal components analysis) was performed as well. This analysis supports the pattern found by the cluster analysis (Fig. 5.24). Samples clustering in the clusters 1 and 2 are separated by a small gap along the first axis. Sub-cluster 1-c plots separately from sub-clusters 1a and 1b, but the samples clustering in 1a and 1b show some overlap.

The first axis explains 75% of the total variance in the data set and plots parallel to the direction of the depth at which the samples have been taken. The second axis explains 13% of the total variance, only.

An r-mode cluster analysis shows that there are two well separated assemblages, which both can be subdivided into two groups (Fig. 5.25). Together with the percent perfect indication values as given in Table 5.1, one assemblage can most easily be characterised by the dominating occurrence of *Heterostegina depressa* and *Amphistegina radiata*. In some samples these are associated with other species, like *Operculina ammonoides* and *Baculogypsinoides spinosus*.

The other assemblage is dominated by a group of species that all occur on the inner reef flat. These are *Peneroplis planatus*, *Neorotalia calcar*, *Amphisorus hemprichii*,

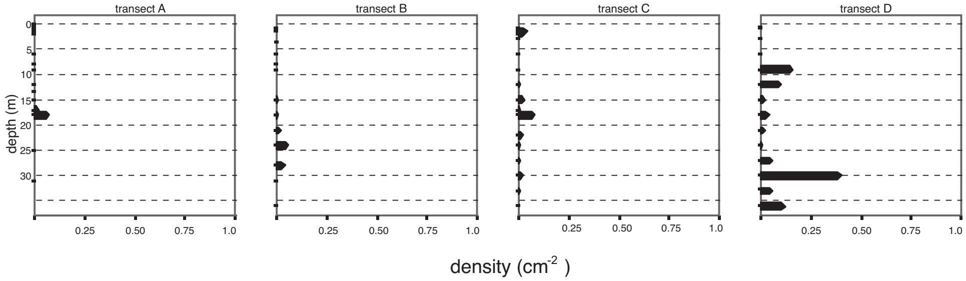


Fig. 5.22: *Operculina ammonoides.*

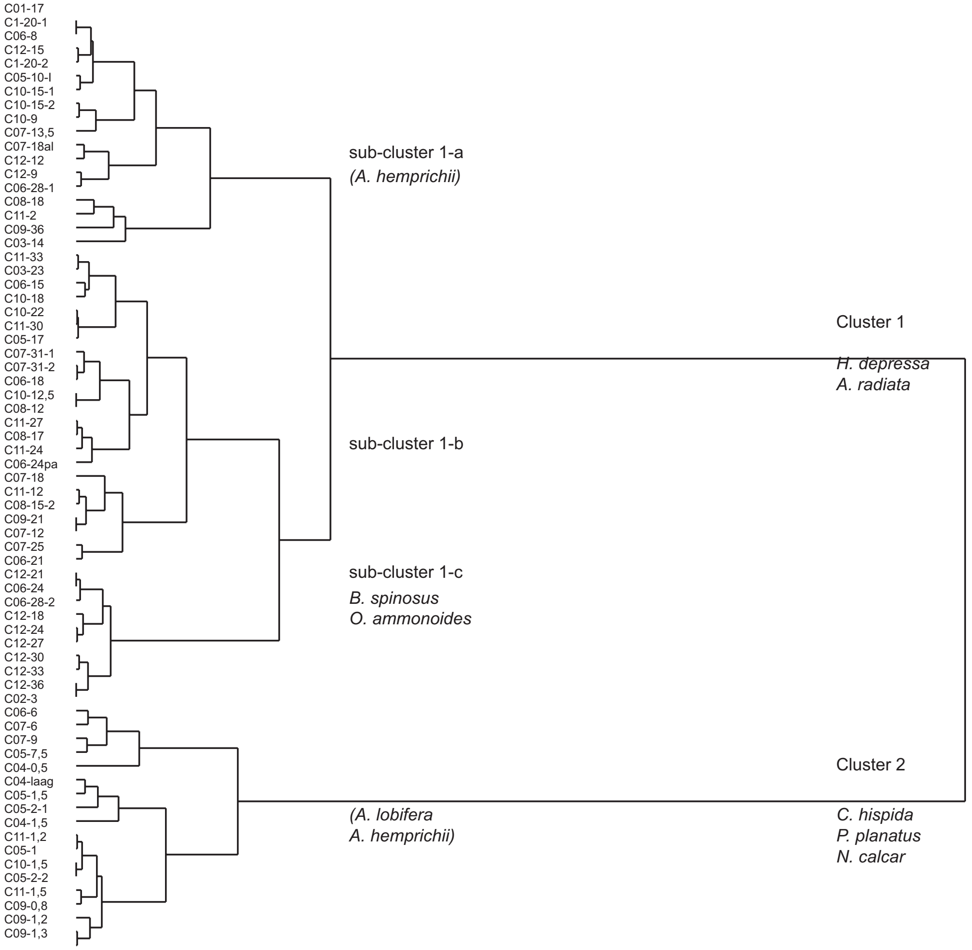


Fig. 5.23. Dendrogram resulting from a Q-mode cluster analysis as described in text. Characteristic species have been indicated for each cluster. Species in brackets have a high indicator value in more than one cluster.

Table 5.1. Percentage perfect indication for the species at a division into four clusters

Species	Cluster 1-a	Cluster 1-b	Cluster 1-c	Cluster 2	% samples
Heterostegina depressa	**28**	**30**	**32**	8	94
Amphistegina lessonii	31	22	23	23	100
A. radiata	**32**	**30**	**37**	0	78
Operculina ammonoides	15	0	**54**	19	50
Baculogypsinoides spinosus	1	0	**85**	1	22
Calcarina mayori	11	1	25	1	24
C. spengleri type A	23	7	24	5	51
Amphisorus hemprichii	29	4	0	55	66
Calcarina hispida	5	4	0	**58**	44
C. spengleri s.s.	11	1	0	**64**	24
Amphistegina lobifera	17	4	0	47	50
Peneroplis planatus	6	0	9	**66**	47
Neorotalia calcar	3	0	0	**61**	24
Sorites orbiculus	0	0	0	34	13
Parasorites orbitolitoides	6	0	2	6	9
Laevipeneroplis proteus	9	0	0	20	15

Calcarina hispida, *Calcarina spengleri* s.s., and *Amphistegina lobifera*. The first two species are nearly exclusive for the reef flat, the others have occasionally been found on the upper slope as well.

Habitat preference of the species found around Cabilao and the Spermonde Archipelago

Of the 22 species of larger benthic foraminifera found in the Spermonde Archipelago, 17 have been found around Cabilao as well (*Dendritina zhengae*, *Alveolinella quoyii, Amphistegina papillosa*, *Operculina complanata* and *O. heterosteginoides* are absent at Cabilao). *D. zhengae* was very rare at the Spermonde, but the other species were common at the base of several reefs in the Spermonde (Chapters 2 and 3, above). Two of the rare species in Cabilao are also rare in the Spermonde (i.e. *Laevipeneroplis proteus* and *Peneroplis pertusus*). Key environmental parameters and the occurrence of all species recorded either at the Spermonde Archipelago or at Cabilao are summarised in Table 5.2.

Peneroplidae

In Cabilao, *Peneroplis planatus* was living at the reef flat in between the thalli of the macroalgae, where it is sheltered from the highest hydrodynamic energy, similar to Okinawa, where it has been recorded from the upper slope, hiding in small filamentous algae (Hohenegger, 1994). In the absence of macroalgae, at the Spermonde Shelf this specimens of this species was mainly living at soft substrate on the upper leeward slope.

Soritidae

Around Cabilao *Parasorites orbitolitoides* is rare and always attached to solid substrates on the upper slope at Cabilao which is a totally different habitat from that of

	found at	transparency of water column		hydrodynamic energy			substrate				depth				remarks
		high	low	very high**	high**	low	rubble	rubble with algae	macroalgae	soft	0-10	11-20	21-30	31-40	
Peneroplis planatus	□ ○ △	□ ○ △		▵	□ △	△	△	△	△	□	□ ○ △	□ ◦ △	△		
P. pertusus	▫ ◦ △	▫ ◦ △		▵	△	△	△	△	△	△	△	△	△	△	
Dendritina ambigua	□ △	□ △			△	□ △				□ △	△	□ △	□ △		
D. zhengae	▫ △	▫ △			△	▫ △				□ △		▫ △	▫ △	□ □ ○ △	
Laevipeneroplis proteus	□ ◦	□ ○			□ ◦			□ ◦			□ ◦	◦			
Alveolinella quoyii	□ △	□ △		▵	△	□ △	△			□ △	△	□ △	□ △	□ △	shallow on firm substrate, deep (Hohenegger, 1994)
Parasorites orbitolitoides	□ ○ △	□ ○ △			○* ▵	□ △	○			□ △	○	□ ○ △	□ △	△	
Sorites orbiculus	□ ○ △	□ ○ △		▵	□ ○ △	△	□ ○ △				▫ ○				10-20 at SO
Amphisorus hemprichii	□ ○ △	□ ○ △		▵	□ ○ △	□ ○ △	□ ○ △	□ ○ △	○	□ △	□ ○ △	□ ○ △	□ △	△	in shallow water not on soft substrate
Amphistegina lobifera	□ ○ △	□ ○ △	■	□ ○ △	■ □ ○ △	△	■ □ ○ △	■ □ ○ △	○ △		■ □ ○ △	□ ○ △			anywhere in shallow, highly illuminated areas, in these areas soft substrates are not stable enough to facilitate LF occurrence
C. mayori															
A. lessonii	■ □ ○ △	□ ○ △	■	▵	□ ○ △	□ ○ △	■ □ ○ △	■ □ ○ △	○ △	□ △	■ □ ○ △	□ ○ △	□ ○ △	□ ○ △	not on shallow soft substrate
A. radiata	■ □ ○ △	□ ○ △	■		△	□ ○ △	□ ○ △	■ □ ○ △		▵	■ □ ○ △	■ □ ○ △	□ ○ △	□ ○ △	preference for solid substrates, but also found in low density on soft substrate
A. papillosa	□ △	□ △			△	□ △						□	□	□ ▵	>30m, abundant >40m in J
Neorotalia calcar	□ ○ △	□ ○ △		△	□ ○ △	□ △	△	△	○	□ △	□ ○ △	□ △	□ ▵		I.
Calcarina gaudichaudii s.l.	□ ○ △	□ ○ △		△	□ ○ △	□ △	□ ○ △	□ ○ △	○ △		○ △	□ ○ ▵	□ ○		on sand
C. gaudichaudii type A	○	○				○		○				○	○		
C. gaudichaudii s.s.	○ △	○ △		△	○ △*	○	△	△	○	▵	○ △	▵			maximum at reef edge, lower distribution limit at 20m
C. hispida	■ □ ○ △	□ ○ △	■	▵	□ ○ △	■ □ ○ ▵		■ □ ○ △	○ △		■ □ ○ △	■ □ ◦ △	□	□ △	peference for shallowest slope parts, but never on reef flat in J
	○ △	○ △		▵	△	○ ▵	△	○ △	○	▵	▵	△		△	preference for solid substrates, but also found in low density on soft substrate in J
Baculogypsinoides spinosus	□ ○ △	□ ○ △			△	□ ○ △		□ ○ △		△		□	□ ○ ▵	□ ○ △	no substrate preference in J, preference for solid substrate in C and SO
Operculina ammonoides	□ ○ △	□ ○ △			▵	□ ○ △	○ △			□ △	○	□ ○ △	□ ○ △	□ ○ △	
O. complanata	▫ △	▫ △				▫ △				▫ △			▫	▫	>45m, max at 65m in J (Hohenegger et al. 2000)
O. heterosteginoides	▫ △	▫ △				▫ △				▫ △			▫	▫	>25m, max at 65-75m in J (Hohenegger et al. 2000)
Nummulites venosus	□ △	□ △			▵	□ △				□ △		□	□ ▵	□ △	
Heterostegina depressa	□ ○ △	□ ○ △		▵	□ ○ △	□ ○ △	□ ○ △	□ ○ △	◦	□ △	■ □ ○ △	■ □ ○ △	□ ○ △	□ ○ △	rare at reef edge, sudden increase at about 10m specimens on soft substrate are larger than those on firm in J
Elphidium craticulatum	□ □ ○	□ ○	■		■ □	■ □	■ □	■ □		■ □	■ □	■ □	□	□	

* very high compares with extreme, high with high and moderate in Hohenegger et al., 1999 table 4
** only hidden between macroalgae
SN = Spermonde Nearshore (southern near shore zone in Renema and Troelstra, in press), SO = Spermonde Outershelf (remaining three zones at Spermonde Shelf),
C = Cebu, J = Japan (Sesoko Island, Okinawa) data from Hohenegger et al. 1999, unless otherwise stated
small symbol : the species has been found but in low abundance
Of both Dendritina ambigua and Nummulites venosus only one specimen was observed from Cebu, both records are not included in this table.

Table 5.2. Overview of records of larger benthic foraminifera from Cabilao (this study), the Spermonde Archipelago (chapters 2 and 3) and Okinawa (Hohenegger *et al.*, 1999).

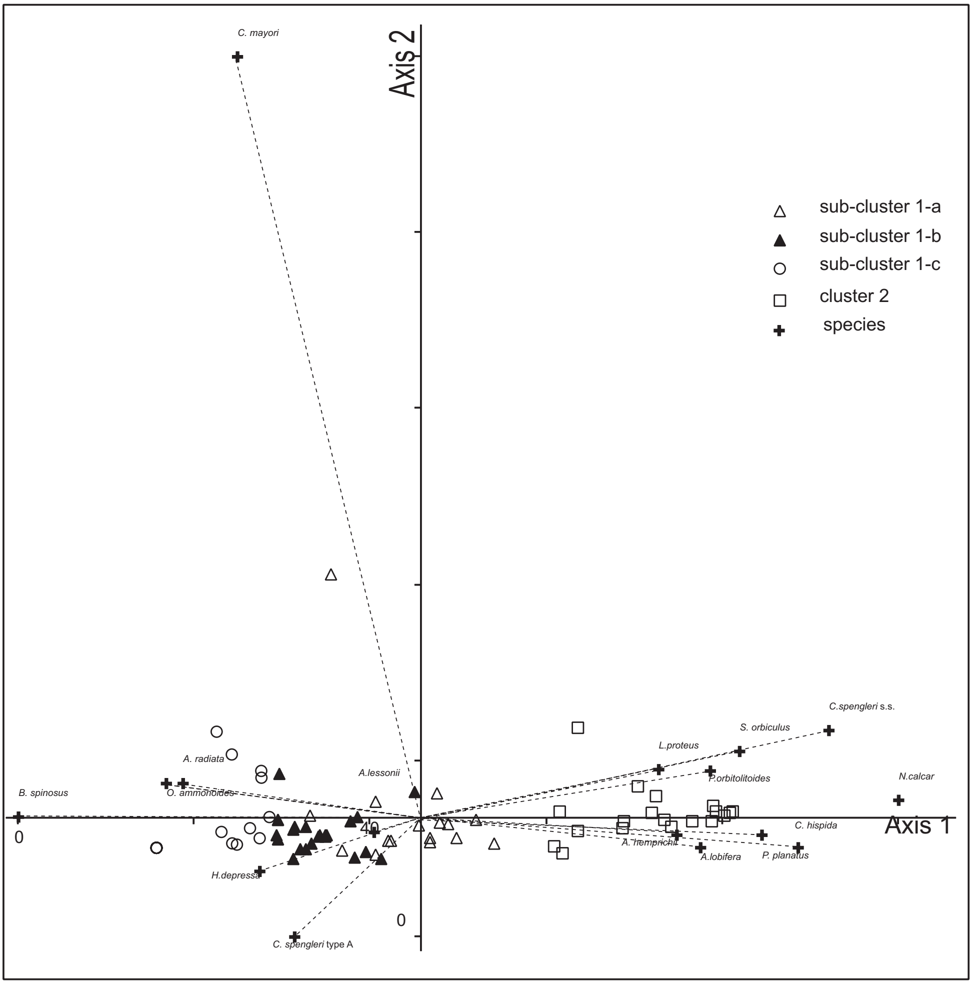


Fig. 5.24. DCA ordination showing scores for the sampling units and vectors for the species. Sampling units grouped by cluster analysis are plotted with the same symbols.

the Spermonde Archipelago, where it occurred preferentially on soft substrate at the reef base. In Cabilao it was recorded in low density. At Sesoko Island, Hohenegger *et al.* (1999) found *P. orbitolitoides* at both substrate types, but in significant higher density on soft substrate. They *(op cit.)* found that *P. orbitolitoides* "clearly avoided" the upper reef slope. The discoidal tests are easily transported from relatively high energy environments, unless they attach to the substrate.

The main substratum of *Amphisorus hemprichii* is formed by thalli of macroalgae on the reef flat, yet it was also found attached to sea grasses, coral rubble and large solid surfaces. The most important substratum of *A. hemprichii* in Okinawa (Hohenegger, 1994; Hohenegger *et al.*, 1999, 2000) and the Spermonde Archipelago (Chapter 2, above) is coral rubble. In higher energy settings *Marginopora vertebralis* occurred on the reef crest in Sesoka Island (Hohenegger, 1994). *A. hemprichii* is predominantly an

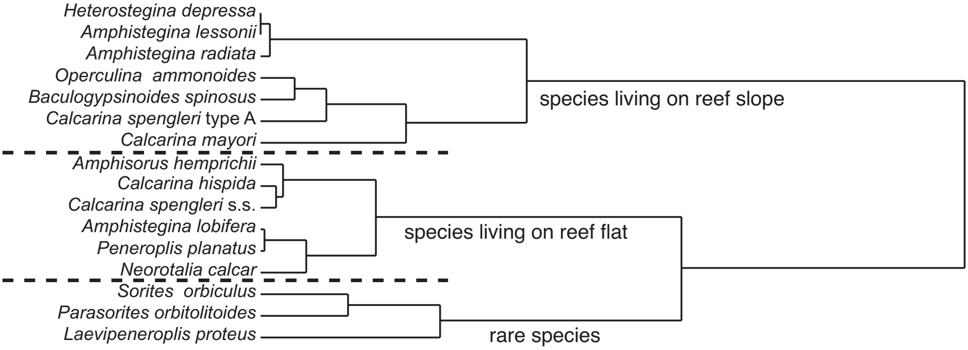


Fig. 5.25. Dendrogram resulting from an r-mode cluster analysis.

epiphytic species (on both macroalgae and sea grass), but can also occur on soft substrates (Langer & Hottinger, 2000; Hohenegger *et al.*, 1999). Another soritid, *Sorites orbiculus* used only a limited number of macroids, which are characterised by flat, bare surfaces to which it may semi-permanently adhere (Fujita & Hallock, 1999). The seagrass leaves in the Spermonde all were covered by epiphytic algae, providing no suitable substrate for soritids to live on.

Amphisteginidae

The three amphisteginids show a very similar habitat preference in the Spermonde Archipelago and around Cabilao. *Amphistegina lessonii* and *A. lobifera* do not show any clear preference for substrate type, in both the Spermonde and Cabilao both species occur in many samples. *A. lobifera* is restricted to shallow water, and is only occasionally found below 15 m depth. In the depth range sampled in this study, *A. lessonii* is the most common amphisteginid in other areas as well (Hansen & Buchardt, 1977; Hallock, 1984; Hohenegger, 1994; Hohenegger *et al.*, 1999; Chapter 2, above). *Amphistegina radiata* has hardly been found in the shallowest samples. Because of its smaller apertural field compared to *A. lessonii* and *A. lobifera*, *A. radiata* is not able to withstand the highest hydrodynamic energy regimes (Hohenegger, 1994). It has a preference for solid substrate (Hohenegger *et al.*, 1999) and it often lives cryptic between coral rubble in order to avoid high energy regimes (Chapter 2, above).

Calcarinidae

Neorotalia calcar has a rather different distribution pattern in the two areas. In the Spermonde *N. calcar* predominantly occurred on the upper leeward slope of the reefs, while around Cebu it was predominantly found at the inner reef flat. On the more gentle slopes of transects C and D it was not found on the reef slope as well. This distribution pattern is more similar to that in other areas (Hallock, 1984; Hohenegger, 1994, 1996). According to Hohenegger *et al.* (1999) *N. calcar* prefers solid substrates in the upper part of the reef slope (<20 m). In Cabilao and Hawaii (Hallock, 1984) this species occurs between thalli of macroalgae, whilst at the Spermonde Archipelago *N. calcar* was predominantly found on sandy substrate.

In the Spermonde Archipelago no *C. hispida* was found on the reef flat, but it is present on either side of the reefs down to 30 m depth. At Cabilao *C. hispida* is associated with an epiphytic lifestyle on macroalgae, while *C. mayori* is mainly found on a substrate of coral rubble. Hohenegger (1994) found a similar morphological gradient on the reefs around Okinawa. On the reef moat, *C. hispida* was globular with short spines and long spikes, similar to those found on the reef flat of Cabilao. However, Hohenegger *et al.* (1999) found this form (which they called *C. hispida* forma *spinosa*) never on the reef flat, but preferred the upper reef slope (maximum at 10 m depth). On the reef slope *C. hispida* became increasingly flattened, with longer spines and shorter spikes (Hohenegger, 1994; see also Hohenegger *et al.*, 1999).

The shell and spines of *C. mayori* are more fragile than the shell of *C. hispida*, and render poorer capabilities to attach to substrate in high hydrodynamic energy. *C. mayori* lives predominantly attached to coral rubble covered by algae in low energetic environments, a similar environment as in Okinawa (Hohenegger, 1994; Hohenegger *et al.*, 1999).

Calcarina spengleri occurs in high density on the relatively sheltered inner reef flat. The smooth form (*C. spengleri* s.s.) occurs mainly on the reef flat, while *C. spengleri* type A is more abundant on the reef slopes. An intermediate form (with the spines of *C. spengleri s.s.* and the pustules of *C. spengleri* type A) occurs on the Spermonde Shelf. There it is found on the exposed slope of the reefs in between coral rubble, and shallow living *C. spengleri* is absent. The shape of *C. spengleri* is very variable and highly dependent on environmental parameters, *C. spengleri* living on the reef flat has a more robust, thick shell that protects the animal from damage by UV light (Hottinger, 1997). This is enhanced by the shade provided by the thalli of the macroalgae. Robust shells are stronger, and the more robust spines provide stronger attachment to the algae. *Calcarina spengleri*, for example, occurs in more sheltered parts of the reef flat and below the fair weather wave base. Above the fair weather wave base, no cryptic habitats are available and *C. spengleri* does not occur in this area. In the Spermonde Archipelago coral rubble on the exposed slope provides shelter for waves and *C. spengleri* is found there below larger pieces of rubble.

Baculogypsinoides spinosus is one of the most consistent species in habitat preference. It occurs at larger depth on coral rubble (Hohenegger, 1994, 1996; Hohenegger *et al.*, 1999; Chapter 2, above).

A striking difference in abundance is seen in *Elphidium craticulatum*. This species is present in almost all samples taken from the Spermonde Archipelago, where it constitutes on average about 1/10 of the total number of specimens in the samples, and in samples taken at larger depth and nearshore even more, but is almost absent from Cabilao. *Elphidium craticulatum* does not house symbionts, but retains chloroplasts from otherwise digested algae. These chloroplasts produce photosynthetates that are used by the foraminifera. Retention of chloroplasts is profitable in places where otherwise the housing of symbionts is not profitable. This can be either in areas too cold or too rich in nutrients (Lopez, 1979; Hollaus & Hottinger, 1997). The conditions at the Spermonde Archipelago, especially in the deeper parts, are at the margin of the window in which endo-symbiosis is profitable for both symbiont and host. In Cabilao conditions fall well within this window and *Elphidium craticulatum* is hardly found.

Table 5.3. Comparison between assemblages found at the Spermonde Archipelago (Chapter 3) and Cabilao.

Spermonde Archipelago	**Cabilao**	**environment**
Calcarina spengleri	*Amphistegina radiata*	exposed reef slope
Amphistegina radiata	*Heterostegina depressa*	
Heterostegina depressa		
Baculogypsinoides spinosus	*Baculogypsinoides spinosus*	deep reef slope
Amphisorus hemprichii	*Operculina ammonoides*	
Amphistegina papillosa		reef base
Palaeonummulites venosus		
Operculina ammonoides		
Amphistegina lobifera	*Amphistegina lobifera*	upper reef slope
Neorotalia calcar	*Neorotalia calcar*	
Peneroplis planatus		
Peneroplis planatus		
	Amphisorus hemprichii	inner reef flat
	Calcarina hispida	
	C. spengleri s.s.	

Nummulitidae

Heterostegina depressa is one of the better studied larger foraminifera species. Its habitat preference is consistent between all areas. It is found in a large depth range on solid substrates, but is occasionally found on soft substrates as well (Hottinger, 1977a; Hallock, 1984; Vénec-Peyré, 1991; Hohenegger, 1994, 1995,1996; Hohenegger *et al.*, 1999; Chapter 2, above).

Hottinger (1977a) and Pecheux (1995) describe two ecophenotypes of *Operculina ammonoides*, a semi-involute and an evolute form. The more robust semi-involute form prefers shallow soft substrates (and is rarely found in the Spermonde Archipelago), while the evolute specimens predominantly occurred on coarse sand and rubble. Hohenegger *et al.* (1999) found a third form with elevated septal traces, which occurred on muddy substrate. All specimens from Cabilao were of the semi-involute type, but were rather loosely coiled compared to the coiling rate given by Hohenegger *et al.* (2000). Hohenegger *et al.* (2000) found this morphotype between well-structured coral rubble too (as well as on coarse sand). The specimens from Cabilao have been found on soft substrate in transect D, at similar depths as in the Spermonde Archipelago, but also attached to coral rubble on the reef slopes.

The assemblages from Cabilao and the Spermonde are rather comparable. In both areas there is a cluster which is characterised by the co-occurrence of *Heterostegina depressa* and *Amphistegina radiata*. In the Spermonde these two species are often accompanied by *Calcarina spengleri*. In both areas, *Baculogypsinoides spinosus* occurs together with these two species in deeper samples. Though not shown in Table 5.2, *Amphisorus hemprichii* occurs in both areas together with *H. depressa* and *A. radiata* in the upper slope samples (with solid substrate, Table 5.1).

Also both areas host an assemblage with *Amphistegina lobifera*, *Neorotalia calcar* and *Peneroplis planatus* which lives on the upper slope on the leeward side of reefs in the Spermonde Archipelago, while in Cabilao it is found on the reef flat between macroalgae. *Amphisorus hemprichii, Calcarina hispida*, and *C. spengleri* s.s. were often found together with the above mentioned species.

The Spermonde reef base assemblage, including species that have a preference for soft substrates, is almost absent at Cabilao. Only one species that is characteristic for this cluster, *Operculina ammonoides*, has been found around Cabilao. It is found in another assemblage however.

Conclusion

The distribution and assemblage composition of larger foraminifera respond to several environmental parameters, like light intensity (directly related to depth and transparency), hydrodynamic energy, substrate type and environmental stability. However, some species show always similar habitat preferences, whilst others are more flexible and occur in other habitats in response to different combinations of environmental conditions, resulting in large variations in habitat in which species occur (within and between regions).

Calcarinids (except *Baculogypsinoides spinosus*) and soritids are groups that show large differences in habitat preference between regions, while nummulitids, amphisteginids and *Baculogypsinoides spinosus* occur in similar habitats in all regions examined.

The largest difference in fauna characteristic between the Spermonde Archipelago and the Cebu islands is the almost total absence at the latter of *Elphidium craticulatum*, which is the second most whidespread species in terms of sample number and the most abundant in terms of number of individuals in the Spermonde Archipelago. The most important ecological trait that characterises *Elphidium craticulatum* with respect to larger symbiont-bearing foraminifera is that they are not obligate algal-host systems but show chloroplast retention. Chloroplast retention is profitable in systems where light is still available, but due to adverse conditions endosymbiosis is not profitable for either host or symbiont (Lopez, 1979; Hollaus & Hottinger, 1997). Because chloroplast retention is a non-obligate system, *Elphidium* is also able to survive during longer periods of conditions in which endosymbiosis is not profitable anymore.

6. Palaeogene nummulitids (Foraminiferida) from the Indonesian Archipelago: a review

Willem Renema; Andrew Racey, BG Group, 100 Thames Valley Park Drive, Reading, Berkshire, RG6 1PT, England; Peter Lunt, Coparex Blora b.v., Jalan H.R. Rasuna Said, Kav. X-2, No 1, Jakarta 12950, Indonesia.

In press: Cainozoic Research **2** (2).

Introduction

Larger foraminifera, especially of the genera *Nummulites* and *Assilina*, have a long history of being used for stratigraphy, starting with De la Harpe (1877). More recently, Blondeau (1972) and Schaub (1981) have summarised the stratigraphic and geographic distribution of numerous species of these genera. Blondeau's work covered the Tethys, Indo-West Pacific and North and South Americas, occasionally referring to Indonesia, Japan, and the West Pacific whilst the much more elaborate review by Schaub (1981) dealt with species from around the Mediterranean and Europe. Racey (1995) described nummulitids from Oman, an area located at the boundary between two of the main Cainozoic larger foraminiferal faunal provinces, i.e., the Mediterranean and Indo-Pacific, and integrated these with Schaub's zonal scheme.

Schaub (1981) proposed a series of biozones for the Palaeogene based on species of *Nummulites* and *Assilina*, which were combined with the biozones proposed by Hottinger (1960) for *Alveolina* and calibrated against nannoplankton data. These zonations were eventually integrated into the shallow benthic zones (SBZ) covering the Palaeocene to Eocene of the Mediterranean region by Serra-Kiel *et al.* (1998). All this work was based mainly on the western Tethys. The most recent revisions of *Nummulites* and *Alveolina* from Indonesia were by Doornink (1932; the genus *Nummulites* in Java) and Bakx (1932; Alveolinidae in Indonesia). The principal objective of the present study is to improve the correlation of the Eocene strata from Indonesia with the timescale of Berggren *et al.* (1995). This could only be satisfactorily attempted when coupled with a revision of the taxonomic status of the various nummulititids previously recorded from the region. Many of these taxa are, by modern standards of taxonomy, inadequately described and, in many cases, poorly illustrated in the original publications. Our work, in part, rectifies these omissions.

In Indonesia, Martin (1881) originally followed the Lyellian method of European biostratigraphy, which was based on the ratio between extant and extinct molluscs, including selected foraminifera. Direct comparison between Europe and Indonesian outcrops led to different conclusions, based either on the occurrence of larger foraminiferal genera or the extant/extinct ratio. The extant/extinct molluscan ratio resulted in an Oligocene age being assigned to the Nanggulan section, though the abundant occurrence of non-reticulate *Nummulites* suggested an Eocene age (e.g., Martin, 1881). However, Martin's view was blurred by the fact that the samples he received from the Nanggulan section comprised a mixture of Eocene to Miocene samples from the nearby Djonggranan beds. When he collected samples himself in 1910, he immediately revised his view to Eocene.

Discrepancies in molluscan biostratigraphy led the Geological Survey in the then Netherlands East Indies to use larger benthic foraminifera for correlation, which resulted in the application of van der Vlerk & Umbgroves (1927) letter stages. Originally there were six letter stages (Ta-Tf), which later increased to eight (Ta to Th). A total of 16 subzones were also included, of which 7 zones and 13 subzones were based on larger foraminiferal ranges (Leupold & van der Vlerk, 1931). The number of letter stages was then revised back to six (Ta-Tf) again by van der Vlerk (1955). The most recent revision of the letter stages for the entire Cainozoic was by Adams (1970), whilst the Oligocene to Pliocene was revised again by Boudagher-Fadel & Banner (1999). The Palaeogene is covered by letter stages Ta to lower Te. The Ta and Tb stages cover the Palaeocene and Eocene, when compared with the European sequence (Adams, 1970). The Ta stage is subdivided into three parts, Ta_{1-3} corresponding broadly to the Late Palaeocene, Early Eocene and Middle Eocene, respectively. The Tb-stage is equivalent to the Late Eocene. However, the subdivision of the Eocene and Palaeocene in Southeast Asia is mainly based on sections in India (Adams, 1970).

The use of planktonic biostratigraphy has improved the correlation between European and Indonesian stratigraphic units, leading, for example to a more detailed stratigraphic scheme proposed by Boudagher-Fadel and Banner (1999) for the Neogene. To date, the application of planktonic biostratigraphy to the Eocene and Lower Oligocene deposits of Indonesia and strontium isotope dating for the Oligocene has been restricted to in-house studies by some oil companies, published here for the first time.

This paper addresses several taxonomic problems regarding nummulitids in Indonesia and discusses their revised stratigraphic ranges following new age data for the various studied sequences, leading to an improved correlation with European deposits.

Morphology of *Nummulites*

Nummulite morphology has been discussed previously by Blondeau (1972), Schaub (1981) and Racey (1995). Their terminology is applied herein and briefly summarised below. Additonal discussion on morphological characters and their relative value in classification can be found in Adams (1988), Haynes (1988), Racey (1992) and Haynes *et al.* (in press). Figure 6.1 shows the most important features of *Nummulites* and related genera. The terminology outlined below is also used for *Planocamerinoides* and *Palaeonummulites* in the present paper.

Septa and chambers

The septum forms a bilamellar, canaliculate, but primarily apertureless curved plate (partition) between successive chambers. A basal foramen, formed by the secondary resorption of wall-material at the base of the apertural face of the penultimate chamber, is almost invariably visible in accurately oriented equatorial sections. Other secondary pores may also be present near the peripheral margin (Adams, 1988). Septa may be regularly and closely spaced as in *N. boninensis* or widely and more irregularly as in some parts of *Nummulites djokdjokartae*. Several chamber and septa shapes are illustrated in Fig. 6.3. Although septa and chamber shape is affected by food availability and temperature, they nevertheless constitute reliable characters for the discrimination of species since abberations from the norm are easily recognised (Racey, 1992).

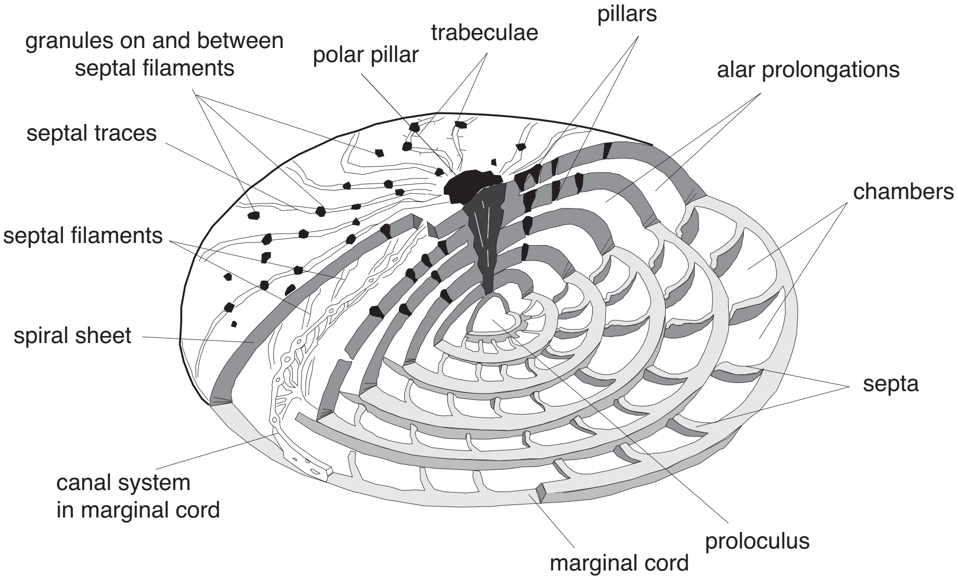


Fig. 6.1. Structure and elements of *Nummulites* test, based on a macrospheric generation (modified from Racey, 1995).

Septal filaments

Extension, sometimes thread-like, of a septum over the lateral surface of the test between the spiral laminae (Adams, 1988). The traces of the septa and septal filaments can often be observed on the test surface. Adams (1988) described the use and taxonomic significance of septal filaments and septal traces and distinguished the following forms:

1. Radial: straight or slightly curved, extending from the pole to the periphery. All septal filaments are necessarily slightly curved at the peripheral margin.
2. Sigmoidal: curved forwards at the periphery and backwards near the pole. If there is no polar twist, the shape is described as falciform.
3. Meandrine: appearing to wander haphazardly over the lateral surface of the spiral sheet.
4. Subreticulate: uniting to form a crude network within the spiral cavity, and showing as septal and filament traces on the outer surface of the spiral wall. Usually associated with pillars.
5. Reticulate: forming a complex network of filaments in which the individuality of the primary filaments is largely or completely lost.

In species with radial and sigmoidal septal filaments and septal traces, these become crowded towards the poles, where they terminate against a central pillar or boss (long septal filaments) or sometimes against a preceding septal filament (short septal filaments). Secondary septal filaments comprise the distal walls of the blister-like chamberlets which form over the lateral surfaces of the test (Adams, 1988). On the outside of a test, secondary filaments are recognised because they run from one (primary) septal filament to another.

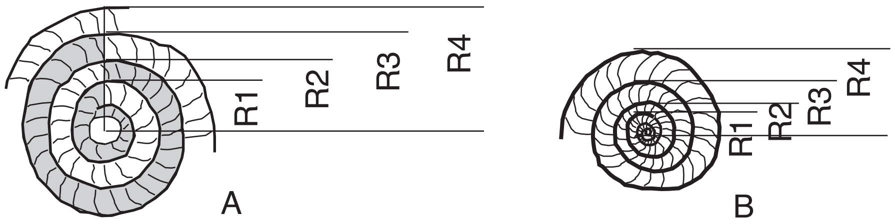


Fig. 6.2. Equatorial section of *Nummulites* showing the method of measurement of the radius per whorl. A: Macrospheric generation (A-form), B: microspheric generation (B-form).

Septal filaments change ontogenetically and may show some variation with environmental parameters (Racey, 1992). Quantitative use (number of septal traces, long/short septal traces, secondary septal traces etc.) is highly variable and thus unreliable for species discrimination, but in adult specimens presence/absence criteria serve well to discriminate between speciesgroups.

Spiral shape

The shape of the spire is important in distinguishing species of *Nummulites*. The spire may be regularly or irregularly coiled, open or tightly coiled and may show tripartition, doubling and/or reversals (Racey, 1995).

In tight whorls, the same radius contains more whorls than in open whorls. Following Schaub (1981) and Racey (1995) the radius of each whorl has been measured (fig. 6.2), and not the number of whorls in a certain radius (e.g., Henrici, 1934) or the radius to a certain number of whorls (e.g., Doornink, 1932) or the number of whorls contained in onethird, twothirds or the full spire (e.g., Blondeau, 1972). The slope and shape of the coiling diagram provides additional information (Racey, 1995). Errors may occur in counting of whorls at the centre (especially in B-forms), since it is difficult to section large, undulating specimens through the proloculus, and/or because the first whorls are often poorly preserved and/or are difficult to see clearly (Racey, 1995).

Regular whorls are even in height and chamber shape, whilst irregular whorls show widely varying chamber heights. The opening rate is the ratio of the diameter of whorl x over whorl x-1 and is expressed as, e.g., 1.5d. In this example the next whorl has a diameter that is 1.5 times larger. Therefore, higher values indicate more rapidly opening spires.

Tripartite spires show a threefold subdivision, each division being characterised by a marked change in tightness, which always follows the sequence tight-loose-tight. No Indonesian species shows this feature. *Nummulites javanus* comes nearest to this character, but the first whorls gradually increase in height, instead of showing a more or less abrupt change as seen in *N. perforatus* or *N. deshayesi* from the western Tethys.

Intercalatory whorls can form through the bifurcation of the spire by splitting of the marginal cord, so that two whorls are created simultaneously (Racey, 1995). This character usually involves thinning of the marginal cord. In Indonesian species this

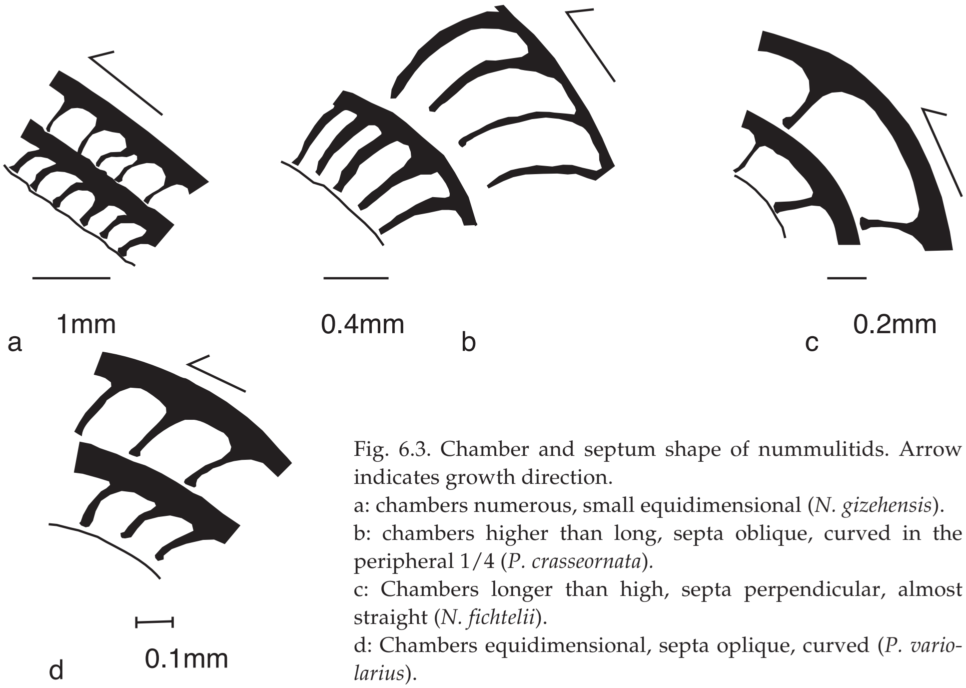


Fig. 6.3. Chamber and septum shape of nummulitids. Arrow indicates growth direction.
a: chambers numerous, small equidimensional (*N. gizehensis*).
b: chambers higher than long, septa oblique, curved in the peripheral 1/4 (*P. crasseornata*).
c: Chambers longer than high, septa perpendicular, almost straight (*N. fichtelii*).
d: Chambers equidimensional, septa oplique, curved (*P. variolarius*).

character is rather rare and is only seen in *Nummulites djokdjokartae* and *N.* nov. spec., in which the intercalatory whorls generally occur after the 7th-9th whorl, and are usually incomplete. *Nummulites boninensis* from Indonesia and Japan sometimes shows one or two intercalatory whorls.

Temporary reversals in the coiling direction (often associated with doubling, i.e., growing two whorls simultaneously) were not observed in any of the Indonesian species.

The spiral shape is summarised in a coiling diagram for the A and B form. In the coiling diagram the range of diameter of the studied specimens is shown for each whorl, as well as the average when more than one specimen was measured.

The character of the spire (especially in the early and middle part of the specimen) is generally constant and is considered to be a feature of diagnostic importance in identifying to which species group a species belongs. Abnormalities in the spire, however, are common and are usually caused by environmental influence (e.g., high hydrodynamic energy resulting in breakage) and are thus of no taxonomic value. Damaged animals usually quickly heal the broken part in order to get back to the normal growth character.

Marginal cord

The marginal cord forms a thickened, imperforate equatorial rim, containing a three-dimensional network of canals that communicate between the chambers. The thickness of the marginal cord (absolute or relative to the chamber height) can be used as a species character (Schaub, 1981). Tightening of the later whorls as seen in, e.g., *N. djokdjokartae* is often caused by the thinning of the marginal cord or its replacement by the spiral sheet. Several of the lineages as defined by Schaub (1981) show similar trends in the thickness of the marginal cord.

Proloculus size in macrosphere

Proloculus size in the macrosphere is often regarded as an important character for species discrimination. However, proloculus size is shown to vary widely within populations (Khan & Drooger, 1970; Drooger *et al.*, 1971; Racey, 1992). Successive populations show an increase in proloculus size with time (Drooger *et al.*, 1971). Racey (1992) concluded that proloculus size was affected by temperature, water depth and food supply, and that variation was marked, resulting in poor reliability for species discrimination, especially when used on its own.

Pillars

The presence and size of pillars (seen as granules or pustules) on the exterior of the test is important, as are their size and arrangement with respect to the septal filaments, filamental traces and the spire as a whole (Racey, 1995). Two main types of pillars occur in *Nummulites*: textural and inflational (Racey, 1995 and references therein). Textural pillars are produced by local changes in the texture of the laminae and are visible in axial thin sections, but usually do not reach the surface of the test. Inflational pillars are produced by local thickening of the laminae by lamellar superposition. Such pillars may reach the surface to form granules/pustules. Possible pillar arrangements are:

1. arranged so that they form a spire on the outer surface.
2. Scattered "randomly" all over the test surface either
   a. on septal filaments (Fig. 6.1), or
   b. on and between septal filaments (Fig. 6.1).
3. Concentrated at the poles to form a large polar pillar (Fig. 6.1).

The intensity of pillar development is strongly affected by environmental parameters in extant populations of *Operculina ammonoides* and correlates with depth and substrate type (Pecheux, 1995; WR, pers. obs.). Pillar location and shape characters (e.g., extending to test surface or not) varies less within populations and may thus constitute valid characters for species discrimination.

Test shape

The test shape was defined as a diameter/thickness (D/T) ratio as follows:

Diameter/thickness	shape
1.5- 2.5	inflated lenticular
2.5- 4.5	lenticular
4.5- 7	flattened lenticular
> 7	flat

Some species show a highly undulose periphery, whilst others have inflated polar regions and/or variations in the shape of the test margin. Test shape is influenced by environmental parameters and is, as such, of limited taxonomic use (Racey, 1992).

Review of previous work

Indonesia

Sumatra — Very few fossiliferous Eocene and Oligocene deposits are known from Sumatra. There are scattered reports of *Nummulites* bearing deposits in North Sumatra (e.g., Verbeek *et al.*, 1881; Tobler, 1923). The only specimens studied herein were collected by Schröder from Nias (Fig. 6.4, no1) and described by Douvillé (1912b, Table 6.1) and are deposited in the National Museum of Natural History in Leiden (The Netherlands, NNM). Most samples comprise very coarse packstones assigned to Ta (Ta_3 of Adams), equivalent to the Lutetian or earliest Bartonian (Fig. 6.5).

Java — The Palaeogene deposits of Java are the best-studied in Indonesia (Fig. 6.4, no 2, 3, 4; Fig. 6.5) and are consequently covered in more detail. Early workers, such as van Dijk (1872), surveying for coal at Nanggulan, recognised the importance of the *Nummulites* they found. Verbeek (1891) and Verbeek & Fennema (1896) located nearly all the now known nummulites-bearing outcrops on Java, of which Nanggulan is the most famous because of its exceptional preservation.

Nanggulan, just west of Yogyakarta and type location of *N. djokdjokartae* (Martin) (Table 6.2) was first dated as Oligocene (Martin, 1881). Martin collected new samples himself in 1910 (Martin, 1915) and concluded a Late Eocene age. Even this age was not easily acquired, and Martin followed with many papers suggesting that the Cainozoic faunas of the Indo-Pacific had developed separately from those of Europe, and therefore the European stratigraphic scheme could not be used in the Far-East. This was the fundamental reason for development of the Indonesian Letter Stages that appeared in 1927 (van der Vlerk & Umbgrove, 1927). Most recent studies have shown the Nanngulan section, and certainly all the locations that have yielded larger foraminifera, are of

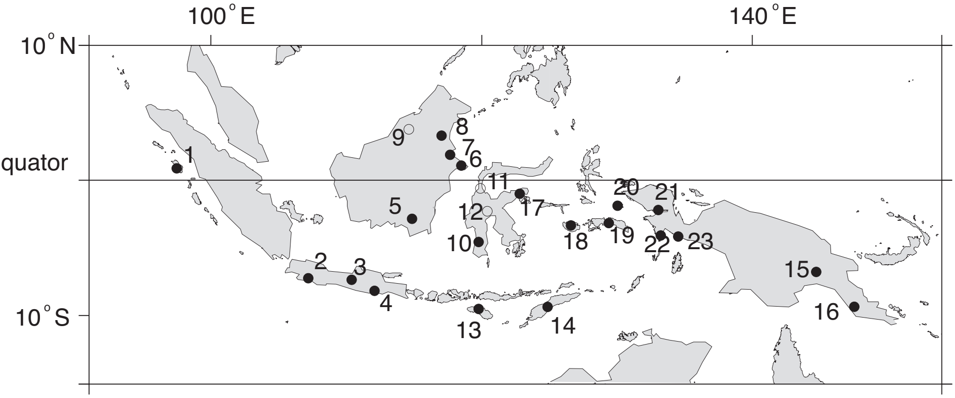


Fig. 6.4. Map showing the localities of studied samples (closed symbol) and known from literature only (open symbol). 1: Nias, 2: Banten/Bantam, 3: Wirosari area, 4: Nanggulan and Jiwo area, 5: SE Borneo, 6: Mangkalihat, 7: Tidoengsche landen, 8: Boeloengan, 9: Melinau Gorge, 10: Tonasa limestone, 11: Donggala, 12: Palossi, 13: Sumba, 14: Timor, 15: Chimbu Lst, 16: New Britain, 17: Poh, 18: Buru, 19: Seram, 20: Misool, 21: Sabang, West Irian 22: Lorentz River, West Irian, 23: Putri Adri, West Irian.

Middle Eocene age, well within zones P 12 – P 14, with the planktonic foraminiferal genera *Morozovella, Acarinina* and *Truncorotaloides* present throughout. More detailed work, including a revision of the nannofossil data of Okada (1981), has shown that the *Nummulites*-bearing sections are from the upper part of NP16 (early part of Okada's CP14), with *Helicosphaera salebrosa* and *Cribrocentrum reticulatum* occuring to the centre of the anticline (Lunt, 2000b). This narrow age range straddles the Lutetian-Bartonian stage boundary (Berggren *et al.*, 1995). A selection of clasts from the Ta *Nummulites* fauna described above have been analysed for $^{87}Sr/^{86}Sr$ ratios. These appear to give consistent results, but it must be stressed that sea-water calibration curves in Middle Eocene times have such a low gradient that the error in calibrating a $^{87}Sr/^{86}Sr$ ratio to GPTS age is very high. An exceptionally well preserved, on apparently pristine, glassy tests of *Nummulites djokjokartae* from a mudstone sample also containing nacrous aragonitic mollusc fragments, from 12 m deep in a core at the centre of the Nanggulan anticline yielded a $^{87}Sr/^{86}Sr$ ratio = 0.707722; 2 sem (%) 0.000017, age 38.8 (37.6-41.5)

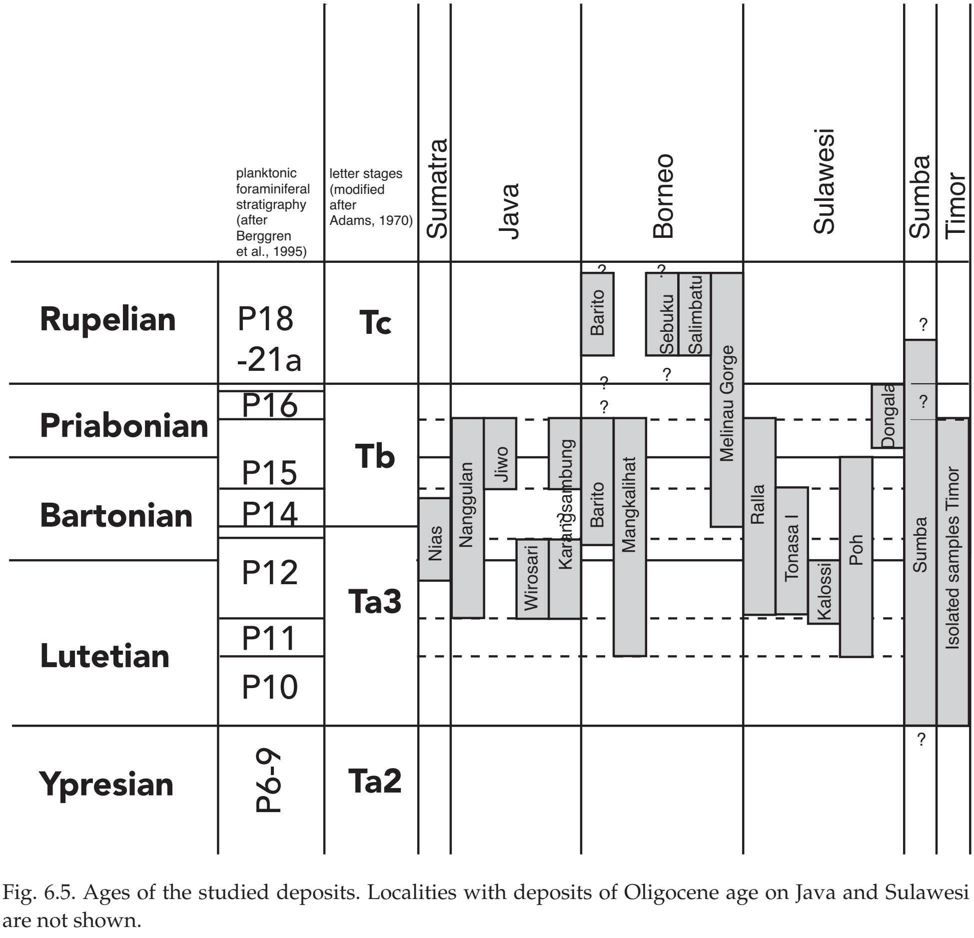


Fig. 6.5. Ages of the studied deposits. Localities with deposits of Oligocene age on Java and Sulawesi are not shown.

Table 6.1. Previously published records of *Nummulites* and *Assilina* from Nias.

Nias	Douvillé, 1912b	reinterpretation
N. bagelensis	x	oblique section of a striate species
N. lamarcki	x	A-form of *Nummulites djokdjokartae*
N. laevigatus	x	B-form of *Nummulites djokdjokartae*
N. pengaronensis	x	*Palaeonummulites pengaronensis*
N. kelatensis	x	*Palaeonummulites beaumonti*
A. orientalis	x	*Planocamerinoides orientalis*
A. granulosa	x	*Planocamerinoides* spec 1

Ma. All Sr isotope ratios used in this paper were done by the same laboratoy using the following parameters:

$^{87}Sr/^{86}Sr$ ratios normalised to $^{86}Sr/^{88}Sr = 0.1194$

$^{87}Sr/^{86}Sr$ ratios normalised to NBS987 $^{87}Sr/^{86}Sr = 0.710235$

Measured NBS987 $^{87}Sr/^{86}Sr = 0.710251 \pm 0.0020\%$ (± 0.000014) (95% confidence limits). The sea water calibration curve of Howard & McArthur (1997) (SIS look-up table version 3, oktober 1999) is used for age calibration to the GPTS of Berggren *et al*. (1995). The given error range is larger than the range resulting from the look-up table since errors in the measurement and the nearest linkage method for calibration of the ages has been taken into account.

Other *Nummulites*-bearing localities in Java include sections with a history as old as Nanggulan, such as the several outcrops around Karangsambung and Lukulo, and areas to the north in the district of Bagelen, type location of *N. bagelensis* and the Jiwo Hills west of Yogyakarta, a primary site for *N. javanus*. In the Bagelen areas, apart from Karangsambung, a very soft scaly clay dominates (but rarely outcrops because of its softness). New samples from Verbeek's Kali Gua are from here and yielded the

Table 6.2. Previously published records of *Nummulites* and *Assilina* from Nanggulan. Records published originally as *Camerina* are shown as *Nummulites*.

Nanggulan						reinterpretation
N. cf *lamarcki*		x				A-form of *Nummulites djokdjokartae*
N. djokdjokartae	x		x		x	
N. djokdjokartae				x		pars *Nummulites djokdjokartae*, pars *Nummulites* nov. spec. (A-form)
N. laevigatus		x		x		pars *Nummulites djokdjokartae*, pars *Nummulites* nov. spec. (B-form)
N. spec indet			x			B-form of *Nummulites djokdjokartae*
N. vredenburgi	x					*Nummulites djokdjokartae*
N. nanggoelani				x		B-form of *Palaeonummulites pengaronensis*
N. pengaronensis	x				x	*Palaeonummulites pengaronensis*
N. pustulosa					x	*Palaeonummulites songoensis*
N. variolarius					x	*Palaeonummulites taballarensis*
N. orbignyi					x	*Palaeonummulites crasseornatus*
N. irregularis					x	*Palaeonummulites crasseornatus*
N. cf *lucasana*					x	no material available, not sufficiently well figured by Doornink
N. semiglobula					x	*Palaeonummulites variolarius*

Table 6.4. Previously published records of *Nummulites* and *Assilina* from Central Java, excluding Nanggulan. Records published originally as *Camerina* are shown as *Nummulites.*

Central Java (excluding Nanggulan)	Verbeek, 1891, Verbeek & Fennema, 1896	Doornink, 1932	reinterpretation
N. javanus	x		pars *Nummulites javanus* pars *Nummulites boninensis*
N. bagelensis	x	x	pars *Nummulites javanus* A form, pars *Palaeonummulites variolarius*
N. perforatus		x	*Nummulites javanus*
N. gizehensis		x	*Nummulites boninensis*
N. laevigatus		x	B-form of *Nummulites* nov. spec.
N. pengaronensis		x	*Palaeonummulites pengaronensis*
N. intermedia		x	B-form of *Nummulites fichteli*
N. pustulosa		x	*Palaeonummulites* nov. spec.
N. densa		x	*Palaeonummulites beaumonti*
N. cf *lucasana*		x	no material available, not sufficiently figured by Doornink
N. semiglobula		x	*Palaeonummulites variolarius*
A. spira	x	x	*Planocamerinoides* spec. 1
A. leymeriei	x	x	*Planocamerinoides* spec. 1

N. boninensis, examined for this paper. These specimens were from very large boulders, although coin-like loose specimens are common in the soil here. While the slightly argillaceous limestone was found to be of NP16 age based on associated nannofossils, with a consistent Sr date from a *Nummulites* clast (see below), the host scaly mudstone is corellated with similar lithologies nearby and also a few kilometres away at Worowari, Kali Bongbong and at Sigugur, where planktonic foraminfera, nannofossils and Sr dating all point to an Early Oligocene age for the scaly clay olistotrome.

In the main Karangsambung section the short publication of Paltrinieri *et al.* (1976) did not extend down to the nummulitic limestone upon which the LIPI geological field camp is built. Below this limestone are conglomerates and silts, but a short way above are open marine mudstones containing diverse planktonic foraminifera including *Chiloguembelina cubensis* (P12 to mid P21), *Morozovella lehneri* (no younger than P14), *Truncorotaloides* and *Acarinina* (no younger than P14), and species of the *Turborotalia cerroazulensis* lineage in the range of the *pomeroli — cerroazulensis* subspecies which characterise P12-13. Nannofossils suggest the older part of this range (P12 overlapping with upper NP15) as based on *Helicosphaera seminulum, Cruciplacolithus dela, Blackites gladius*, and others (nannofossils; A. Baky, by permission of Coparex Banyumas b.v.). There is no sign of scaly clay in the Eocene in Karangsambung. The Jatibungkus limestone at the top of the Karangsambung section is at least a laterally discontinuous olistolith several hundred metres wide and 50-70 m thick, set within later Middle Eocene turbidites. Work has not been concluded on this anomalous bed, of which the age is still unclear.

The survey of Verbeek & Fennema (1896) detailed several localities in the west Java Banten (Bantam) area with both Eocene sedimentary rocks and younger strata characterised by reticulate *Nummulites*. The geologist W.C.B. Koolhoven (1933) collected specimens which were made available to Doornink for inclusion in his 1932 review of Javan nummulitids. Doornink (1932) described seven new species, and argued that *N. javanus* was closely related to both *N. perforatus* and, in part, *N. gizehensis*. Among his new species was *N. densa,* the A-form of *N. subbrongniarti.* He also discussed the taxonomic status of *N. subbrongniarti* and argued that that species was synonymous with *N. intermedius* (now the B-form generation of *N. fichteli*).

From the nummulites-bearing strata in the Watu Perahu locality at Jiwo Hills, distinct *Morozovella* planktonic forams can be recognised in the limestones and subsequent processing of weathered limestone in soil yielded loose specimens from this genus, as well as ?*Acarinina*. The brown mudstones that overlie the Watu Perahu *javanus*-limestone yielded sparse nannofossils including *Helicosphaera compacta* and *H. seminulum*, indicating an upper NP15 through NP16 age, but no planktonic forams have been found in this mudstone. About 600 m south of Watu Perahu is a short dry valley (Pendul section) known for its abundant loose *N. javanus* as well as metre-size boulder of dark gray *javanus*-limestone, often containing large *Planocamerinoides*. Another 400 m south is the Gamping village location famous for loose *Discocyclina* tests to several centimeters released by the thousand into the brown soil, as well as rarer *N. pengaronensis*. This facies is mapped as the Gamping Formation, and is traditionally considered Late Eocene on no specific evidence. The Pendul section contains clasts from centimetre to meter size suspended in the grey mudstone, and the nummulitids to be a major part of those clasts (along with fragments of basement). The *Nummulites*-bearing sediment here is a pebbly mudstone or olistotrome. Low grade metamorphism from the nearby volcanic intrusion hampers age determination but a concerted recent effort appears to have confirmed a general Eocene age (Lunt and Baky, pers. obs.) and therefore contrasts with the olistostrome from the Bagelan area in which "*N. javanus*" limestone and other boulders are in a mud matrix of Early Oligocene age. The Gamping Beds at Jiwo (a few hundred metres south of Watu Perahu), and traditionally considered Late Eocene, have been re-dated as Middle Eocene, NP15-16 (based on the presence of *Acarinina* sp.and the nannofossils *Discoaster* cf. *saipanesis*, *Helicosphaera dineseenii*, *Pemma* sp. in a poor assemblage).

Outcrops of other Eocene localities are less geographically and stratigraphically extensive and less complete. Several isolated occurrences have also been dated using nannofossils and dinoflagellates. The new Kali Gua samples, containing *N. boninensis,* examined for the present paper, was found to be of NP16 age based on associated nannofossils. Note, however, that these northern Lukolo sites (Kali Gua, Worowari, Kali Bongbong and at Sigugur) are characterised by boulders of limestone embedded in a mudstone which is currently under investigation as a possible scaly clay melange of Early Oligocene age, which contains olistoliths of basement and Eocene lithologies.

The survey of Verbeek & Fennema (1896) detailed several localities in the west Java Banten area (Bantam district in the obsolete administrative terminology) with both Eocene sediments, as well as slightly younger strata characterised by reticulate *Nummulites*. The geologist W.C.B. Koolhoven collected specimens which were made available to Doornink for inclusion in his 1932 review of Java nummulitids. Of the Eocene samples some of the best came from a small section in the Cicarucup Beds (Tji Karang location of Doornink). Samples from this location contained common *Pellatispira* as well as Doornink's *Nummulites gerthi* (considered here synonymous with *N. pengaronensis*). The type, and only other, location for *N. gerthi* is the Gamping

Barat or Gunung Gamping location east of Yogya (not to be confused with Gamping village and beds at Jiwo). The Gamping Barat location was lost (quarried away), but has been re-located for this paper. Here *N. pengaronensis* is seen with abundant *Pellatispira* suggesting a younger Eocene age than the other Javanese faunas described above. In the xenoliths brought to surface by the mud volcano at the core of the Sangiran Dome are some head-size boulders of very similar *Pellatispira*-rich limestone with *N. gerthi / N. pengaronensis* as well as frequent planktonic foraminifera including *Porticulosphaera semiinvoluta* (P15 restricted).

Also in Banten, West Java, are some of the better preserved Tertiary C localities, made famous by Tan Sin Hok in his 1932 monograph on *Cycloclypeus*, and containing an appendix on the heterostegines of this area. This, plus nearby sections at Cikalong (Cimandiri) and Gunung Walat contain locally abundant *Nummulites fichteli* and *N. subbrongniarti*. These classic Lower Oligocene sites have almost no plankton, just sparse nannofossils, and have also been dated using Sr isotopic analysis. Overlying mid-Oligocene, Td, samples from this area have been treated similarly, as have other Td sites from eastern Java, records of which have not been published before (Pelang and Kujung locations). These Sr analyses are on picked *Nummulites* tests from mudstone or whole rock, and while slight diagensis is likely (especially the whole rock samples) the data seems highly consistent between samples. All three Tc samples have $^{87}Sr/^{86}Sr$ ratios that fall in a range from 0.707787 34.1 (33.9-34.4) Ma, Cihara, 0.707792 33.9 (33.7-34.2) Ma, Cikalong, to 0.707832 33.2 (32.7-33.7) Ma, Cimanggu. The Td sample from Ciapus is from just above the first appearance of *Eulepidina* (the first appearance of which defines the Tc-Td boundary) and has the lowest $^{87}Sr/^{86}Sr$ ratio from this Letter Stage, 0.707892 corresponding to 32.0 (31.8-32.2) Ma. In eastern Java there are five Td data points, four from the same Kujung area, known from a nearby oil well (Kujung-1) shown to be well above the base Td, and possibly near its upper limit. These, plus the small Pelang outcrop 150 km west, all share $^{87}Sr/^{86}Sr$ ratios between 0.707955 to 0.708084, corresponding to 30.4-27.1 Ma. Of these samples the near basal Td sample from Ciapus has been dated as the lower part of NP24, based on the co-occurrence of *Helicosphaera recta*, *H. bramlettei*, *H. compacta* and *Sphenolithus pseudoradians*. The samples from within (possibly later) Td, in the Kujung area are of a very similar age, zone P21 (lower part) by the presence of *Globigerina angulisuturalis* and *Chiloguembelina cubensis*. Work is still in progress on the Tc-Te transitions, and details are outside the scope of the present paper.

The *Nummulites* material studied herein includes samples collected by van Dijk, Doornink, Martin and Verbeek deposited in the NNM. Samples containing isolated specimens of *N. javanus* from West Java (Bantam, Fig. 6.4, no. 2), were also studied together with new samples collected from the Eocene at Nanggulan, Jiwo Hills and Karangsambung and the Kali Gua area (Fig. 6.4, nos 3, 4). There are a total of 25 samples from various nummulites-bearing Oligocene sites including Cijengkol and Cinagnang in southern Bantam, and the nearby Cikalong (also called Cimandiri) sites in the old Priangker district.

Borneo — Borneo has many deposits of Eocene to Oligocene age. Verbeek (1871, 1874) was the first to describe *Nummulites* from the area around Banjarmasin, describing several new species of Middle Eocene to Early Oligocene age, including *P. pen-*

Table 6.5. Previously published records of *Nummulites* and *Assilina* from Borneo. Records published originally as *Camerina* are shown as *Nummulites*, records originally publishes as *Nummulites (Assilina)* are recorded as *Assilina*.

Borneo	Pengaron district (Verbeek, 1871, 1874)	Tidoengsche Landen (van der Vlerk, 1929)	Boeloengan (vander Vlerk, 1929)	Mangkalihat (van der Vlerk, 1929)	Marah (Yabe, 1921)	Melinau Gorge (Adams, 1965)	reinterpretation
N. javanus						x	*Nummulites javanus*
N. bagelensis		x					*Palaeonummulites variolarius*
N. sp *(striate)*						x	?
N. striatus	x						A-form of *Nummulites beaumonti*
N. biaritzensis	x						B-form of *Nummulites beaumonti*
N. pengaronensis			x		x		*Palaeonummulites pengaronensis*
N. kelatensis				x			*Palaeonummulites beaumonti*
N. nutalli				x			*Palaeonummulites taballarensis*
N. thalicus				x			*Palaeonummulites taballarensis*
N. mamilla		x					*Palaeonummulites variolarius*
N. variolarius				x			*Palaeonummulites variolarius*
N. cf *divina*							A-form of *Nummulites subbrongniarti*
N. subbrongniarti					x		
N. fichteli		x	x				pars A-from of *Nummulites fichteli*, pars A-form of *Nummulites subbrongniarti*
N. fichteli						x	
N. intermedius			x				B-from of *Nummulites fichteli*
A. orientalis					x		*Planocamerinoides orientalis*
A. granulosa					x		*Planocamerinoides* spec. 1

garonensis and *N. subbrongniarti* (Fig. 6.4, no 5; Table 6.5). Subsequent studies on Eocene deposits by van der Vlerk are summarised in his 1929 paper in which he described samples from the area between Sangkuliran and Tarakan (NE Borneo), which contained abundant *Nummulites* comprising nine species (Fig. 6.4, nos 6-8). However, he named the A and B forms of each species separately and two of his species (*N. thalicus* and *N. nuttalli*) are now referred to *Palaeonummulites taballarensis.* The strata studied range in age from early Lutetian to Oligocene. These samples, together with additional material from field surveys, are filed in the NNM.

Adams (1965) described the Ta through Te (basal Bartonian to Chattian), succession in the Melinau Gorge, Sarawak, one of the few places with a continuous Middle Eocene to Oligocene section, though around the Eocene-Oligocene boundary the sediments are poorly fossiliferous (Fig. 6.4, no. 9, Table 6.5).

Sulawesi — Previously, little attention has been paid to the *Nummulites* fauna of Sulawesi. Dollfus (1917) briefly examined the fossil content of carbonates found on

Table 6.6. Previously published records of *Nummulites* and *Assilina* from Sulawesi. Records published originally as *Camerina* are recorded here as *Nummulites*.

Sulawesi	Tonasa (van der Vlerk & Dozy, 1934; Crotty & Engelhardt, 1993; Wilson, 1995)	Donggala (Osimo, 1908)	Central Sulawesi (Rutten in Waterschoot van der Gracht, 1915)	Central Sulawesi (Dollfus, 1917)	reinterpretation
N. javanus	x	1	1	1	pars *Nummulites javanus*, pars *Nummulites boninensis*
N. elegans		0			*Palaeonummulites variolarius*
N. heeri		0			*Palaeonummulites variolarius*
N. guettardi		0			*Palaeonummulites variolarius*
A. umbilicata			x		*Planocamerinoides umbilicata*
N. djokdjokartae				x	
N. laevigata				x	*Nummulites* nov. spec.
N. bagelensis				x	pars *Nummulites javanus*, pars *Nummulites boninensis*
N. kelatensis				x	*Palaeonummulites beaumonti*
N. cf *globula*	x				*Palaeonummulites* spec. 1

Sulawesi. Crotty & Engelhardt (1993) studied the larger foraminifera and palynomorphs in the Tonasa II quarry, whilst Wilson (1995) studied the sedimentology of the Tonasa Formation in south-west Sulawesi. Several of Wilson's localities were visited and sampled in 1997, and some of these samples have been dated using dinoflagellates by H. Brinkhuis (University Utrecht, pers. com.) as approximately late Lutetian to Priabonian. In the Ralla area nummulites-bearing deposits range from at least upper Lutetian to Priabonian in age, with abundant isolated specimens in the P15-P17 interval (stratigraphic data in Wilson, 1995; Fig. 6.4, no. 10).

Osimo (1908) described a Priabonian fauna from Donggala (North Sulawesi, Fig. 6.4, no. 11) though these specimens have not been re-studied. Other specimens studied herein comprise Eocene larger foraminifera from several localities in central and east Sulawesi (Kalossi and Poh) that have not been published, but are deposited in the NNM. Based on the nummulitids found, these strata range from middle Lutetian to Bartonian in age (Fig. 6.4, no. 12). The previously published records of *Nummulites* and *Assilina* from Sulawesi are summarised in Table 6.6.

In the Institut für Paläontologie, Universität Bonn samples collected and published by Wanner (1912) from the eastern branch of Sulawesi were available for study. These contain numerous thin sections and rock samples.

From location 257, Bach Pang 5 thin sections of a small miliolid-algal bioclastic packstone were available for study. These contained numerous *Alveolina timorensis*, a large and a small species of *Alveolina*. Also present were *P. variolarius*, *P.* cf. *pengaronensis*, *N. javanus* A form, and a discocyclinid resembling *Discocyclina timorensis*.

Samples labelled "250 Liangbolo" and "251 Liangbolo nach Tuhan" contained *P. variolarius*, *P. pengaronensis*, *Borelis*, large *Discocylina* and *Spiroclypeus*, a typical Priabonian assemblage. Wanner (1907) gives a different species list (the same large alve-

Table 6.7. Previously published records of *Nummulites* and *Assilina* from Sumba. Records published originally as *Camerina* are recorded here as *Nummulites*.

Sumba	Caudri, 1934	reinterpretation
A. aff *granulosa-exponens*	x	*Planocamerinoides* spec. 1 and/or *Planocamerinoides umbilicata*
A. orientalis	x	*Planocamerinoides orientalis*
N. bagelensis	x	not described, nor figured
N. borneensis	x	*Palaeonummulites taballarensis*
N. discoidea	x	*Planocamerinoides* spec.
N. djokdjokartae	x	
N. fichteli	x	pars A-from of *N. fichteli*, pars A-form of *Nummulites subbrongniarti*
N. aff *irregularis*	x	*Palaeonummulites crasseornatus*
N. javanus var alfa	x	B-form of *Nummulites boninensis*
N. javanus var beta	x	B-form of *Nummulites javanus*
N. kemmerlingi	x	see remarks *Palaeonummulites crasseornatus*
N. kelatensis	x	*Palaeonummulites beaumonti*
N. pengaronensis	x	*Palaeonummulites pengaronensis*
N. aff *taballarensis*	x	*Palaeonummulites taballarensis*
N. cf *variolaria*	x	*Palaeonummulites variolarius*

olinids as recorded in Bach Pang, together with miliolids, unidentified nummulitids and *Lithothamnium*).

Sumba — Caudri (1934) studied the larger foraminifera from Sumba and described faunas of Ta, Tb, Tc, Td and younger, with definitions consistent with modern usage (Ta being undivided except into fossiliferous and unfossiliferous parts, equivalent to Ta3 of Adams 1970). Because *N. taballarensis* and *N. borneensis* were later reassigned to *Ranikothalia*, a genus restricted to the Late Palaeocene and earliest Early Eocene, Ta of Caudri (1934) is sometimes interpreted as Early Eocene, but there is no evidence for assigning this age to these rocks.

There is probably a hiatus at the end of the Eocene with much of the Priabonian missing, which would correlate with new biostratigraphic work on Java, at Nanggulan and Karangsambung. *Nummulites* were found in Middle Eocene to Oligocene deposits (Table 6.7). Some of these samples were deposited in the NNM, and these have been restudied (Fig. 6.4, no. 13).

Moluccas — The Eocene of the Molucas is poorly known. Wanner (1907, 1910, 1922) published on the general geology of the islands of Buru, Misool and Seram. On Buru and Seram, Eocene deposits are rare. In Wanner's collections at the Institut für Paläontologie, Universität Bonn, thin sections comprise a small miliolid packstone with some alveolinids, together with *P.* cf. *variolarius* (thin sections labelled 118, 119). No isolated specimens were available for study to verify this identification. Thin sections (labelled 170, Kamaka Wallar) from another locality contained numerous *P. variolarius*, large *Discocyclina*, *Borelis, Operculina* and *Pellatispira*, a typical Late Eocene assemblage.

Table 6.8. Previously published records of *Nummulites* and *Assilina* from Timor. Records published originally as *Camerina* are recorded here as *Nummulites*.

Timor	Henrici, 1934	reinterpretation
N. perforata	x	*Nummulites javanus*
N. bonleonensis	x	A-form of *Nummulites javanus*
N. bagelensis	x	*Palaeonummulites variolarius*
N. guettardi	x	A-form of *Palaeonummulites* spec. 1
N. variolaria	x	*Palaeonummulites variolarius*
N. cf *globula*	x	*Palaeonummulites* spec. 1
N. pengaronensis	x	*Palaeonummulites pengaronensis*
N. kelatensis	x	*Palaeonummulites beaumonti*
N. crasseornata	x	*Palaeonummulites crasseornatus*

All Eocene samples available for study from Misol and Ceram comprise small miliolid packstones, with alveolinids, rare *N. javanus* A-forms and *N. boninensis* A-forms (sample labelled Wai Sasifu).

Timor — The only work concerning Eocene larger foraminifera of Timor is the thesis of Henrici (1934), who reported nine (after revision five) species of *Nummulites* (Table 6.8). These range in age from lowest Lutetian to Priabonian. His original samples are deposited in the Geologisch Museum (Technische Universiteit Delft) and the Institut für Paläontologie, Universität Bonn, and these have been restudied (Fig. 6.4, no. 14). This led to the recognition of some species previously unrecorded from Timor, among which *N. boninensis* (several localities in the Molengraaff Collection), and *N.* nov. spec.(only from Uwaki, collected by Wanner).

Samples labelled Bonleo, Miomaffo and Harmeno, contained the planktonic foraminifera *Cibrohantkenina* cf. *inflata*, and are of probable P16 age. All three samples have a very similar larger benthic foraminiferal fauna with *P. variolarius, Discocyclina* and *Borelis*. Other species present are *P. pengaronensis* in samples from Miomaffo and Harmeno and *Orthocyclina soeroeanensis* and *Pellatispira* only from Miomaffo, a typical Tb, Priabonian assemblage. A sample (labelled Uwaki) contained the planktonic foraminifera *Morozovella lehneri* and *Acarinina* sp.of P12-P14 age, together with *N. javanus* and *Alveolina timorensis*.

West Papua — Several samples from the Birds Head, Lorentz River and Bibis River collected by Wanner are present in the collection from the Institut für Paläontologie, Universität Bonn. Most of these samples are of Middle Eocene age. A sample labelled 142 from 'Arguni Bai, Abfall Gusi Gebirges' (Fig. 6.4, no. 21) contains *Lacazinella* and *P. variolarius*, another sample (labelled 24) from the same area contains *N. javanus* (A-form) and *N. boninensis* (A-form, identified as *N. bagelensis* by Wanner).

In samples from Pulau Adi (Fig. 6.4, no. 22) *P. pengaronensis* together with *N. javanus* were observed, whilst samples from Etna Bai (Fig. 6.4, no. 23) contained several specimens of *N. djokdjokartae* (A and B forms, identified as *N.* cf. *laevigatus* by Wanner). The single recognisable species from another sample is *P. variolarius*.

Around Indonesia

Philippines — Very little is known about the occurrence and distribution of larger foraminifera, especially *Nummulites* in the Philippines. Douvillé (1911) reported on larger foraminifera, but did not describe any Palaeogene deposits. During 1978-1985 several papers by a group of Japanese scientists (Hashimoto & Matsumaru, 1978, 1981b,c, 1984; Hashimoto *et al.*, 1978a-c, 1979) describing the larger foraminifera from the Philippines appeared, which in part dealt with Eocene and Oligocene deposits. Their specimens were not available for restudy. Moreover, their figured specimens often comprise oblique sections or fragments of specimens, which do not allow positive identification. Cosico *et al.*. (1989) described larger foraminifera from the Visayas Islands, central Philippines and summarised the history of larger foraminiferal research in the Philippines. The oldest unit they described was the Late Eocene *Pellatispira* zone, which did not contain any *Nummulites*. The only species of *Nummulites* they recorded is *N. fichteli* from the overlying Early Oligocene biozone.

Papua New Guinea — Binnekamp (1973) and Bain & Binnekamp (1973) comprise the main studies dealing with the Cainozoic (mainly Palaeogene) larger foraminifera from Papua New Guinea. Several other studies have been undertaken mainly dealing with Upper Oligocene to Miocene deposits. Binnekamp (1973) found *Palaeonummulites pengaronensis* co-occurring with *Pellatispira,* indicating a probable Priabonian or late Bartonian age. In Bain & Binnekamp's (1973) study a larger stratigraphical interval was covered, and they found *Nummulites javanus* and *N. fichteli* together with the only published record of *N. vascus* known from the Indo-West Pacific. Their *N. vascus* specimens resemble *P. pengaronensis*, but lack an axial plug. However, the presence of an axial plug is highly variable in *P. pengaronensis* which led Doornink (1932) to separate *N. semiglobulus* from *P. pengaronensis* based on the presence of an axial plug in the latter. Doornink's specimens of *P. semiglobulus* show the beginning of the development of an axial plug as do the specimens of *P. vascus* figured by Bain & Binnekamp. Their specimens were not available for study.

West Pacific — Numerous studies have been undertaken on atolls in the West Pacific, but Palaeocene-Eocene sedimentary rocks are generally lacking. Cole & Bridges (1953) and Cole (1954, 1956, 1957, 1963) described the larger foraminifera from various boreholes in Saipan, Eniwetok and Bikini. Cole described *N. saipanensis* in Cole & Bridges (1953), and recorded *N. djokdjokartae* on Saipan (Cole, 1954). On Bikini, Cole (1954) recorded *P. pengaronensis,* and in his synonymy of this species, he included *N. saipanensis*. Hanzawa (1957) described the foraminifera from Micronesia including Saipan, recording *P. pengaronensis*, *N. bagelensis* (= *N. javanus)* and *P. striatus*. In his opinion the latter is a senior synonym of *N. saipanensis*. Deprat (1905) described the larger foraminifera from New Caledonia, comprising *N. djokdjokartae, N. nangoulani* (= *P. pengaronensis*), *N. bagelensis* (= *N. javanus)* and *Palaeonummulites variolarius* (recorded as *N. variolarius)*.

Japan — Studies on Japanese *Nummulites* are mainly from the Bonin Islands. Hanzawa (1947) described *N. boninensis* whilst Matsumaru (1984, 1994, 1996) restudied these specimens as well as additional material. Matsumaru (1996) subdivided *N. boninensis* into five species. Matsumaru (1996) described the complete Eocene larger foraminifera fauna from the Bonin Islands dividing the fauna into three assemblages, two of which contain *Nummulites*. The nummulites-bearing part of the Eocene on the Bonin islands can be assigned a P12-P14 age, based on the occurrence of planktonic foraminifera (*Morozovella* sp., *Acarinina* sp. and *Turborotalia cerroazulensis*, *Morozovella* sp. and hantkenids; Matsumaru, 1996), and is thus contemporaneous with the Nanggulan section on Java.

The oldest assemblage comprises *N. boninensis*, *N. javanus* and *P. pengaronensis,* and is assigned a late Ta_3 (late Lutetian) age. The middle assemblage comprises mainly *P. pengaronensis* and *N. javanus,* and is assigned a Bartonian age. The uppermost assemblage contained no *in situ Nummulites* and was assumed to be late Bartonian or earliest Priabonian in age on the basis of the presence of planktonic foraminifera.

Systematic palaeontology

Order Foraminiferida
Suborder Rotaliina Delage & Hérouard
Superfamily Nummulitoidea de Blainville
Family Nummulitidae de Blainville
Subfamily Nummulitinae de Blainville

Diagnosis — Test planispiral, involute or evolute with numerous median chambers which may be simple or divided into chamberlets, with or without lateral chamberlets; complex canal system of septal, marginal and axial canals; aperture an arched slit over the apertural face (after Loeblich & Tappan, 1987).

Discussion — The family Nummulitidae occurs from the Palaeocene to Recent (Loeblich & Tappan, 1987) in dominantly tropical marine environments. The family contains 16 genera, 11 of which have been found in the Indo-Pacific. Of these, only those with simple undivided chambers are relevant to the present study.

The generic descriptions in the following sections are based on Haynes (1988) and Haynes *et al.* (in press).

Genus *Nummulites* Lamarck

Type species — *Camerina laevigata* Bruguière, 1792.

Diagnosis — Test discoidal to globular, commonly large, up to 12 cm in diameter in B-form. Dimorphism pronounced in larger species. Planispirally, rather tightly coiled, involute. Primary septa straight, curved or undulate. Secondary septa present. Chambers undivided with a distinct, fine to moderately thick marginal cord. Pillars often present and may appear as pustules on the outer test surface.

Range — Palaeocene to mid Oligocene in the Tethys.

Discussion — Most records of *Nummulites* from the Caribbean, North and South Americas should be reassigned to *Palaeonummulites* (see Blondeau, 1972; Haynes, 1988). Large species showing marked dimorphism are especially common in the Middle Eocene. The group comprises numerous lineages in the Eocene, with only a few species extending into the Oligocene.

Nummulites boninensis Hanzawa, 1947
Fig. 6.6; Pl. 9, figs. A-C.

* 1891 *Nummulites javanus* var α Verbeek — p. 105.
1896 *Nummulites javanus* var α Verbeek, 1891 — Verbeek & Fennema, p. 1096.
1915 *Camerina gizehensis* (Forskål, 1775) — Rutten *in* Waterschoot van den Gracht, p 54.
1926a *Camerina gizehensis* (Forskål, 1775) — Nuttall, p. 139.
1931 *Camerina gizehensis* (Forskål, 1775) — Umbgrove, p.50.
1932 *Camerina gizehensis* (Forskål,1775) — Doornink, p. 272.
* 1947 *Nummulites boninensis* Hanzawa, p. 254, pls 39-40.
1970 *Nummulites gizehensis* (Forskål, 1775) — Adams, p. 122.
1995 *Nummulites boninensis* Hanzawa — Racey, p. 36.

Material — Over 25 specimens from Kali Gua (central Java) including 5 axial sections and 5 equatorial sections of A forms and 2 axial and 5 equatorial sections of B-forms (RGM 202020). Over 25 specimens from Sungai Ular (Southwest Sulawesi),

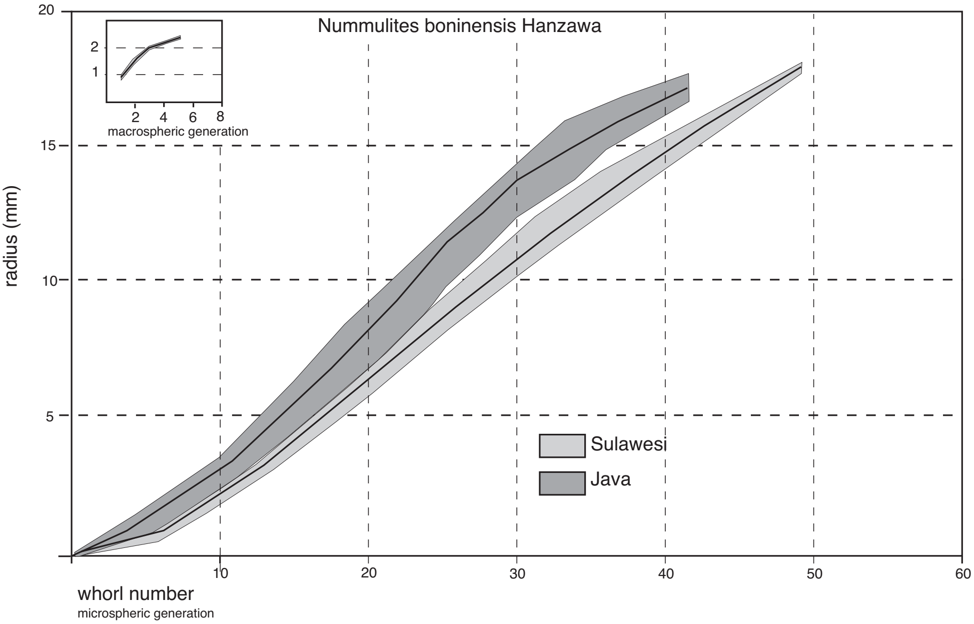


Fig. 6.6. Coiling diagram of *Nummulites boninensis* Hanzawa.

including 5 equatorial and 1 axial sections of B-forms, and 4 equatorial sections of A-forms (RGM 202016-202017).

Five specimens from Timor, including one axial section of an A-form, and 4 equatorial sections of B-forms (Geologisch Instituut, TU Delft).

A-form — Test lenticular with a sharp margin, diameter up to 7 mm, thickness up to 2.5 mm. D/T = 3. Septal filaments radiating, and strongly curved with granules over entire test surface on and between septal filaments, becoming denser and larger towards the poles. Spire comprises five whorls, the first two rather high, the latter more tightly coiled (Fig. 6.6). Chambers initially 1.5-2 × higher than broad becoming isometric in the later whorls. Marginal cord 1/4 of chamber height. In axial section, pillars are concentrated in the polar region occasionally reaching the test surface. Proloculus large, 0.55-1.0 mm in diameter.

Whorl number	**1**	**2**	**3**	**4**	**5**
Radius (mm)	0.8	1.4	1.9	2.2	2.5
Chambers	7	12	21	23	–

B-form — Test discoidal, with an undulose, sharp periphery, diameter 26 to 45 mm, thickness up to 6 mm. D/ T = 6.5 (5.8-9.1). Numerous granules occur on and between the meandriform septal filaments over the entire test surface, but are more common in the polar region. In equatorial section the spire opens regularly, tightening in the last few whorls (Fig. 6.6) and consisting of up to 40 whorls. Chambers higher than broad in the initial whorls, 1.5-2 × broader than high in the final whorls. Septa oblique, straight. Marginal cord thick, half the chamber height in the outer whorls. In axial section, there are numerous pillars, some reaching the surface of the test.

In axial section with many very fine pillars, especcially in the polar region, of which most do not reach the outer surface. Spiral laminae thick in the peripheral region, but very thin in the polar region.

Whorl number	1	2	3	4	5	6	7	8	9	10	11	12	13
Radius (mm)-Java	0.16	0.36	0.58	0.80	1.1	1.4	1.8	2.29	2.62	3.1	3.5	4.0	4.5
Radius (mm)-Sulawesi	0.17	0.31	0.48	0.63	0.92	1.28	1.55	1.86	2.23	2.69	3.05	3.44	3.94

	14	15	16	17	18	19	20	21	22	23	24	25	26
Radius (mm)-Java	5.0	5.7	6.4	7.0	7.6	8.0	8.6	9.2	9.9	10.5	11.0	11.7	12.2
Radius (mm)-Sulawesi	4.48	4.75	5.16	5.58	6.12	6.46	6.88	7.48	8.00	8.53	8.98	9.37	10.0

	27	28	29	30	31	32	33	34	35	36	37	38	39
Radius (mm)-Java	12.9	13.5	14.0	14.4	14.9	15.5	16.1	16.6	16.9	17.2	17.5	–	–
Radius (mm)-Sulawesi	10.5	11.0	11.4	11.7	12.2	12.7	13.0	13.5	13.9	14.3	15	15.6	15.9

	40	41	42	43	44	45
Radius (mm)-Java	–	–	–	–	–	–
Radius (mm)-Sulawesi	16.0	16.1	16.2	16.3	16.4	16.4

Remarks — Some of the specimens used in the type-description of *Nummulites javanus* Verbeek are actually referable to *N. boninensis.* For example, though *N. javanus* var a and b of Verbeek (1891) are slightly smaller than the specimens found at Kali Gua and on Sulawesi, they have the same internal structure and surface ornaments and should be included in *N. boninensis*. *Nummulites bagelensis* Verbeek was also described as comprising several variations and *N. bagelensis* I Verbeek is very similar to the A-form of *N. boninensis*.

The type description of *N. boninensis* refers to a species in which the B-form differs from *N. gizehensis* (Forskål) by its sharper periphery, more regular coiling without intercalatory whorls, thicker marginal cord (equalling chamber height, versus half of chamber height in *N. gizehensis*). In axial section, the pillars are more pronounced than in *N. gizehensis*. The specimens from Sulawesi exactly match this description although the maximum size of the specimens is less (diameter up to 40 mm vs 60 mm in Ogasawara Island).

Matsumaru (1984, 1996) restudied *N. boninensis* and concluded that specimens described under this name from Ogasawara Island, Japan would be better attributed to three different taxa, *N. aturicus* Joly & Leymerie, *N. aturicus-perforatus,* and *N. perforatus* (Montfort) in 1984. In 1996, Matsumaru recognised four larger *Nummulites* species: *N. aturicus*, *N. gizehensis* (Forskål), *N. millecaput* (Boubée) and *N. perforatus* (Montfort).

The species mentioned by Matsumaru as *'N. gizehensis'* , does not fit the description given by Schaub (1981, 1995) and Racey (1995) in that it lacks intercalatory whorls (1-11 in the specimens of Schaub (1981, 1995) and Racey (1995)), have a thicker marginal cord and a thicker test. These characteristics are sufficient to distinguish *N. boninensis* from *N. gizehensis.*

Geographic distribution — Indonesia: Ralla (SW Sulawesi), Kali Gua (central Java) and several localities in Timor. Elsewhere: Hillsborough Island (Japan) and Oman (Racey, 1995).

Stratigraphic range — Bartonian in Sulawesi (nannoplankton (NP17) and dinoflagellate age (H. Brinkhuis, pers. com.). Bartonian (P13-P14) in Hillsborough Island (Hanzawa, 1947; Matsumaru, 1996) and together with *N. perforatus* and *N. lyelli* in Oman, suggesting an early Bartonian age (SBZ17, Serra-Kiel *et al.*, 1998).

The stratigraphic range in Indonesia is interpreted to be Middle Eocene, Ta3 or Bartonian.

Nummulites djokdjokartae (Martin, 1881)
Fig. 6.7; Pl. 6, figs. A-B, G-J; Pl. 7, figs. D-E.

* 1881 *Nummulina djokdjokartae* Martin, p. 109.
1891 *Nummulites jogjakartae* [sic] Martin, 1881 — Verbeek p. 116.
1896 *Nummulites jogjakartae*[sic] Martin, 1881 — Verbeek & Fennema, p. 1106.
1896 *Nummulites javanus* var β Verbeek & Fennema, p. 1098.
1899 *Nummulites djokjokartae* [sic] Martin, 1881 — Newton & Holland, p. 255.
1905 *Nummulites jogjakartae* [sic] Martin 1881 — Deprat, p. 495.
* 1906 *Nummulites douvillei* Vredenburg, p. 79 .
* 1908 *Nummulites vredenburgi* Prever *in* Vredenburg, p. 239 (new name for *N. douvillei*).

1908 *Nummulites djokjokartae* [sic] Martin, 1881 — Osimo, p. 33.
1912a *Nummulites vredenburgi* Prever, 1908 — Douvillé, p. 280.
1912a *Nummulites djokdjokartae* Martin, 1881 — Douvillé, p. 283.
1915 *Nummulites djokdjokartae* Martin, 1881 — Martin, p. 194.
1917 *Nummulites djokjakarta* [sic] Martin, 1881 — Dollfus, p. 973.
1917 *Nummulites laevigatus* Lamarck var *vredenburgi* Prever — Dollfus, p. 972.
1926a *Nummulites acutus* (Sowerby, 1840) — Nuttall, p. 133.
1929 *Nummulites vredenburgi* Prever, 1908 — Gerth, p. 598.
1932 *Camerina djokdjokartae* Martin, 1881 — Doornink, p. 281-282.
1957 *Camerina djokdjokartae* (Martin, 1881) — Cole, p. 329.
1959 *Nummulites acutus* (Sowerby, 1840) — Nagappa, p. 145-192.

Material — Numerous individuals, comprising 18 equatorial sections of A-forms, and 15 of B-forms plus five axial sections of A forms and 5 axial sections of B-forms from Nanngulan (Java). RGM 47196, 3320, 3334). Two equatorial sections of B-forms from Poh (Sulawesi, Geologische Institut, Universität Bonn) and five equatorial sections of A-forms and 5 of B-forms from Banten (Java, RGM 202021).

A- form — Lenticular with rounded periphery. Diameter up to 5 mm, thickness up to 2.2 mm. D/T = 1.6-2.4. Trace of septal filaments radiating, S-shaped, occasionally branching with coarse granules on and between the septal filaments, granules concentrated on, but not limited to the central part of the test.

In equatorial section, spire regular consisting of 4 1/2 to 6 whorls (Fig. 6.7) with the first whorl wider than subsequent whorls. Marginal cord thick, 1/4 – 1/3 of chamber height. Chambers rectangular, initially almost isometric, becoming 1 1/2 × as broad as high. Septa perpendicular to marginal cord, curving backwards.

In axial section, pillars occur over entire test surface from centre to periphery, and often reach the test surface to form granules. Proloculus 0.6-0.9 mm in diameter.

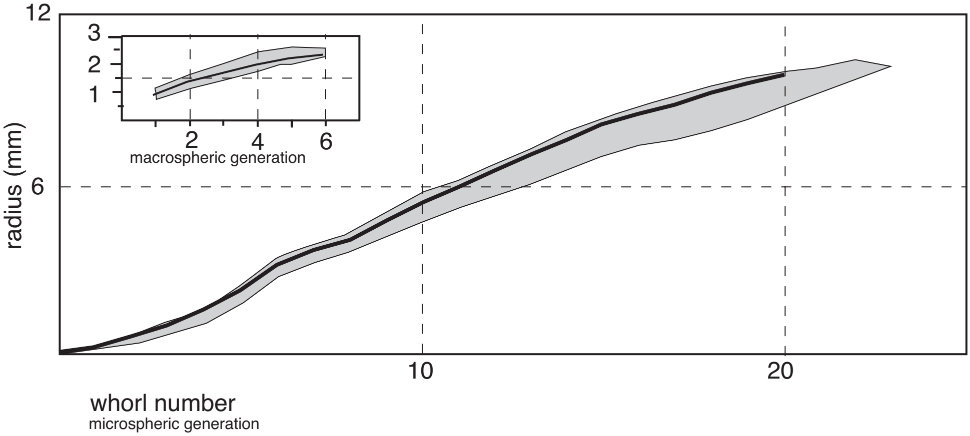


Fig. 6.7. Coiling diagram of *Nummulites djokdjokartae* Martin.

Whorl number	1	2	3	4	5	6
Radius (mm)	0.97	1.36	1.70	2.06	2.19	3.32
Chambers	8	17	23	26	22	–

B-form — Test flat lenticular, with sharp to rounded periphery. Test diameter up to 25 mm, thickness up to 6 mm with D/ T = 3.5-4.5. Septal filaments meandriform, with large granules on and between them. In equatorial section, spire regularly increasing in width, up to the 6-8th whorl (Fig. 6.7), after which the spire becomes irregular, with partial intercalatory whorls developed. Marginal cord thick in the first 6-8 whorls (about 1/4 of chamber height), equally thick (0.15-0.2 mm) and thinner (or absent) in remaining whorls. Chambers 2-6 × as high as long in first 4 whorls (on average 3, s.d = 1.4), 1.5 to 3 × higher than long in whorl 5-6 (8), about 1.5-2 × longer than high in the later whorls. Septa straight, sharply curved backwards at the peripheral margin, perpendicular to marginal cord in first whorls and curved in later (>8) whorls, irregularly spaced.

In axial section, chamber height increases in height towards margin. Spiral laminae thickest near marginal cord, then much thinner, lateral splitting of the spiral laminae is common, sometimes into 3 thin laminae, but usually only into 2. Splitting occurs near the marginal cord. Alar prolongations very narrow. Pillars of varying size and shape, distributed from pole to periphery. Most pillars do not protrude up to the surface, i.e. they are buried.

Whorl number	1	2	3	4	5	6	7	8	9
Radius (mm)	0.16	0.54	0.91	1.5	2.18	3.08	3.60	3.96	4.65
Chambers	8	14	24	30	32	36	40	44	–

Whorl number	10	11	12	13	14	15	16	17	18
Radius (mm)	5.30	5.82	6.41	6.98	7.49	8.04	8.41	8.73	9.16
Chambers									

Whorl number	19	20	21	22
Radius (mm)	9.49	10.0	10.4	11.1
Chambers				

From the 9th whorl onwards the chamber number was unclear, due to irregularities in the spire.

Remarks — This is a species that has been subject to a lot of confusion in the literature. The A-form was described as *N. djokdjokartae* by Martin in 1881, and in the same year Verbeek reported *N.* cf. *laevigatus* (B-form) and *N.* cf. *lamarcki* (A-form) from the same area (Verbeek, 1891). In 1896 Verbeek & Fennema recorded only *N. laevigata* (B-form) and *N. djokdjokartae* (A-form).

In 1840 *N. acutus* (Sowerby) was described from Lakhpat (Cutch) in India. In the same area Vredenburg (1906) found another species that he described as *N. douvillei*. Prever pointed out to him that this name was pre-occupied and proposed the name "*N. vredenburgi* Vredenburg" (Vredenburg, 1908; Samanta, 1982). Since Prever published this, the name formally is *N. vredenburgi* Prever. Many later authors synonymised *N. acutus, N. vredenburgi* and *N. djokdjokartae*. Although *N. acutus* is the oldest available name, the (youngest) name *N. vredenburgi* is used for this taxon as well.

The intial whorls of *N. vredenburgi* are quite tight, but the 4th to 7th whorl are wider and the chambers are 2-3 times higher than wide, and the marginal cord thins after the 10th-12th whorl (said in description, not visible in figured specimens). In axial section, the spiral laminae split frequently into two-three thin laminae, a character also seen in the Indonesian specimens (Samanta, 1982). The measurements provided by Samanta (1982) for *N. vredenburgi* all fall within the range of the Indonesian specimens, although his A-forms are generally slightly flatter.

We agree with Samanta (1982) that the type specimen of *N. acutus* is morphologically distinct from *N. vredenburgi* and *N. djokdjokartae*. Samanta did not discuss the similarities and differences between *N. vredenburgi* and *N. djokdjokartae*, though as discussed above, they are very similar in nearly all characters and we consider them to be synonymous, with the name *N. djokdjokartae* having priority over *N. vredenburgi*.

The B-forms figured by Nagappa (1959) as *N. acutus* have all the characters in common with *N. djokdjokartae*, and, therefore, should be re-assigned to *N. djokdjokartae*. Some small specimens of *N. djokdjokartae* (B-forms, diameter 9-11 mm) in the NNM collection (RGM 3334), identified by Douvillé as *N. vredenburgi*, turned out to have exactly the same coiling pattern as *N. djokdjokartae* for the first six whorls, but do not have intercalatory whorls or the very thin marginal cord in the latter whorls. These specimens are otherwise similar to *N. djokdjokartae* and probably are juveniles of *N. djokdjokartae*.

Geographic distribution — Indonesia: Central Java, West Java, Sulawesi, Sumba, Nias and West Papua. Elsewhere: West India (Vredenburg, 1906, 1908; Nagappa, 1959), New Caledonia (Deprat, 1905) and Saipan (Cole, 1956).

Stratigraphic range — Known from upper Middle Eocene sediments (later P12 / NP16, latest Lutetian / earliest Bartonian) in Nanggulan. The Harudi Formation from which *N. vredenburgi* was described is assigned an P12 age (Samanta, 1982). The stratigraphic range in Indonesia is interpreted as late Lutetian to early Bartonian (P12).

Nummulites fichteli Michelotti, 1841
Fig. 6.8; Pl. 12, figs. D-E.

* 1841 *Nummulites fichteli* Michelotti, p. 44.
1905 *Nummulites subbrongniarti* Verbeek, 1871 — Douvillé, p. 439.
1909 *Nummulites fichteli* Michelotti, 1841 — Provale, p. 92.
1909 *Nummulites intermedia* d'Archiac, 1846 — Provale, p. 93.
1929 *Nummulites intermedius* d'Archiac, 1846 — van der Vlerk, p. 18.
1929 *Nummulites fichteli* Michelotti, 1841 — Gerth, p. 598.
1929 *Nummulites intermedius* d'Archiac — Gerth, p. 598.
1931 *Camerina fichteli* (Michelotti, 1841) — Umbgrove, p. 49.
1931 *Camerina intermedius* d'Archiac, 1846 — Umbgrove, p. 50.
1932 *Camerina intermedia* (d'Archiac) — Doornink, p. 285.
1934 *Camerina fichteli* (Michelotti, 1841) — Caudri, p. 72.
1970 *Nummulites fichteli* Michelotti, 1841– Adams, p. 122.
1973 *Nummulites fichteli* Michelotti, 1841– Bain & Binnekamp, p. 8.
1981c *Nummulites fichteli* Michelotti, 1841 [pars] — Hashimoto & Matsumaru, p. 75.

1993 *Nummulites fichteli* Michelotti, 1841– Crotty & Engelhardt, p. 77.
1995 *Nummulites fichteli* Michelotti, 1841– Racey, p. 44.

Material — Over 30 specimens from Sungai Mesalai and Sungai Taballar (Kalimantan), including 2 axial and 5 equatorial sections of A-forms, and 2 axial and 5 equatorial sections of B-forms (RGM 19061-19070, RGM 19115-19120).

A-form — Test flat lenticular, diameter 2.5-5.5 mm, thickness 1-1.5 mm and D/T = 2.0-3.5. Septal filaments strongly reticulate. In equatorial section spire regular, fairly uniform and tightly coiled (Fig. 6.8). Chambers initially isometric, in the last few whorls 3 × as broad as high. Septa straight, inclined to the marginal cord. Marginal cord 1/5 of the chamber height in the first whorls, 1/3 in the last whorls. In axial section pillars from the median layer do not reach the surface of the test. Proloculus 0. 25-0.30 mm in diameter.

Whorl number	1	2	3	4	5	6	7	8
Radius (mm)	0.45	0.72	1.1	1.4	1.7	2.0	2.3	2.7
Chambers	7	12	15	18	22	22	24	–

B-form — Test flat lenticular, diameter 8-14 mm, D/T = 3.5-4.5. Septal filaments reticulate with occasional very fine granules on and between the septal filaments, especially towards the polar region. In equatorial section spire is uniform and fairly tightly coiled (Fig. 6.8). Marginal cord 1/2-1/3 of the chamber height. Chambers increasing in length from the inner towards the outer whorls, becoming up to 3 × longer than high in outer whorls. Septa slightly inclined in the inner whorls, more inclined in the outer whorls.

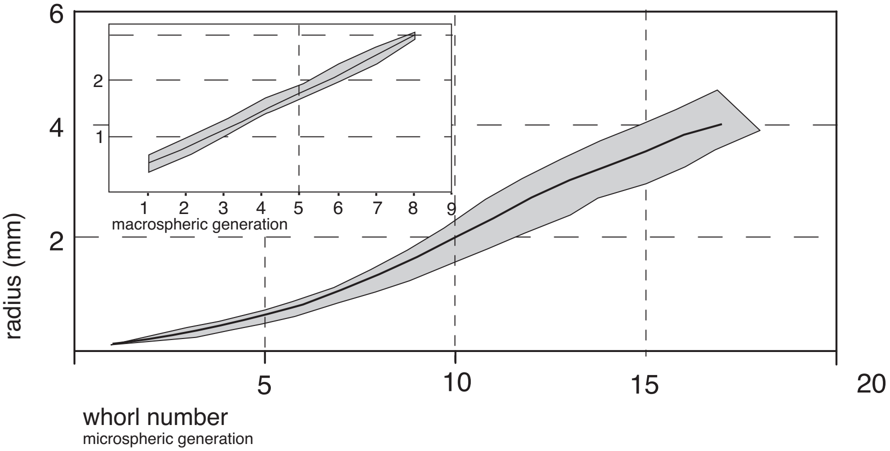


Fig. 6.8. Coiling diagram of *Nummulites fichteli* Michelotti.

Whorl number	1	2	3	4	5	6	7	8	9	10	11
Radius (mm)	0.13	0.22	0.34	0.48	0.65	0.83	1.09	1.37	1.68	2.03	2.37
Chambers	–	16	18	22	24	24	23	24	26	28	28

Whorl number	12	13	14	15	16	17
Radius (mm)	2.74	3.30	3.56	3.33	3.86	4.05
Chambers	30	–	–	–	–	–

Remarks — The Indonesian A-forms of this species are somewhat more tightly coiled than the European and Omani specimens figured by Schaub (1981) and Racey (1995), respectively. The B-forms match the European specimens, although the Indonesian specimens fall in the lower range of the variation shown in the coiling diagrams of Schaub (1981) and Racey (1995), i.e. they show less variation and are more tightly coiled than the western Tethyan specimens.

In addition to *N. fichteli* and *N. subbrongniarti*, Doornink (1932) recognized a third species of reticulate *Nummulites*, *N. absurda* Doornink (p. 299-300) from Java, distinguished from the other reticulate species by its larger and more irregular shaped of the proloculus and the form of spire. So far this species is only known from one locality where it is found with 'typical' *N. fichteli* so that it can not be excluded that this is an ecophenotypic variant of *N. fichteli*. The predecessor of this species in Europe, *N. fabianii* Prever, 1905 has not been found in Indonesia, though it is widespread and often abundant in the Priabonian of Europe and the Middle East (Schaub, 1981; Racey, 1995 and references therein).

Geographic distribution — Indonesia: Java, Sumatra, Borneo, Sulawesi, Sumba and Irian Jaya. Elsewhere: Widely distributed throughout the Tethys. For records on distribution see Blondeau (1972), Schaub (1981) and Racey (1995). There are additional eastern Asiatic records from Mindanao (Hashimoto & Matsumaru, 1984), Mindoro and Luzon (Philippines; Cosico *et al.*, 1989) and Papua New Guinea (Bain & Binnekamp, 1973).

Stratigraphic range — Characteristic species of Tc and Td (Early Oligocene) in the East Indian Letter Classification (Adams, 1970). The last appearance of this species is in zone P21a in the Kujung area of NE Java (dated as 29.4 Ma using strontium isotopes). A single younger Sr date of 28.4 Ma has been obtained from the Pelang limestone of central Java, but at this locality there are no independent planktonic foraminiferal data. The interpreted stratigraphic range is Letter Stage Tc to Td, Rupelian.

Nummulites javanus Verbeek, 1891
Fig. 6.9; Pl. 8, figs. A-F.

1891 *Nummulites javanus* var γ,δ Verbeek, p. 105-106.
* 1891 *Nummulites bagelensis* Verbeek, p. 107.
1896 *Nummulites javanus* Verbeek, 1891 — Verbeek & Fennema, p. 1096.
1896 *Nummulites bagelensis* Verbeek, 1891 — Verbeek & Fennema, p. 1101.
1905 *Nummulites bagelensis* Verbeek, 1891 — Deprat, p. 493.
1912a *Nummulites bagelensis* Verbeek, 1891 — Douvillé, p. 262.

1929 *Nummulites bagelensis* Verbeek, 1891 — van der Vlerk, p. 18.
1929 *Nummulites javanus* Verbeek, 1891 — Gerth, p. 598.
1929 *Nummulites bagelensis* Verbeek, 1891 — Gerth, p. 598.
1931 *Camerina javana* Verbeek, 1891 [sic] — Umbgrove, p. 50.
1931 *Camerina bagelensis* (Verbeek) — Umbgrove, p. 49.
1932 *Camerina perforata* Denys de Montfort, 1808 — Doornink, p. 273.
1932 *Camerina bagelensis* Verbeek, 1891 — Doornink, p. 277.
1934 *Camerina javana* (Verbeek, 1891) — Caudri, p. 64.
1934 *Camerina bagelensis* Verbeek, 1891 — Henrici, p. 25.
1934 *Camerina perforata* Denys de Montfort, 1808 — Henrici, p. 21.
1948 *Camerina perforata* Denys de Montfort, 1808 — van Andel, p. 1013.
1979 *Nummulites perforatus* (Denys de Montfort, 1808) — Hashimoto *et al.*, p. 155.
1981b *Nummulites perforatus* (Denys de Montfort, 1808) — Hashimoto & Matsumaru, p. 67.
1993 *Nummulites javanus* Verbeek, 1891 — Crotty & Engelhardt, p. 77.
1995 *Nummulites javanus* Verbeek, 1891 — Racey, p. 50.

Material — Over 30 specimens including 5 equatorial and 3 axial sections of B-forms, and 10 equatorial and 2 axial sections of A forms from Karangsambung (Central Java; RGM 202019, RGM 202022). Over 30 specimens including 10 equatorial and 3 axial sections of B-forms from Banten (West Java, RGM 202023). Twenty specimens, including 5 equatorial sections of B-forms from Jiwo Hills (Central Java, RGM 202018, RGM 202024). Ten equatorial and 3 axial sections of B-forms and 4 equatorial and 2 axial sections of A-forms from several localities on Timor (Institut für Paläontologie, Universität Bonn).

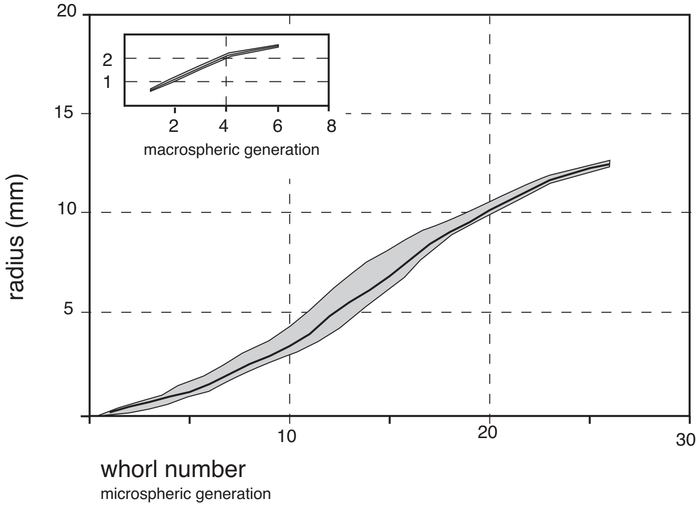


Fig. 6.9. Coiling diagram of *Nummulites javanus* Verbeek.

A-form — Lenticular with a rounded periphery, diameter up to 4.5 mm, thickness up to 2 mm and D/T = 1.8 (1.5-3.1). Septal filaments gently, curved radiating from the centre with granules on and between septal filaments. In equatorial section spire regular, comprising 4-5 whorls (Fig. 6.9). First two whorls fairly lax tightening in the 3rd-4th whorl. Septa oblique, curving gently in the proximal part, distally straight. Marginal cord 1/5 of chamber height. Chambers equidimensional to broader than high. Proloculus 0.55-0.8 mm in diameter.

Whorl number	1	2	3	4	5
Radius (mm)	0.6	1	1.6	1.9	2.2
Chambers	7	12	23	25	–

B-form — Test lenticular, up to 30 mm in diameter, maximum thickness 9 mm with D/T = 3.1 (2.6-5.2). Septal filaments meandriform with fine granules on and between them, especially over the polar region. In equatorial section, spire regularly opening, tightening in the last whorls in some specimens giving it a tripartite appearance (Fig. 6.9). Septa slightly oblique, straight to gently curved in the distal part. Chambers higher than broad in the first whorls, becoming 2-3 × as broad as high in the outer whorls. Marginal cord thick, 1/3-1/2 of the chamber height.

In axial section, strongly pillared with thin pillars, especially over the centre of the test, with most pillars not reaching the test surface.

Whorl number	1	2	3	4	5	6	7	8	9	10	11	12	13
Radius (mm)	0.18	0.47	0.7	0.97	1.2	1.6	2.1	2.6	3.0	3.5	4.1	5	5.7

Whorl number	14	15	16	17	18	19	20	21	22	23	24	25	26
Radius (mm)	6.3	7.0	7.8	8.6	9.2	9.7	10.3	10.8	11.3	11.8	12.1	12.4	12.6

Due to flexure of the shell, the number of chambers could not be counted.

Remarks — Initially, all Indonesian 'larger' *Nummulites* were grouped under the name *N. javanus*. In his original description, Verbeek (1891) had already described 4 varieties, a, b, g and d. a and g are the largest forms, a has a rounded periphery, whilst g is more flattened and has a sharp periphery; b and d are smaller, b is a thick form with a rounded periphery, whilst d is a small, flat form with a very sharp periphery. Subsequently there has been a lot of discussion about these species. Doornink (1932) suggested that the two forms with the sharp periphery should be included in *N. gizehensis* (Forskål), whilst the specimens with the rounded periphery, i.e., var d and var b, should be included in *N. perforatus* (Montfort). The present study confirms that the large sized *Nummulites* from Indonesia belong to two species, *N. boninensis* (equivalent to var a of Verbeek) and *N. javanus* (equivalent to var g of Verbeek).

The smaller variety with the blunt edge has subsequently been identified as *N. laevigatus* (Bruguière) by Douvillé (1912a); a transitional form between *N. laevigatus* and *N. perforatus* by Dollfus (1917); *N. obtusus* Sowerby by Gerth (1929) and, *N. perforatus* (Denys de Montfort) by Doornink (1932). Racey (1995) discussed the status of the smaller specimens with the blunt edge. The B-forms of *N. perforatus* have a tripartite spire, which is not seen in the Javanese specimens. In the middle, looser, part of the spire *N. perforatus* also has occasional intercalatory whorls. *Nummulites javanus* has a gradually opening spire, with some very tight last whorls (usually three, sometimes up to five). In none of the specimens of *N. javanus* are intercalary whorls present (own obs; Racey, 1995). The spire of *N. obtusus* (Sowerby) is also tripartite, but always has 3-4 intercalary whorls, features absent in the Javanese specimens. *Nummulites laevigatus* has a gradually opening spire, which does not tighten in the outer whorls, and has a flatter test with sinuous septal filaments and can thus be differentiated from *N. javanus*.

Geographic distribution — Indonesia: Karangsambung and Jiwo (Central Java, the type locations), Bayah (West Java), Ralla, Tonasa (SW Sulawesi), Batu Gading, Melinau Gorge (Sarawak) and several localities at Sumba, Timor and West Papua. Elsewhere: Oman (Racey, 1995) and Papua New Guinea (Bain & Binnekamp, 1973).

Stratigraphic range — *Nummulites javanus* is assigned a Ta_3 age (Middle Eocene in Adams, 1970; Lutetian in Haak & Postuma, 1975), though Bartonian was not recognised in these studies. In Oman, Racey (1995) found *N. javanus* together with *N. perforatus* and *N. brongniarti* in the “Biaritzian”, equivalent to the upper Lutetian to Bartonian (SBZ 17 in Serra-Kiel *et al.* 1998, top P12-P14). Outcrops in Karangsambung, Java, containing *N. javanus* could not be dated directly, though samples taken just above them have yielded planktonic foraminifera and nannoplankton indicative of a Middle Eocene, late Lutetian to early Bartonian (P12, upper NP15) age. Limestones with *N. javanus* and *Pellatispira* from Jiwo Hills (Watu Perahu) were successfully dated as P14 or older based on the presence of *Morozovella* sp. Overlying mudstones were also dated as Middle Eocene on nannofossils (see earlier notes). Samples from Ralla containing both *N. javanus* and *Pellatispira* were dated as Bartonian on the basis of associated dinoflagellates (H. Brinkhuis pers. com. to WR). Crotty and Engelhardt (1993) also found samples containing pollen indicative of Bartonian age immediately above *N. javanus* bearing sedimentary rocks. The suggested stratigraphic range for this species in Indonesia is therefore considered to be Middle Eocene, late Lutetian to early Bartonian.

Nummulites spec. nov.

Fig. 6.10; Pl. 6, figs. C-E; Pl. 7, figs. A-C.

1881	*Nummulites* cf. *lamarcki* d’Archiac & Haime, 1853 — Verbeek *et al.*, p. 39.
1881	*Nummulites* cf. *laevigata* Lamarck, 1801 [sic] — Verbeek *et al.*, p. 39.
1891	*Nummulites laevigatus* Lamarck, 1801 [sic] — Verbeek, p. 117.
1896	*Nummulites laevigata* Lamarck, 1801[sic] — Verbeek & Fennema, p. 1104.
1912b	*Nummulites vredenburgi* Prever, 1908 — Douvillé, p. 260.
1932	*Camerina laevigata* Bruguière, 1792 — Doornink, p. 279-280.
1934	*Camerina djokjokartae* (Martin, 1881) — Caudri, p. 67.
1972	non *Nummulites acutus* (Sowerby, 1840) — Blondeau, p. 149.
1995	*Nummulites acutus* (Sowerby, 1840) — Racey, p. 30.

Material — Numerous individuals from Nanggulan (Java), comprising 12 equatorial sections of A-forms, and 10 of B-forms plus five axial sections of A forms and 5 axial sections of B-forms.

One equatorial section from Uwaki, West Timor (Institut für Paläntologie, Universität Bonn).

Type locality — Kali Puru, Nanggulan, Central Java, Indonesia.

Type horizon — *Djokdjokartae* beds of the Nanggulan Formation, later Middle Eocene (uppermost Lutetian or basal Bartonian).

Diagnosis — Medium sized *Nummulites*, septal filaments meandriform, densely covered by granulae. Spiral laminae infrequently split in the polar region, not near the marginal cord. Coiling regular up to the 8-10th whorl, then more irregular with thinning marginal cord. A-forms are difficult to distinguish from *N. djokdjokartae*, except that they are smaller and have fewer whorls.

A- form — Lenticular with rounded periphery. Diameter up to 4.5 mm, thickness up to 2.5 mm. D/T= 1.6-2.0. Trace of septal filaments radiating, S-shaped, occasionally branching with coarse granules on and between the septal filaments. In equatorial section, spire regular consisting of up to 4-4 1/2 whorls (Fig. 6.10), with the first whorl wider than subsequent whorls. Marginal cord thick, 1/4-1/3 of chamber height. Chambers rectangular, initially almost isometric, becoming 1 1/2 × as broad as high. Septa perpendicular to marginal cord, curving backwards. In axial section, pillars occur over entire test surface from the centre to the periphery, and often reach the test surface to form granules. Proloculus 0.48-0.7 mm in diameter.

Whorl number	1	2	3	4
Radius (mm)	0.97	1.36	1.69	1.88
Chambers	8	17	22	–

B-form — Test flat lenticular, with sharp to rounded periphery. Test diameter up to 18 mm, thickness up to 6 mm with D/ T = 3.5-4.5. Septal filaments meandriform, with large granules on and between them. In equatorial section, spire regularly increasing

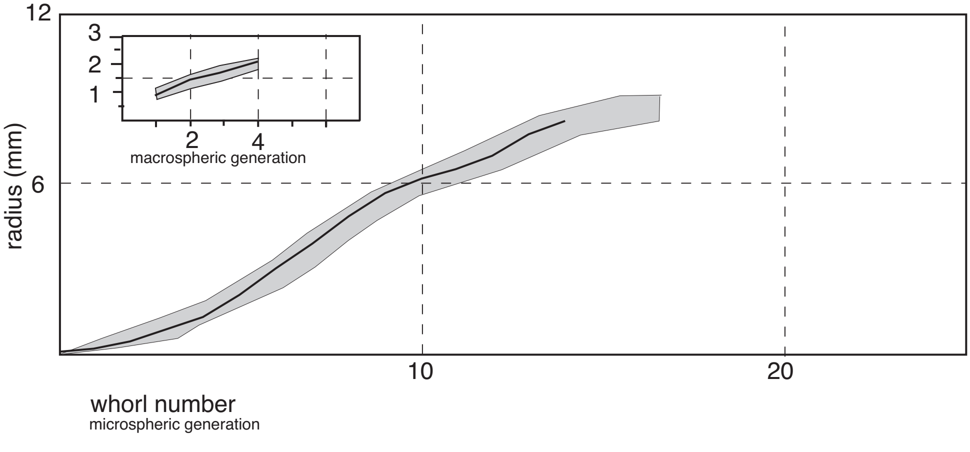


Fig. 6.10. Coiling diagram of *Nummulites* spec. nov.

in width, up to the 8-10th whorl (Fig. 6.10), after which the spire becomes irregular, with partial intercalary whorls developed. Marginal cord thick in the first 8-10 whorls at about 1/4 of chamber height and thinner in remaining whorls. Chambers 2 × higher than long in the first 4 whorls, about 1.5-2.0 × higher than long in whorl 5-8 (10) and finally 1.5-2 × longer than high in the later whorls. Septa straight, sharply curved backwards at the peripheral margin, perpendicular to marginal cord in first 8-10 whorls and curved in later whorls.

In axial section, chamber height increases in height towards margin. Spiral laminae thickest near marginal cord, then much thinner, but lateral splitting of the spiral laminae is rare, occurring nearer to the central axis of the test than to the marginal cord. Alar prolongations very narrow. Pillars of varying size and shape, distributed from pole to periphery. Most pillars do not protrude to the surface of the test.

Whorl number	1	2	3	4	5	6	7	8	9
Radius (mm)	0.21	0.47	0.90	1.3	2.1	3.0	3.9	4.88	5.85
Chambers	9	12	22	27	27	33	38	48	64

Whorl number	10	11	12	13	14	15	16
Radius (mm)	6.22	6.55	7.02	7.78	8.25	8.55	9.04
Chambers	68	70	76	92	90	92	–

Remarks — The A-form typically has 4-4.5, the B-form 14-17 whorls. In the Nanggulan (Java) section, A-forms are abundant, whilst B-forms are rare. *Nummulites* spec. nov. differs from *N. djokdjokartae* in that it is slightly more loosely coiled, the chambers are isometric to twice as high as long (2-3 times as high as long in *N. djokdjokartae*) and the lateral laminae thin, but do (usually) not split. If they split, it is in the polar egion, whilst in *N. djokdjokartae* they split near the periphery. Additionally, the maximum size of *N.* spec. nov. is 16-18 mm, while *N. djokdjokartae* can get as large as 25 mm.

In India and Indonesia, three species of the *N. laevigatus*-lineage (*N. acutus*, *N. djokdjokartae* and *N. vredenburgi*) have been described, which have been confused during the last century. The types of *Nummulites acutus*, mixed A- (which Sowerby regarded as juveniles) and B-forms are lost, except for the largest specimen that is preserved in NHM (London). Samanta (1982) resampled the type area and studied the remaining type specimen of *N. acutus* and the type specimens of *N. vredenburgi* and discussed the differences between these two species, that both were synonymised together with *N. djokdjokartae* by Umbgrove (1931).

Samanta (1982) showed that *N. acutus* and *N. djokdjokarte* (= *N. vredenburgi*) are two distinct species that often have been confused. Samanta (1982) did not find new specimens of *N. acutus*, so his description of that species is solely based on the type specimen. This specimen reaches only 10 mm in diameter, the coiling pattern is tighter than the Indonesian specimens and the marginal cord does not thin or disappear, thus not justifying the synonymy between *N. acutus* and *N. djokdjokartae*.

Blondeau (1972) described and figured specimens under the name *N. acutus* that fit the description of Sowerby precisely. The maximum diameter is 13 mm, with only 12 whorls, all chambers isometric or only slightly higher than long, marginal cord not thinning in the outermost whorls, whilst the maximum diameter in Indonesia is 18 mm, specimens have up to 17 whorls and the initial chambers are higher than long.

Blondeau shows Indonesian A-froms (*N. djokdjokartae*) as the accompanying macrospheric generation, but the microspheric forms shown by him originate from Madagascar and differ from the Indonesian B- forms.Thus, *N. acutus* (Sowerby) is a different species, warranting the small Indonesian specimens to be described as a new species.

The A and B forms shown by Racey (1995) as *N. acutus* are similar to *N.* spec. nov. in size, coiling pattern and number of whorls, as well as external characters, and should be included in this species.

Geographic distribution — Indonesia: Central Java; Timor. Elsewhere: Oman (Racey, 1995).

Stratigraphic range — In Oman, *Nummulites* spec. nov. (recorded as *N. acutus*) was found in middle Lutetian deposits, which are approximately equivalent to zone P11. In Indonesia it is found in the oldest sedimentary rocks containing larger foraminifera from the Nanggulan section, that have been dated as upper P12 (Lunt 2000a,b), but also in the Nummulite beds 2, thus the range of *N.* spec. nov. overlaps with the range of *N. djokdjokartae*.

The stratigraphic range in Indonesia is interpreted as Letter Stage Ta (P11-P12), correlating with the Lutetian Stage.

Nummulites subbrongniarti Verbeek, 1871
Fig. 6.11; Pl. 12, figs. A-C.

* 1871 *Nummulites sub-brongniarti* Verbeek, p. 6.
1874 *Nummulites subbrongniarti* Verbeek — Verbeek, p. 152-155.
1929 *Camerina fichteli* Michelotti — van der Vlerk, p. 18.
* 1932 *Camerina divina* Doornink, p. 299-300.
1934 *Camerina divina* Doornink — Caudri, p. 78.

Material — Fifteen specimens including 1 equatorial section of a B-form and 5 equatorial and one axial section of A-forms from Sungai Seilor (Borneo, RGM 10949, RGM 19051-19060). Five specimens including 5 equatorial sections of A-forms from Tji Dengkol (Java, RGM 202025).

A-form — Lenticular test with a sharp margin, diameter 3.5-5.0 mm, thickness 1.6-2.4 mm and D/ T = 2.1 (1.8-2.5). Septal filaments reticulate comprising a rather coarse mesh. The equatorial section comprises 7-9 compact whorls of almost equal height (Fig. 6.11). Marginal cord 1/3 of chamber height in initial whorls and approximately 1/2 chamber height in later whorls. Chambers 1.5 × broader than high in the initial whorls, becoming 3-5 × broader than high in the outer 3-4 whorls. In axial section fine pillars diverge from the equatorial plane to the outer whorl. Proloculus 0.2-0.36 mm in diameter.

Whorl number	1	2	3	4	5	6	7
Radius (mm)	0.6	0.78	0.98	1.19	1.42	1.67	1.89
Chambers	8	9	10	11	13	14	–

B-form — Description based on the type description of Verbeek (1871) and figures in Hashimoto *et al.* (1973), together with data from one thin section present in the NNM collection.

Test flattened lenticular, with a subrounded, often undulated periphery. Diameter up to 28 mm (commonly 14 mm), thickness up to 6 mm and diameter/ thickness = 4-5. Septal filaments reticulate. In equatorial section, comprises up to 50-60 whorls in a diameter of 14 mm (Fig. 6.11), with a large variation in both the diameter and the number of whorls. Marginal cord in the inner whorls as high as the chamber height, in the latter whorls about 1/3 of the chamber height. Chambers up to 4 times longer than high, especially in the outer whorls. Septa slightly inclined and straight.

Whorl number	1	2	3	4	5	6	7	8	9	10
Radius (mm)	0.1	0.2	0.3	0.5	0.6	0.7	0.9	1.1	1.3	1.5

Whorl number	11	12	13	14	15	16	17	18	19	20
Radius (mm)	1.6	1.9	2.3	2.6	3.1	3.5	3.7	3.9	4.2	4.4

Whorl number	21	22	23	24	25	26	27	28	29	30
Radius (mm)	4.7	4.9	5.2	5.5	5.8	6.1	6.3	6.5	6.8	7.1

Whorl number	31	32	33	34	35	36	37	38	39	40
Radius (mm)	7.3	7.5	7.6	7.8	8.0	8.2	8.4	8.6	8.7	8.9

Whorl number	41	42	43	44	45	46	47	48	49
Radius (mm)	9.0	9.1	9.3	9.4	9.5	9.6	9.7	9.8	10

Due to flexure of the test, number of chambers could not be counted.

Remarks — *Nummulites subbrongniarti* differs from *N. brongniarti* d'Archiac & Haime in being more tightly coiled in both the A and B-forms. Furthermore *N. subbrongniarti* lacks granules on the surface of the test and has reticulate rather than subreticulate septal filaments.

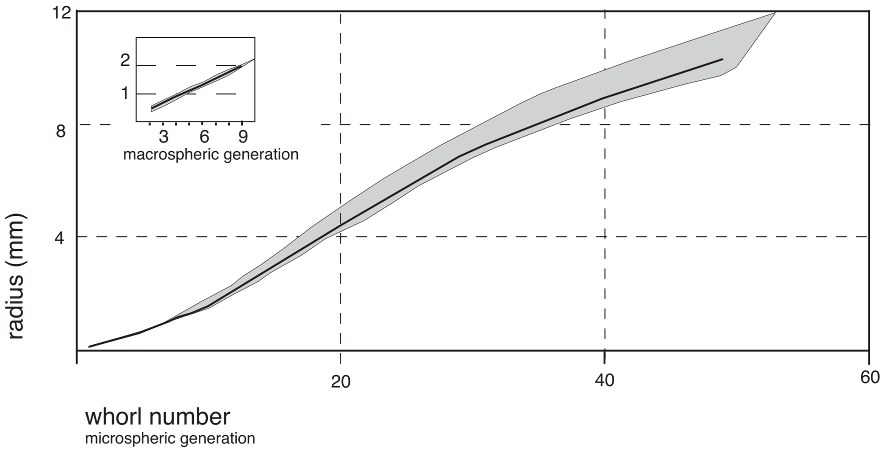


Fig. 6.11. Coiling diagram of *Nummulites subbrongniarti* Verbeek.

Much confusion has arisen following the type description by Verbeek in 1871. His drawings were not clear, and though he mentioned that the proloculus was small, but visible, this species was subsequently interpreted as an A-form. However, Verbeek's specimens are clearly B-forms, based on their size and the number of whorls. Starting with Douvillé (1905), several authors have regarded *N. subbrongniarti* as the Indonesian representative of *N. intermedius-fichteli*. Doornink (1932) restudied the Javanese *Nummulites* and acknowledged the existence of more than one species among the Oligocene reticulate *Nummulites*, describing two new species and discussing the status of *N. subbrongniarti.* He did not recognise *N. subbrongniarti*, but described *N. divina* Doornink from Java, which is an A-form similar to the A-form of *N. fichteli*, but has broader chambers (3-5 × as broad as high) in the outer whorls and has whorls of similar height. The reticulate septal filaments (mesh) on the test surface are coarser than in *N. fichteli* (see Caudri, 1934). Specimens figured and collected by van der Vlerk (1929) match Doornink's description. Verbeek (1871) distinguished *N. subbrongniarti* from *N. fichteli* by its tighter coiling, larger number of whorls and longer chambers. He also mentioned the coarse mesh on the outer surface. The similar character distinguishing *N. divina* and *N. subbrongniarti* from *N. fichteli* indicate that these are in fact A and B forms of a single species, i.e., *N. subbrongniarti*. *Nummulites divina* must therefore be considered a junior synonym of *N. subbrongniarti.*

Hashimoto *et al.* (1973) restudied many reticulate nummulitids to examine the relationship between *N. subbrongniarti* and *N. fichteli.* Although they looked at many characters, they did not take the form of the spire into account and their fig. 6.11 clearly shows all the characters of *N. subbrongniarti*.

Nummulites subbrongniarti is closely related to *N. fichteli*. In India, Pakistan and Egypt two other species occur that also are as closely related to *N. fichteli*: *N. sublaevigatus* and *N.* cf. *fichteli* (Sen Gupta, 2000), showing a radiation of the reticulate *Nummulites* lineage after the Eocene-Oligiocene boundary, but terminated prior to the Chattian.

Geographic distribution — Indonesia: Cijengkol (Java, Doornink, 1932), Sungai Seilor. Antjam, Borneo (van der Vlerk, 1929), Pengaron, SE Kalimantan (Verbeek, 1871; Hashimoto *et al.*, 1973) and East Sumba (Caudri, 1934). Elsewhere: Mindoro (the Philippines).

Stratigraphic range — Co-occurring with *N. fichteli* and *P. pengaronensis* in SE Borneo in Tc faunas (Rupelian). Suggested stratigraphic range: Lower Rupelian, Tc.

Genus *Palaeonummulites* Schubert

Type species — *Nummulina pristina* Brady, 1874.

Diagnosis — Planispiral, involute, semi-compressed to globular; spire moderately tightly coiled; whorls relatively few, generally no more than four or five in the A-form; coiling tight; chambers up to twice as high as long in equatorial section; primary septa and extensions ("filaments") only; septal sutures radial to sigmoidal; marginal cord finely to moderately strong developed. Mid-Palaeocene to Recent with a Cosmopolitan distribution.

Discussion — Distinguished from *Nummulites* by its simple septal filaments that are straight to sigmoidal. In *Nummulites* secondary septal filaments are present.

Palaeonummulites beaumonti (d'Archiac & Haime, 1853)
Fig. 6.12; Pl. 11, figs. A-D.

* 1853 *Nummulites beaumonti* d'Archiac and Haime, p. 133.
1874 *Nummulites biarritzensis* d'Archiac and Haime, 1853 — Verbeek, p. 155.
1874 *Nummulites striata* d'Orbigny var f — Verbeek, p. 157.
1912a *Nummulites kelatensis* Carter, 1861 — Douvillé, p. 262.
1929 *Nummulites kelatensis* Carter, 1861 — van der Vlerk, p. 19.
1929 *Nummulites kelatensis* Carter, 1861 — Gerth, p. 598.
* 1932 *Camerina densa* Doornink, p. 295.
* 1932 *Camerina hoogenraadi* Doornink, p. 297.
1934 *Camerina kelatensis* (Carter?) Douvillé — Caudri, p. 53.
1934 *Camerina kelatensis* Carter, 1861 sensu Douvillé — Henrici, p. 30.
1940 *Nummulites beaumonti* d'Archiac and Haime — Davies, p. 206.
1972 *Nummulites beaumonti* d'Archiac and Haime — Blondeau, p. 149.
1981 *Nummulites beaumonti* d'Archiac and Haime — Schaub, p. 135.
1995 *Nummulites beaumonti* d'Archiac and Haime — Racey, p. 34.

Material — Five specimens from Nias including one equatorial section of a B-form (RGM 202026). Four specimens from Taballar including three equatorial sections and one axial section of B-forms (RGM 19112-19114). Five specimens, including three equatorial and one axial section of B-forms from Timor (Institut für Paläontologie, Universität Bonn).

A-form — Not found.

B-form — Test lenticular, with rounded margin. Test diameter 6.5-9.0 mm, thickness 3.5-4 mm, D/T ratio = 2.1-3.1. Septal filaments straight, radiating and curving

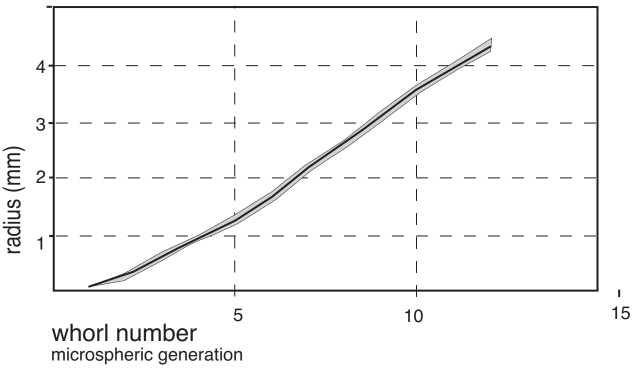


Fig. 6.12. Coiling diagram of *Palaeonummulites beaumonti* (d'Archiac & Haime).

around a polar pillar. In equatorial section, spire regularly opening (Fig. 6.12). Chambers numerous, uniform, rectangular, 1.5-2.0 as high as long in the initial whorls, equidimensional to slightly higher than broad in the outer whorls, with almost straight septa. Marginal cord about 1/4-1/5 of the chamber height. In axial section alar prolongations thin, spiral laminae all of the same thickness. Fine pillars reach about half way to the exterior, maily concentrated over the polar region and often buried.

Whorl number	1	2	3	4	5	6	7	8	9	10	11	12
Radius (mm)	0.11	0.26	0.59	0.93	1.25	1.67	2.21	2.59	3.07	3.55	3.97	4.33
Chambers	–	21	26	30	34	40	42	48	55	57	60	65

Remarks — According to Davies (1940) and Blondeau (1972), *P. kelatensis* Carter is in part synonymous with *P. beaumonti* (d'Archiac & Haime). Davies (1940) redescribed *P. kelatensis* from topotypes, whilst Racey (1995) restudied these and concluded that *P. kelatensis* is a smaller species with fewer whorls than *P. beaumonti*. Furthermore, in the description of *P. kelatensis* Davies stated that the septal filaments are clearly twisted, while the septal filaments are nearly straight and only curved around the polar region in *P. beaumonti*. The buried pustules in the polar region are a good features to help distinguish *P. beaumonti* from other species.

The specimens from all localities in Indonesia match the description of *P. beaumonti* in nearly all characters, and should therefore be included in that taxon, though they have previously been reported as *N. kelatensis* (see references in synonymy list).

Geographic distribution — Indonesia: Nias, Borneo, Java, Sumba and Timor, but rare in all localities. Elsewhere: Oman (Racey, 1995), Senegal, Libya (Blondeau, 1972), Egypt (De la Harpe, 1883), India (Nuttall, 1926a, b) and Pakistan (Davies, 1940).

Stratigraphic range — In Nias *P. beaumonti* is found together with *Alveolina ovicula* and *Planocamerinoides* sp. 1, indicating a (late) Lutetian age. In Timor it co-occurs with *N. javanus* and planktonic foraminifera indicating a P12-P14 age. In Oman it is restricted to the late Lutetian (Racey, 1995), while in the western Tethys it is found in the late Lutetian- Bartonian (Serra-Kiel *et al.*, 1998). The stratigraphic range in Indonesia of this species is therefore suggested to be upper Lutetian-Bartonian.

Palaeonummulites crasseornatus (Henrici, 1934)
Fig. 6.13; Pl. 13, figs. A-B, H-J.

1932 *Camerina irregularis* Deshayes, 1838 — Doornink, p. 290.
1932 *Camerina orbignyi* (Galeotti) — Doornink, p. 289.
* 1934 *Camerina crasseornata* Henrici, p. 32.
1934 *Camerina* aff. *irregularis* Deshayes, 1838 — Caudri, p. 62.

Material — Ten specimens including four equatorial sections of B-forms from Nanggulan. Over 30 specimens including five equatorial and three axial sections of both A and B-forms from Timor (Geologisch Instituut, TU Delft). Two specimens including 1 axial section of a B-form from Jatibungkus (RGM 202032).

A-form — Diameter up to 3 mm, thickness 1.5 mm. Involutely coiled with a pronounced marginal cord. From the coarsely granulated (70-130 mm) centre straight septal filaments radiate. In equatorial section, spire regular, fairly constant in width (Fig. 6.13). Chambers rectangular with rounded tops. Septa thin, perpendicular to the marginal cord, with intraseptal canal visible, slightly bent backwards. In axial section, a small umbilical plug is visible. The marginal cord is thick, and coarsely canalised. Proloculus 0.20-0.32 mm in diameter.

Whorl number	1	2	3	4
Radius (mm)	0.42	0.93	1.7	2.6
Chambers	13	16	19	25

B-form — Diameter up to 8 mm, thickness 1.7 mm and D/T = 3.4 (2.5-4.4). Test lenticular, involute. The centre of the test has a large number of coarse pillars, out of which 30-35 S shaped septal filaments radiate. In equatorial section the spire is irregular, showing large differences in whorl height within and between whorls (Fig. 6.13). Test outline often elongated. Chambers rectangular, slightly bent backwards with rounded tops. Septa thin, perpendicular to the marginal cord and distally curved backwards, in outer whorls with intraseptal canal visible. Chambers higher than broad (up to 3 ×). In axial section an umbilical plug (pillar) is visible. The marginal cord is swollen and coarsely canalised.

Whorl number	1	2	3	4	5	6
Radius (mm)- Java	0.29	0.58	0.98	1.46	1.92	2.1
Chambers- Java	7	15	24	30	34	39

Remarks — There have been several records of *N. irregularis* Deshayes or related taxa from Tb strata in Indonesia, many of which should be assigned to other genera in our opinion. For example, the specimens figured by Provale (1908) as *N. heeri* De la

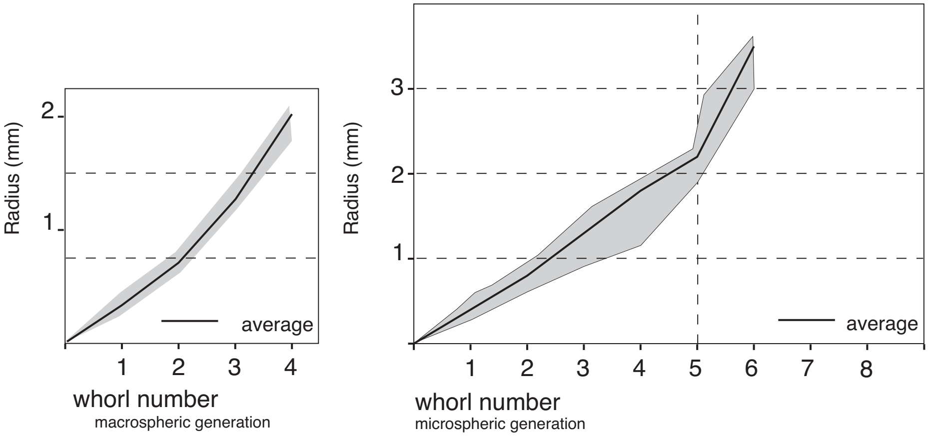


Fig. 6.13. Coiling diagram of *Palaeonummulites crasseornatus* (Henrici).

Harpe and *N. sub-heeri* De la Harpe, are, in fact, *Operculina*, based on the rapidly opening spire and lack of alar prolongations, features which do not occur in *Nummulites* and are characteristic for *Operculina*.

Doornink (1932) first reported this species from Indonesia as *N. orbignyi* (Galeotti), referring to a more complete description of *N. elegans* (Jones, 1887), which includes *N. prestwichianus* (Jones), and *N. elegans* Sowerby. However, Jones (1887) showed that some of the specimens described by Sowerby as *N. elegans* were juveniles of *N. planulatus* Lamarck. In both the descriptions of *N. elegans* and *N. prestwichianus*, no granulations in the centre of the test are mentioned, nor on their plates. Jones (1887) shows *N. prestwichianus* as lacking granulations and having a poorly developed umbo in the centre of the test. In the Indonesian specimens no umbo is present, and in many specimens a polar depression is observed. Thus, neither *N. elegans* nor *N. prestwichianus* are identical with the Indonesian specimens. Boussac (1911) synonymised all these species under *N. orbignyi*, but did not give any supporting illustrations, though his description matches the previous description. Blondeau (1972) separated *N. orbignyi* and *N. prestwichianus* (= *N. elegans*) as distinctive species. Both species differ from the Indonesian specimens by either the absence of granulations and the presence of an evolute last whorl (*N. orbignyi*) or by having a more robust test (*N. prestwichianus*).

Schaub (1981, p. 160) mentioned that the granulated specimens from the the Isle of Wight, southern England, are *N. aquitanicus* Benoist, 1889 (previously described as *N. orbignyi* var *granulosa* Jarzeva) though according to Schaub (1981), *N. aquitanicus* is much larger and more regularly coiled than *N. orbignyi*).

Doornink (1932) described specimens from Central Java as *N. irregularis* because of their similarity to *N. irregularis* material from India. His description refers to granules, a common morphological character of the Nummulitidae. However, *Nummulites irregularis* does not have granules (Schaub, 1981; Racey, 1995). Granules are present in the Javanese specimens, and are formed by small pustules, comparable to those in Recent *Operculina ammonoides*. The Javanese specimens, therefore, cannot be assigned to *N. irregularis* Deshayes. The description given by Caudri (1934) is similar to that of the above-mentioned specimens. Although she did not give any measurements, she stated that the coiling is tighter than that of the Indian and European specimens.

The Javanese specimens studied herein exactly match the type specimens of *Camerina crasseornata* Henrici. In equatorial section, the septa are thinner and the chambers higher than in *P. taballarensis*. They are larger than both *Palaeonummulites thalicus* and *P. taballarensis,* have a more inflated test and more numerous coarse pillars over the poles. In the largest B-forms the last whorl is evolute and the coarse marginal cord forms a ridge that is visible on the test surface, which is otherwise only seen in *Ranikothalia*. Unlike *Ranikothalia*, the alar prolongations do not extend towards the poles in axial section and are much higher.

Nummulites kemmerlingi Caudri (1934, p. 60-62) was recognised by Caudri from only seven specimens. It is very similar to *P. crasseornatus* but larger (8.5-15 mm). No specimens could be relocated in museum collections and the specimens shown by Caudri (1934) are only slightly larger than the largest *P. crasseornatus* B-form described herein. Thus, *N. kemmerlingi* is regarded herein as synonymous with *P. crasseornatus*.

Geographic distribution Indonesia: Java (Nanggulan, Jatibungkus Lst), Timor (Henrici, 1934), Sumba (Caudri, 1934) and Sulawesi (Ralla bridge section). Elsewhere: specimens from Pinugay Hill, Luzon, the Philippines (Hashimoto *et al*., 1978c) resemble *P. crasseornatus* though the figures provided are insufficient to allow positive identification.

Stratigraphic range — Recorded from Timor together with *Alveolina ovicula* Nuttall and *N. javanus* Verbeek (Ta stage). In Java *P. crasseornatus* is found in the *Discocyclina* layers at Nanggulan (upper P12, upper NP16), from the Lutetian- Bartonian boundary. In the Jiwo Hills area they are dated as P12-14, upper NP15-16 age, i.e., latest Lutetian to earliest Bartonian. Letter Stage Ta and in the Middle Eocene. *Palaeonummulites crasseornatus* is found in Sumba together with *P. beaumonti*, *P. taballarensis* and *Planocamerinoides orientalis*, indicative of an upper Lutetian age. The stratigraphic range in Indonesia is therefore considered to be Middle Eocene, Ta, late Lutetian — Bartonian.

Palaeonummulites pengaronensis (Verbeek, 1871)
Fig. 6.14; Pl. 10, figs. A-E.

* 1871 *Nummulites pengaronensis* Verbeek, p. 3.
1874 *Nummulites pengaronensis* Verbeek, 1871 — Verbeek, p. 145-148.
* 1891 *Nummulites nanggoelani* Verbeek, p. 161.
1896 *Nummulites nanggoelani* Verbeek, 1891 — Verbeek & Fennema, p. 1105.
1896 *Nummulites pengaronensis* Verbeek, 1871 — Verbeek & Fennema, p. 1107.
1905 *Nummulites nanggoulani* Verbeek, 1891 — Deprat, p. 494.
1912b *Nummulites pengaronensis* Verbeek, 1871 — Douvillé, p. 284.
1929 *Nummulites pengaronensis* Verbeek, 1871 — van der Vlerk, p. 6-7.
1929 *Camerina nanggoelani* Verbeek, 1891 — Gerth, p. 598.
1931 *Camerina pengaronensis* Verbeek, 1871 — Umbgrove, p. 50.
1932 *Camerina pengaronensis* (Verbeek, 1871) — Doornink, p. 283.
1932 *Camerina pustulosa* Douvillé, 1919 — Doornink, p. 286.
* 1932 *Camaerina gerthi* Doornink, p. 296.
1934 *Nummulites* cf. *pengaronensis* Verbeek, 1871 — Caudri, p. 52.
1934 *Camerina pengaronensis* (Verbeek, 1871)- Henrici, p. 29.
1949 *Nummulites pengaronensis* Verbeek, 1871 — Rutten in van Bemmelen, p. 85.
1968 *Nummulites pengaronensis* Verbeek, 1871 — Samanta, p. 677-680.
1973 *Nummulites pengaronensis* Verbeek, 1871 — Binnekamp, p. 10.
1979 *Nummulites pengalonensis* [sic] Verbeek, 1871 — Hashimoto *et al*., p. 155
1981b *Nummulites* cf *pengaronensis* Verbeek, 1871 — Hashimoto & Matsumaru, p. 68.

Material — Ten specimens including 5 equatorial and 2 axial sections of B-forms from Pengaron (Borneo). Fifteen specimens, including 5 equatorial sections of B-forms, and 4 equatorial and 1 axial section of A-forms from Nanggulan (Central Java, RGM 202026). Numerous specimens from Sangiran, including 10 equatorial and 1 axial of A-forms and 1 B-form (RGM 202027). Ten specimens, including 4 equatorial sections of A-forms and 4 equatorial sections of B-forms from Nias. Three equatorial and 2 axial sections of B-forms from Timor (Institut für Paläontologie, Universität Bonn).

A-form — Test biconical, with a sharp to rounded periphery, 3.1-4.1 mm (average 3.6 mm) in diameter and up to 3.2 mm thick with a D/T = 1.8 (1.3-2.4) Septal filaments radiating, straight to slightly S-shaped. Polar usually pillar present. In equatorial section, up to 5.5 whorls with a regularly opening spire (Fig. 6.14) and has a thick marginal cord (1/3-1/4 of chamber height). Chambers slightly longer than high to equidimensional. Septa thin, perpendicular to marginal cord, curving backwards. Test is distinctly diamond shape in axial section, with an umbilical plug (pillar) which is poorly developed in some specimens. Alar prolongations narrow. Proloculus small, 0.18-0.28 mm in diameter.

Whorl number	1	2	3	4	5
Radius (mm)	0.5	0.63	1.0	1.4	1.7
Chambers	8	14	19	24	30

B-form — Exterior similar to A-form with test diameter up to 9 mm, thickness up to 3 mm and D/T = 2.5 (1.8-3.2).

Spire gradually opening, uniform (Fig. 6.14) with marginal cord thin, about 1/5 of chamber height. Chambers higher than broad to isometric in the outer whorls. Septa perpendicular to the marginal cord, strongly curving backwards in the distal half. Biconical in axial section, with umbilical plug (pillar), alar prolongations narrow.

Whorl number	1	2	3	4	5	6	7	8	9
Radius (mm)	0.15	0.4	0.6	0.83	1.4	1.9	2.6	3.4	3.94
Chambers	-	23	27	35	33	46	-	-	-

Remarks — There has been confusion about whether the type specimen of *P. pengaronensis* was A-form or a B-form (see Doornink, 1932). The types were not available for study though topotypes collected by Verbeek were examined. The diameter of the B-forms is 6-9 mm, which is similar to the diameter of the types. The co-occurring A-forms are much smaller, being up to 4 mm in diameter. Both have a similar external morphology and chamber shape. The holotype is probably a B-form, as originally noted by van der Vlerk (1929), who probably saw the type specimens. In subsequent descriptions the A- and B-forms have often been confused. *Palaeonummulites pengaronensis* is very similar to *N. striatus* d'Orbigny, but is smaller with a smaller proloculus in the A-form. The fourth and fifth whorls are more tightly coiled in the A-forms. Both species have an axial pillar and a distinctive diamond shaped test in axial section.

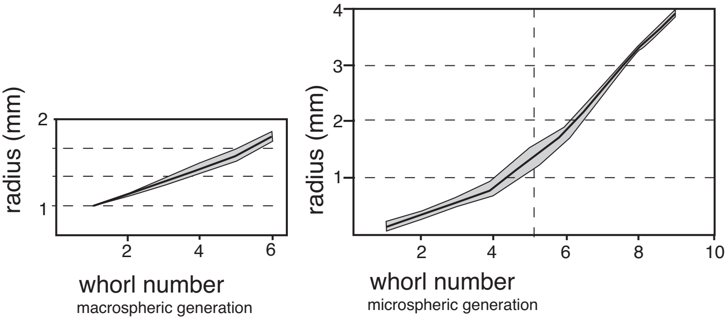


Fig. 6.14. Coiling diagram of *Palaeonummulites pengaronensis* (Verbeek).

Doornink (1932) described *P. gerthi* from Gamping, and noted that "owing to the special character of this form, it is very dificult to name a species which may be related to it". We found a similar facies (rich in *Pellatispira*, some *Sylvestriella*, *Discocyclina, Asterocyclina* and rare *Heterostegina* and *N. pengaronensis* B-form) in Sangiran, with abundant globular *Palaeonummulites*, very similar to the figures of Doornink. In all measurements these are similar to *P. pengaronensis*, and thus *P. gerthi* is regarded as a junior synonym of *P. pengaronensis*.

Geographic distribution — Indonesia: West, Central and East Java, Sumba, Borneo, Sulawesi, Timor and Nias (Sumatra). Elsewhere: Assam (Eastern India, Samanta, 1968); New Caledonia (Deprat, 1905), Papua New Guinea (Binnekamp, 1973) and Saipan (Cole, 1954; 1957).

Stratigraphic range — Most abundant in the (?latest Bartonian and) Priabonian, that is, Tb, Late Eocene, after the extinction of Ta forms. Van der Vlerk (1929) reported *P. pengaronensis* with *N. fichteli* and *Heterostegina reticulata* in Borneo which would indicate an Early Oligocene age. *Palaeonummulites pengaronensis* is also found together with *N. javanus* in Java and in Timor associated with *Cibrohantkenina* and *P. variolarius*, indicating a Late Eocene P16 age. The stratigraphic range in Indonesia is assumed therefore to be late Middle Eocene through Early Oligocene, Ta to Tc, Lutetian - (early) Rupelian.

Palaeonummulites spec. nov.
Fig. 6.15; Pl. 13, figs. C-G.

1932 *Camerina pustulosus* Douvillé, 1919 — Doornink, p. 286-287.

Material — Twentyfive individuals including 10 equatorial and 4 axial sections of B-forms from Nanggulan.

Type locality– Kali Songo, Nanggulan, Central Java, Indonesia.

Type horizon — *Discocyclina* beds of the Nanggulan Formation, Middle Eocene, uppermost Lutetian or basal Bartonian.

Diagnosis — A small tightly coiled *Palaeonummulites*, with all whorls involutely coiled. Septa curved with large granules in the centre of the test. Marginal cord thick, 1/3 of the chamber hight. Differs from *P. taballarensis* in being more loosely coiled. It is less irregularly coiled than *P. crasseornatus* which has straight to slightly curved septa.

A-form — Test lenticular with a flattened periphery. Diameter 3-4 mm, thickness 1.5-2.5 mm, diameter/thickness 1.5-2.4. Septal filaments slightly curved, radiating. Lateral surface covered by coarse pustules, concentrated in the umbonal region. In equatorial section spire gradually opening (Fig. 6.15). Septa thin, perpendicular to slightly inclined, straight and bent backwards in their basal part. Chambers 3-4 × higher than broad. In axial section pillars occur mainly over the umbonal region. Proloculus 0.2-0.3 mm in diameter.

Whorl number	1	2	3
Radius (mm)	0.5	1.1	1.7
Chambers	7	18	26

B-form — Test lenticular, involute throughout, sometimes with an umbonal depression. Diameter 4 to 6 mm, thickness up to 2 mm, diameter/thickness = 1.7-3.2 (12 measured specimens). Umbonal region covered by coarse pustules, 90-210 mm in diameter. The number of granules and the surface area covered by these granules is variable. The granules mainly occupy the centre of the test and are arranged in a spiral in the outer half of the test.

Smoothly curved septal filaments are mainly seen at the outer half of the test (Pl. 13, fig. E). In equatorial section, the spire opens slowly, occasionally with some irregularities (Fig. 6.15). Septa are thin, straight, and bent backwards in their upper part. Intraseptal canal clearly visible. Chambers 2-3 × higher than broad, except in areas showing relatively low whorl height. In axial thin section, densely packed pillars occur over the umbonal region. Marginal cord thick, coarsely canalised.

Whorl number	1	2	3	4	5	6
Radius (mm) holotype	0.36	0.55	0.83	1.12	1.49	1.97
Chambers	8	17	26	31	32	39
Radius (mm) average	0.29	0.58	0.98	1.46	1.92	2.1
Chambers average	7	15	24	30	34	39
Number of measured specimens	5	5	5	5	3	1

Remarks — Doornink (1932) first reported this species as *N. pustulosus* Douvillé, 1919. The European specimens of *N. pustulosus* show a superficial resemblance in external appearance, though the B-form is much larger, as is the proloculus size in the A-form and the chamber shape is much more regular than in *N. pustulosus*. The Javanese specimens show all the characteristics of the genus *Palaeonummulites*, though

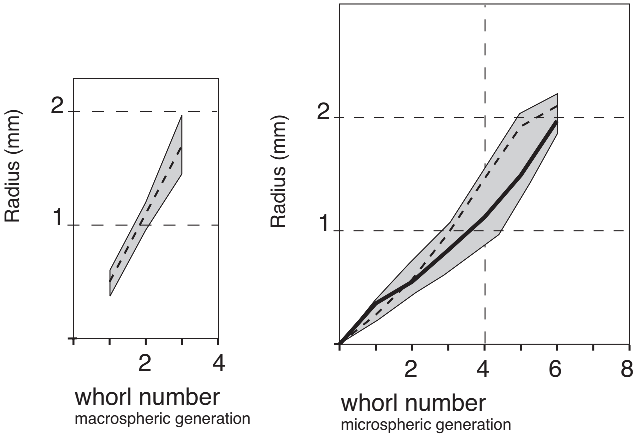


Fig. 6.15. Coiling diagram of *Palaeonummulites* spec. nov.

their marginal cord is more strongly developed and coiling is more open than in the diagnosis of this genus provided by Haynes (1988). It has thin, straight septa with a relatively thick marginal cord. Especially where the chambers are very high, the septa are bent backwards in their topmost quarter.

Geographic distribution — Known only from Central Java: Jiwo, Kali Songo ("Kali Semah") (Doornink, 1932, as *Camerina pustulosa*). Additional specimens have been found in Kali Songo (RGM20200) and "Kali Semah" (B8718).

Stratigraphic range — The few known localities have been dated as zone P12, late NP16, Middle Eocene, latest Lutetian or earliest Bartonian (Lunt, 2000a and herein).

Palaeonummulites sp. 1

Fig. 6.16; Pl. 10, figs. F-G.

1908 *Nummulites guettardi* d'Archiac & Haime, 1853 — Osimo, p. 30.
1908 *Nummulites guettardi* d'Archiac & Haime, 1853 — Provale, p. 82.
1934 *Camerina guettardi* d'Archiac & Haime, 1853 — Henrici, p. 26-27.
1934 *Camerina* cf. *globula* Leymerie1846 — Henrici, p. 28.

Material — Ten specimens from Timor, including 4 equatorial and 3 axial sections of A-forms and 2 equatorial sections of B-forms (Institut für Paläontologie, Universität Bonn).

A-form — Test lenticular, small with rounded periphery. Diameter up to 4 mm, thickness up to 2 mm and D/T on average 2.1. Polar pillar small with septal filaments radiating straight. In equatorial section the spire is tight and regularly coiled (Fig. 6.16). Chambers are higher than broad to equidimensional with marginal cord 1/10 of chamber height. Septa perpendicular, curved backwards. In axial section a weak single polar pillar is present. Proloculus small 0.09-0.18 mm in diameter.

Whorl number	1	2	3	4	5
Radius (mm)	0.3	0.62	0.78	1.02	1.4
Chambers	9	14	21	24	28

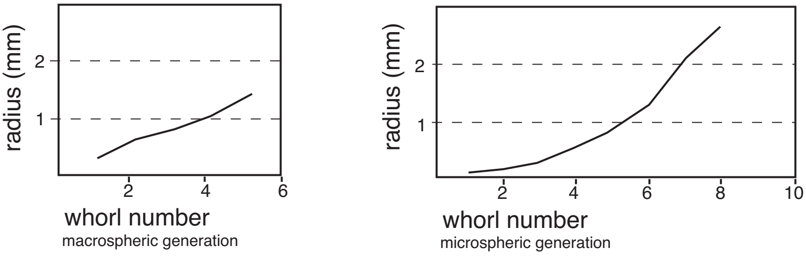


Fig. 6.16. Coiling diagram of *Palaeonummulites* spec. 1.

B-form — Test lenticular, small with rounded periphery, diameter up to 6 mm, thickness up to 3.5 mm and D/T on average 2.0. Polar pillar small with septal filaments curving radially outwards from the polar area and straightening towards the margin. In equatorial section, spire compact, regular (Fig. 6.16). Chambers higher than broad, with rounded tops. Septa curved backwards, almost perpendicular to marginal cord at base. Marginal cord thin, about 1/10 of chamber height. In axial section a weakly developed polar pillar is present.

Whorl number	1	2	3	4	5	6	7	8	9
Radius (mm)	0.08	0.16	0.28	0.52	0.90	1.34	2.1	2.65	3.6
Chambers	12	18	24	26	30	34	38	–	–

Remarks — This species is most similar in appearance to *P. globulus* from which it differs in having more and slightly tighter coiled whorls with fewer chambers in the A-form. The microspheric form is slightly larger and flatter than that of *P. globulus.*

Geographic distribution — Indonesia: Timor (Henrici, 1932), Sumba (Caudri, 1934), Java, and Borneo.

Stratigraphic range — In Borneo and Timor it was found together with *Orbitolites complanatus*. These deposits are interpreted as lower Lutetian in age. Suggested stratigraphic range in Indonesia: the older part of the Middle Eocene, Letter Stage Ta1-2. ?Ypresian - lower Lutetian.

Palaeonummulites taballarensis (Caudri, 1934)
Fig. 6.17; Pl. 13, figs. K-M.

1929 *Nummulites nutalli* Davies, 1927 — van der Vlerk , p. 10.
1932 *Nummulites variolarius* Lamarck, 1804 — Doornink, p. 287.
* 1934 *Camerina borneensis* Caudri, p. 56.
* 1934 *Camerina taballarensis* Caudri, p. 59.

Material — Numerous specimens including 8 equatorial and 3 axial sections of A-forms, plus 4 equatorial sections of B-forms from Sungai Taballar (Borneo, RGM 19126-19141).

A- form — Test involute, small, diameter 2.2-3.2 mm, thickness 1.5-2.1 mm, D/T= 1.5. In the centre of the test, a cluster of pillars (usually fewer than 10) forms an umbo, with 24-25 straight septal filaments radiating towards the margin (often becoming slightly curved near the margin). In rare cases some pillars that are arranged in a spiral over the polar region. Whorls open gradually (Fig. 6.17) and are slightly tighter than in *P. thalicus* Davies. Thick marginal cord, about 0.3-1 × chamber height. Chambers rectangular with rounded top, on average 1.25 × as high as broad. Septa straight, thick with a clearly visible intraseptal canal oriented obliquely to the marginal cord. Proloculus 0.35-0.5 mm in diameter.

Whorl number	1	2	3	4
Radius (mm)	0.62	0.97	1.37	1.88
Chambers	9	18	23	–

B-form — Test lenticular, involute, last whorl partly evolute. Diameter up to 5 mm, thickness 2.3 mm, D/T = 2. Chamber walls in the last whorl are almost parallel, with a well-developed marginal cord. Large polar pillar and several smaller ones, arranged more or less in a spiral over the centre of the test. Spire opening gradually (Fig. 6.17). Marginal cord about 0.2 × chamber height in axial section. Septa straight with an intra-septal canal clearly visible. Chambers are about 1.5-2 × higher than broad and have rounded tops.

Whorl number	1	2	3	4	5	6	7	8
Radius (mm)	0.15	0.3	0.5	0.8	1.2	1.6	2.1	2.6
Chambers	8	9	13	19	25	33	34	40

Remarks — The A-form differs from *Ranikothalia nuttalli* Davies in having thicker and straighter septa, higher chambers, tighter coiling and a larger proloculus. The B-form is characterised by its tighter spire, smaller number of chambers per whorl, less elongate chambers and a marginal cord which does not stand out in relief as strongly as is typical in B forms of *R. nuttalli*.

There is a lot of confusion about the occurrence of this species outside the Indian subcontinent, especially in Indonesia. Van der Vlerk (1929) identified *Nummulites nuttalli* (B-form) and *N. thalicus* (A-form) from East Borneo. Davies described the B-form of *N. nuttalli* and the A-form *N. thalicus* from India. Later these were considered a species pair and Caudri (1934) used *N. nuttalli* as the type species of the genus *Ranikothalia*.

The A-form of *R. nuttalli*, as given by Racey (1995) is more similar to *Palaeonummulites thalicus* Davies, suggesting that *R. nuttalli* and *P. thalicus* Davies do not belong to the same genus (Racey, 1995). The same pairing is also reported to occur in samples from E Borneo by van der Vlerk (1929).

Caudri (1934) restudied van der Vlerk's samples from Borneo and concluded that the B-forms were different from *R. nutalli* in being smaller and more tightly coiled and described these as *Camerina (= Nummulites) borneensis* Caudri. Adams (1970) restudied paratypes of *R. nuttalli* (from India) and concluded that these are different from those found in Indonesia, and agreed with Caudri (1934) in erecting *R. borneensis*.

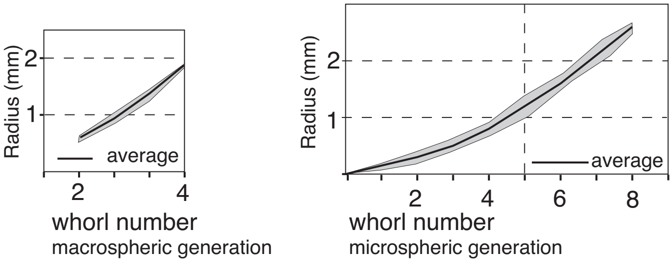


Fig. 6.17. Coiling diagram of *Palaeonummulites taballarensis* (Caudri).

After comparing the figured specimens of van der Vlerk and other specimens of *Ranikothalia* B-forms in Racey (1995), Caudri (1934) and Davies (1927), and studying topotypes of *C. borneensis*, we conclude that the B-form illustrated by van der Vlerk is not *Ranikothalia nuttalli* and should be reassigned to *Palaeonummulites*.

Caudri (1934) reassigned the A-form from Borneo (*N. thalicus* Davies sensu van der Vlerk) to *Camerina (= Nummulites) taballarensis* whilst Adams (1970) agreed with the original identification of *N. thalicus* by van der Vlerk. Racey (1995) re-examined the records of *R. nuttalli* and considered the A-forms of *C. borneensis* (including *C. taballarensis*) as synonymous with *R. nuttalli*. However, because of the larger proloculus and tighter coiling of the Indonesian specimens, we do not agree that *C. taballarensis* (the A-form accompanying *C. borneensis*) is the same as *P. thalicus* Davies. Thus, we conclude that both microspheric and macrospheric specimens should be assigned to a species other than *P. thalicus*. Although Caudri (1934) described *C. borneensis* first, it is more appropriate to use the name *P. taballarensis* Caudri (published in the same publication, but some pages later), since most of the species are macrospheric forms and the microspheric forms are extremely rare. From the above it is clear that the only illustrated and documented record of *Ranikothalia* from the Indonesian region is erroneous and that these specimens should be reassigned to *Palaeonummulites*.

In the type sample from Sungai Taballar one specimen (an axial section) has been found that has a much smaller proloculus and more pronounced pustules extending over a larger part of the test. It resembles *P. cuvillieri* Sander, 1962 from Oman (Racey, 1995), a species that is abundant in India in strata of similar age (Saraswati *et al.*, 2000). Since it is only one specimen, and we have not been able to find more specimens to obtain equatorial sections, consequently we do not report *P. cuvillieri* from Indonesia in this paper.

Geographic distribution — Only known from Borneo (Sungai Taballar; van der Vlerk, 1929) and Sumba (Caudri, 1934). The fact that the only previously published records of *Ranikothalia* from the Indonesian region are now reassignable to a different genus (i.e., *Palaeonummulites*) has important palaeobiogeographic indications in that it lends support to the idea that the genus *Ranikothalia* is restricted to the Indian Subcontinent and the Middle East (see also Racey, 1995; Haynes *et al.*, in press).

Stratigraphic range — In Borneo this species is found together with *P. beaumonti* and *P. variolarius* indicating a middle to late Lutetian age. The stratigraphic range in Indonesia is interpreted as Lutetian.

Palaeonummulites variolarius (Lamarck, 1804)

Fig. 6.18; Pl. 11, figs. E-H.

* 1804	*Lenticulites variolaria* Lamarck, p. 187.
1829	*Nummularia variolaria* (Lamarck, 1804) — Sowerby, p. 76.
1875	*Nummulina variolaria* Lamarck, 1804 — Sowerby, p. 533.
* 1891	*Nummulites bagelensis* var Ib, IIc and IId Verbeek, p. 67.
1896	*Nummulites bagelensis* var. Ib, IIc and IId Verbeek, 1891 — Verbeek & Fennema, p. 1101.

1905 *Nummulites variolarius* Sowerby, 1829 — Deprat, p. 495.
1912b *Camerina variolaria* (Sowerby, 1829) — Douvillé, p. 256.
1929 *Nummulites variolarius* Sowerby, 1829 — van der Vlerk, p. 21.
1929 *Nummulites bagelensis* Verbeek, 1891 — van der Vlerk, p. 18.
* 1932 *Camerina semiglobula* Doornink, p. 292.
1932 *Camerina mamilla* Fichtel and Moll, 1798 — Doornink, p. 290.
1934 *Camerina bagelensis* Verbeek — Henrici, p. 25.
1934 *Camerina variolaria* Sowerby — Henrici, p. 27.

non
1932 *Nummulites variolarius* (Lamarck, 1804) — Doornink, p. 287-288
(= *P. taballarensis* Caudri)

Material — More than 40 specimens, including 10 equatorial and 5 axial sections of both A- and B-forms from Nanggulan (Central Java, RGM 20129). Over 40 specimens, including 10 equatorial and 5 axial sections of both A and B-forms from Ralla (Sulawesi, RGM 20130). Twenty specimens including 5 equatorial sections of A-forms and 10 equatorial sections of B-forms from Sungai Seilor and Taballar (RGM 19076-19105).

A-form — Small, biconical test up to 2.5 mm in diameter and up to 1.7 mm thick, diameter/thickness ratio average of 1.6. Septal filaments straight to S-shaped, radiating from a polar pillar occasionally developing secondary filaments. In equatorial section, tightly coiled, comprising up to 5 whorls that open very regularly (Fig. 6.18). Chambers as high as broad or slightly higher than broad. Septa perpendicular to marginal cord, strongly curving backwards in their distal part. Marginal cord about 1/5 or less of the chamber height. In axial section a clear umbilical pillar is present. Proloculus very small, 0.05-0.15 mm in diameter.

Whorl number	1	2	3	4	5
Radius (mm)	0.2	0.43	0.72	0.95	1.25
Chambers	7	11	13	16	20

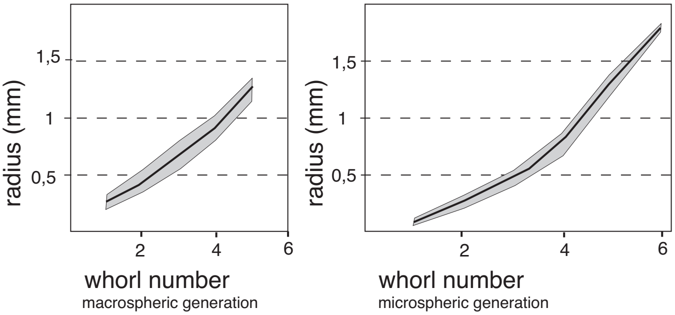


Fig. 6.18. Coiling diagram of *Palaeonummulites variolarius* (Lamarck).

B-form — Similar to the A- form, though slightly larger, up to 4 mm in diameter and up to 2.5 mm thick with D/T of 2.1 on average. Septal filaments straight to S-shaped with polar pillar. In equatorial section comprises of up to 6 whorls, that open gradually (Fig. 6.18). Marginal cord quite thick, irregular. Septa oblique and curved in their distal part. Chambers in the first whorls higher than broad, isometric in the last whorls. Marginal cord 1/6 of the chamber height. In axial section the polar pillar is more pronounced than in the A-form.

Whorl number	1	2	3	4	5	6
Radius (mm)	0.1	0.30	0.45	0.75	1.2	1.8
Chambers	8	12	14	18	26	30

Remarks — This species may be confused with *P. globulus* (Leymerie) which Blondeau (1972) suggests was the precursor of *P. variolarius*. Both A and B-forms are smaller than *P. globulus* and in axial section the polar pillar is less pronounced than in *P. globulus*. Furthermore, the A-form of *P. variolarius* is more tightly coiled and has fewer chambers in each whorl than *P. globulus*. The B-form of *P. globulus* has more whorls and is much larger than the B-form of *P. variolarius*.

The taxonomic status of this species is unclear. It was described by Lamarck (1804) without an accompanying illustration or type locality. Lamarck (1804) placed it in the genus *Lenticulites*, although he had erected the genus *Nummulites* just three years earlier (Lamarck, 1801). Sowerby (1829) who referred in his record to the description of Lamarck (1804) was the first to figure this species. Blondeau (1972) mentioned *P. variolarius* from a broad range of localities including England, the Paris Basin, the Aquitaine basin, northern Africa, the former Soviet Union and New Caledonia.

Specimens of *N. bagelensis* Ib, IIc and IId of Verbeek in the NNM collections all belong to this species, as do specimens identified as *N. bagelensis* from Borneo by van der Vlerk (1929).

Geographic distribution — Indonesia: widely distributed throughout Indonesia, Java, Borneo, Timor, Sulawesi, Nias, and Sumba. Elsewhere: only rarely included in studies dealing with the Nummulitidae (see above). Blondeau (1972) reports it from England, France, Belgium, the former Soviet Union, Egypt, Somalia, Mozambique and New Caledonia.

Stratigraphic range — The oldest occurrences are in association with *N. djokdjokartae*, or P12, whilst the youngest record on Java is from the *Discocyclina* layers in the Nanggulan section, dated as later Middle Eocene (P12, late NP16), lowermost Bartonian (Lunt, 2000a,b). On Sulawesi (Ralla) it is found in P15-P17 sediments, and in Timor in P16 sediments. Blondeau (1972) suggested a range from the Lutetian to Bartonian.

The stratigraphic range in Indonesia is estimated to be Middle-Late Eocene (Ta3-Tb: middle Lutetian — Priabonian).

Genus *Planocamerinoides* Cole

Type species — *Nummularia exponens* Sowerby, 1840.

Diagnosis — Test planispiral, compressed often with an inflated polar region and marked central depression; spire tightly and uniformly coiled, many whorls, quasi –evolute, i.e. alar prolongations pinched off though spiral sheet extends towards the poles; opening rate less than 1.5d; chambers regular more than 1.5 × as high as broad, marginal cord finely developed and generally <1/4 chamber height. In axial cross-section chambers are triangular, often increasing in height towards the periphery. A pronounced difference in diameter between the B-form and the A-form generation is usually noted in larger Eocene species.

Stratigraphic range — Common from the Late Palaeocene to Middle Eocene.

Discussion — *Assilina* d'Orbigny, 1826 (type species *Assilina depressa* d'Orbigny, 1850) differs from *Planocamerinoides* in having a completely evolute, flat to flatly lenticular test, often with a central depression, a more rapidly opening spire (approximately 2d) spire and a thicker marginal cord.

The taxa described below have traditionally been assigned to *Assilina* which was broadly divided by Schaub (1981) into two main groups, the *A. exponens* and *A. spira* groups. All forms described below from Indonesia have been reassigned to *Planocamerinoides* as defined above following Haynes (1988) and Haynes *et al.* (in press). *Planocamerinoides* broadly encompasses most of the species previously assigned to the *Assilina exponens* group by Schaub whilst *Assilina* is used mainly for species previously assigned to the *Assilina spira* group by Schaub (1981).

Planocamerinoides is a rare genus in Indonesia, confined to a limited number of localities, and usually occurs in indurated solid carbonates, making it difficult to isolate and describe. One of the species discussed herein is included though the authors have not seen specimens, but the unique morphology warrants recognition (*P. umbilicata* Rutten *in* van Waterschoot van der Gracht).

Another species that, if proven valid, should be called *P. discoidea* (Caudri) is not included because of its current uncertain status. Specimens similar in appearance to *P. discoidea*, described by Caudri from Sumba, have also been found on Borneo (as *Assilina granulosa* d'Archiac var *minor* Heim; Yabe, 1921) and at Kali Worowari (Java). It is a small, macrospheric *Planocamerinoides* without umbonal depression but with parallel sides. It co-occurs with *P*. spec. 1 and it probably should be assigned to *Operculina* instead of *Planocamerinoides*.

Planocamerinoides orientalis (Douvillé, 1912b)

Fig. 6.19; Pl. 12, fig. F.

* 1912b *Assilina orientalis* Douvillé, p. 263.
1921 *Assilina orientalis* Douvillé, 1912b — Yabe, p. 105.
1934 *Assilina orientalis* Douvillé, 1912b — Caudri, p. 83.
cf. * 1953 *Assilina laminosa* Gill, p. 76-86.

cf. *1953 *Assilina sublaminosa* Gill, p. 76-86.
cf. 1999 *Assilina laminosa* Gill — Akhtar & Butt, p. 136.

Material — One axial section of an A-form from Nias (holotype) and several oblique sections from the same locality (RGM 11879).

A-form — Test inflated lenticular with a sharp edge, diameter 5-5.8 mm, thickness 1.5-2.2 mm and D/T = 1.5-2.5. Some specimens show a poorly developed granulated, umbo (e.g., Caudri, 1934, pl. II, fig. 1). The lateral surface of the test is generally smooth, while radiate, slightly curved septa are visible as a septal ridges.

In equatorial section (Doornink, 1932, text-figs 17-18) spire tight, opening very gradually. Chambers equidimensional, septa perpendicular, slightly recurved towards their tops. Marginal cord 1/4 of chamber height. In axial section, a very thick spiral sheet extends towards the poles and coarse pillars occur in the central part of the test which reach the lateral surface of the test. Chambers in axial section have a strongly tapering, arrow head shape. Proloculus 0.15-0.25 mm in diameter.

Whorl number	1	2	3	4	5
Radius (mm)	0.5	0.9	1.4	1.9	2.3
Chambers	9	21	24	?	?

B-form — Not found.

Remarks — Easily recognised in axial section by the very robust appearance with thick spiral sheet and coarse pillars in the polar region. The Indonesian specimens are larger than *P. sublaminosa* (Gill, 1953), from the lower Eocene of Pakistan (Gill, 1953; Akhtar & Butt, 1999), which reaches only 2-3.6 mm diameter and are otherwise similar. *P. sublaminosa* may be the predecessor of *P. orientalis*.

Geographic distribution — Indonesia: Borneo, Java, Nias and Sumba. Elsewhere: NW Pakistan (Gill, 1953).

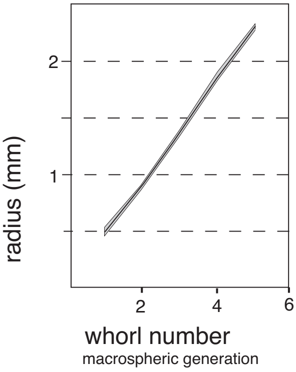


Fig. 6.19. Coiling diagram of *Planocamerinoides orientalis* Douvillé.

Stratigraphic range — Occurs with *P. beaumonti* on Nias (Douvillé, 1912b) with *Alveolina ovicula* and *P. beaumonti* on Sumba (Caudri, 1934); with *Palaeonummulites taballarensis* and *Discocyclina javana* (small form) on Sumba (Caudri, 1934), and with *P. pengaronensis* on Borneo (Yabe, 1921). The suggested range for this species based on the associated microfauna in Indonesia is Letter Stage Ta, Middle Eocene, middle to upper Lutetian to possibly basal Bartonian.

Planocamerinoides sp. 1
Fig. 6.20; Pl. 12, figs. G-K.

1896 *Assilina spira* de Roissy, 1805 — Verbeek & Fennnema, 1896; p. 1102-1103.
1896 *Nummulites (Assilina) leymeriei* d'Archiac & Haime, 1853 — Verbeek & Fennema, p. 1103-1104.
1912b *Assilina granulosa* d'Archiac, 1847 — Douvillé, p. 263.
cf. 1921 *Assilina granulosa* d'Archiac var *minor* Heim- Yabe, p. 105.
1932 *Assilina granulosa* d'Archiac — Doornink, p. 301-303.
1932 *Assilina spira* de Roissy — Doornink, p. 303.
1934 *Assilina* spec. *granulosa-exponens* (pars) — Caudri, p. 34-39.

Material — Rare species, 5 specimens from Jiwo, including 2 equatorial sections of B-forms and 1 of an A-form (RGM 20214).

A-form — Test lenticular to flattened lenticular with a subrounded periphery, diameter 5-7 mm, thickness 1.5-2 mm, D/T = 3.2-4.0. Granules in central part of the test which is occasionally slightly depressed. Septal ridges are visible in relief in the outer part of the test. In equatorial section comprises up to 4.5 whorls of similar height. Chambers regularly spaced of similar length in all whorls, slightly higher than broad. Marginal cord 1/3-1/4 of chamber height. In axial section quasi-evolute with the alar prolongations pinched off by the spiral sheet which extends towards the poles in all whorls. Lateral sides of the test are parallel, without a polar depression. Proloculus 0.3-0.55 mm in diameter.

Whorl number	1	2	3	4
Radius (mm)	1.1	1.6	2.1	2.7
Chamber	11	20	24	32

B-form Test flat with a sharp periphery, with spire and septa visible as ridges on the test surface. Test diameter up to 20 mm, thickness 1.5-2.5 mm and D/T = 4.8-5.2. Polar region finely pillared. In equatorial section the spire opens regularly, and has rectangular chambers which are 1.5-2 × as high as broad. Septa straight, perpendicular to slightly inclined, arcuate in the outermost part. Marginal cord 1/4 of chamber height. In axial section the spiral sheet extends towards the poles, whilst the alar prolongations are pinched-off. Lateral surface of the test parallel, without a polar depression.

Whorl number	1	2	3	4	5	6	7	8	9	10
Radius (mm)	0.2	0.5	0.7	1.1	1.5	2.2	2.8	3.7	4.9	6.3

Remarks First reported by Verbeek & Fennema (1896) as *Nummulites (Assilina) leymeriei* (A-form), which was assigned to *Assilina granulosa* by Doornink (1932). Schaub (1981) discussed the synonymy of *Assilina laxispira* De la Harpe, 1926, which included *Assilina granulosa*. However, *A. laxispira* is fully evolute and the spiral sheet is pinched off on the previous whorl. In the Indonesian specimens labelled as *Nummulites (Assilina) granulosa* and figured by Verbeek & Fennema (1896, fig. 93), the spiral sheet is not pinched off and clearly reaches towards the poles. The Indonesian specimens should therefore be reassigned to *Planocamerinoides*.

The drawings and descriptions of Verbeek & Fennema (1896) represent the only data available on the microspheric generation of this species in Indonesia. In both figures and description it is clear that this species, originally recorded as *Assilina spira*, should be reassigned to *Planocamerinoides*. *Assilina spira* has no extending spiral laminae and is fully evolute, thus the Indonesian specimens should be reassigned to another species. All measurements and figures resemble *P. exponens*, though the size is in the lower part of the range given by Racey (1995). Schaub (1981) suggests that *P. exponens* is replaced by *P. cancellata* in the eastern Tethys. However, *P. cancellata* is even larger than *P. exponens* and more tightly coiled (Racey, 1995). The Indonesian specimens are rather small and have a slightly looser spire than *P. exponens*. Some of the specimens shown by Caudri (1934) match this species, for example her figures 6 and 7. At all localities the A- and B-forms occur together and are therefore inferred to represent a microspheric-megalospheric pair.

Geographic distribution — Indonesia: Java, Borneo, Nias and Sumba.

Stratigraphic range — Occurs with *Nummulites javanus* at some Middle Eocene localities in East and Central Java correlating to the late Lutetian or early Bartonian stages.

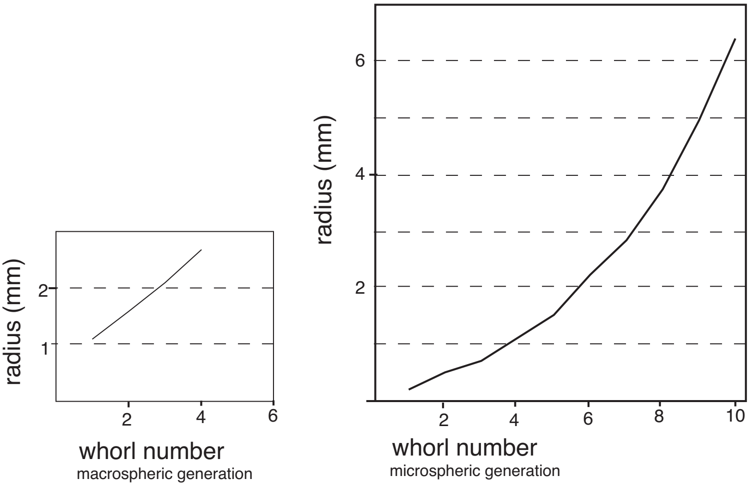


Fig. 6.20. Coiling diagram of *Planocamerinoides* spec. 1.

Planocamerinoides umbilicata (Rutten *in* van Waterschoot van der Gracht, 1915)
Fig. 6.21; Pl. 12, figs. L-P.

* 1915 *Nummulites (Assilina) umbilicata* Rutten *in* van Waterschoot van der Gracht, p. 60.
1934 *Assilina* spec. *granulosa-exponens* type (pars) — Caudri, p. 34.

non:
* 1938 *Assilina umbilicata* de Cizancourt, p. 23.

Material — No specimens were available for study and consequently the description below is based on the drawings provided by Rutten in van Waterschoot van der Gracht (1915). On p. 60 (ibid.) an equatorial and an axial section of a microspheric form and an axial section of a macrospheric form are shown (reproduced as Pl. 12 figs. M-P).

A-form — Not mentioned in the type description, apart from the remark that sometimes the first chamber is rather large. However, a figure of an A-form was provided (p. 60, fig. 6.36) on which the following description is based.

Test lenticular with a polar depression and sharp periphery, diameter cannot be measured, thickness 2.1 mm, D/T unknown. The spire consists of six fairly tightly coiled whorls. In axial section the spiral sheet extends over the previous whorl, though after the third whorl, the spiral sheet does not reach the central part of the test. Proloculus 0.25 mm in diameter.

Whorl	1	2	3	4	5	6
Radius (mm)	0.3	0.7	1.1	1.7	2.4	2.8

B-form — Test lenticular to flattened lenticular with a distinct polar depression and sharp periphery, diameter up to 11 mm, thickness up to 2.5 mm and D/T = 4.4. Granulated in centre, with granules aligned along straight, radiating (septal) ridges in the peripheral part of the test. In equatorial section very uniformly coiled, with chambers

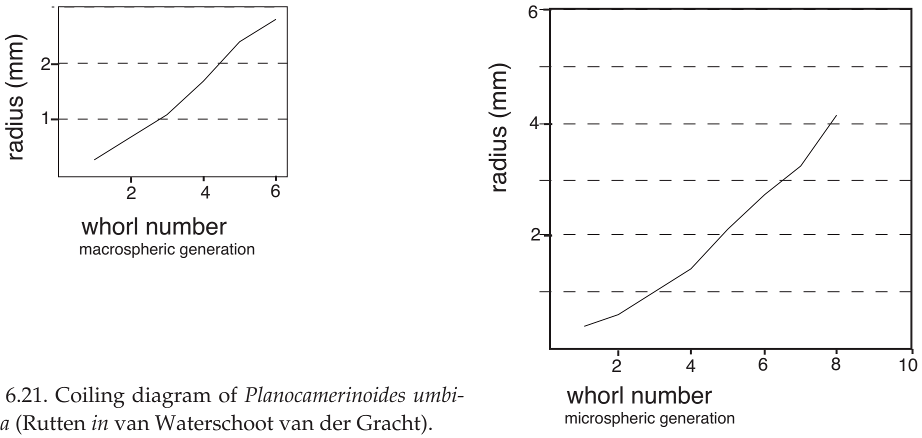


Fig. 6.21. Coiling diagram of *Planocamerinoides umbilicata* (Rutten *in* van Waterschoot van der Gracht).

2 × broader than high to equidimensional. Septa straight, perpendicular. Up to 9 whorls in figured specimens and 11 whorls in the written description.

Whorl	1	2	3	4	5	6	7	8
Radius (mm)	0.4	0.6	1	1.4	2.1	2.7	3.2	4.1
Chambers	8	17	22	24	31	34	37	38

Remarks — Apart from the description by Rutten (*in* van Waterschoot van der Gracht, 1915), little is known about this species. The clear umbilical plug is not seen in any other Indonesian species of *Planocamerinoides* and it might well be a distinct species. Some of the specimens described by Caudri (1934) match the description of this species though she did not provide any illustrations against which this can be confirmed. Caudri (1934) discussed the taxonomy of Indonesian assilinids, and concluded that the specimens from Java and Sumba probably comprised a group of very similar species. The main characters she used were; the test shape in axial section, chamber shape and, number of chambers in each whorl. Her primary conclusion was that none of the specimens studied could be matched with *P. exponens* or *A. granulosa* (= *A. laxispira*) and that these species could not therefore be identified in the Indonesian specimens, a conclusion supported by the present study.

In 1938, de Cizancourt described the A and B-form pair *Assilina umbilicata-A. subumbilicata* from the Early Eocene of Afghanistan. As Schaub (1981) discussed, the species of Rutten (*in* van Waterschoot van der Gracht, 1915) has priority and the species described by de Cizancourt (1938) should be called *P. subumbilicata* (de Cizancourt, 1938). It has many characteristics in common with *P. umbilicata,* is notably smaller with a maximum diameter of about 5.5 mm in the microspheric generation.

Planocamerinoides umbilicata Rutten falls in the group of *P. reicheli* as described by Schaub (1981, p 215-218), which is characterised by a spiral sheet which extends over the previous whorl, but does not reach the centre of the test. None of the species in this group figured by Schaub (1981) show such a clear umbilical depression as seen in *P. umbilicata*. This very characteristic test-shape and coiling mode is the main reason why we regard this species as a valid species, without seeing any new specimens.

Geographic distribution — Indonesia: Sulawesi and probably Sumba.

Stratigraphic range — In Sulawesi this species co-occurs with *P. variolarius* (van Waterschoot van der Gracht, 1915) whilst in Sumba it was found in association with *Nummulites beaumonti* and *Assilina orientalis* (Caudri, 1934) suggesting a Middle Eocene, Ta_3 age, late Lutetian age).

Stratigraphy

The occurrence of a certain species is not always due to its stratigraphical range, but due to facies control. Although contemporaneous, it is remarkable that *N. djokdjokartae* and *N. javanus* never have been found co-occurring in one sample. A range chart for the taxa in this study is given in Figure 6.18 and has been composed from the co-occurrence of species in the various sections shown in Figure 6.5. Independent age dermination of some localities using nannoplankton, planktonic foraminifera, dinoflagellates and, in the Oligocene stable strontium isotopes have been used in this age calibration. The species limits in Figure 6.18 reflect current knowledge and are likely to change as more data become available. As with the occurrence of studied sequences (Fig. 6.5), the boundaries are chosen to coincide with the boundaries of the Letter Stages, as units of faunal stability. The interval of greatest uncertainty is the Ypresian to lower Lutetian due mainly to a lack of sequences containing larger foraminifera. However, modern geological models (cf. Netherwood, 2000) suggest most sedimentary basins in Southeast Asia only came into existence from the middle Middle Eocene onwards (middle Lutetian) so lower Lutetian and older sections may not be present, or rare and would be overlain by a major unconformity. In East Indonesia / Papua New Guinea where there are older Eocene and Paleocene sedimentary rocks, but they are invariably in deep marine facies and tend to lack larger foraminifera.

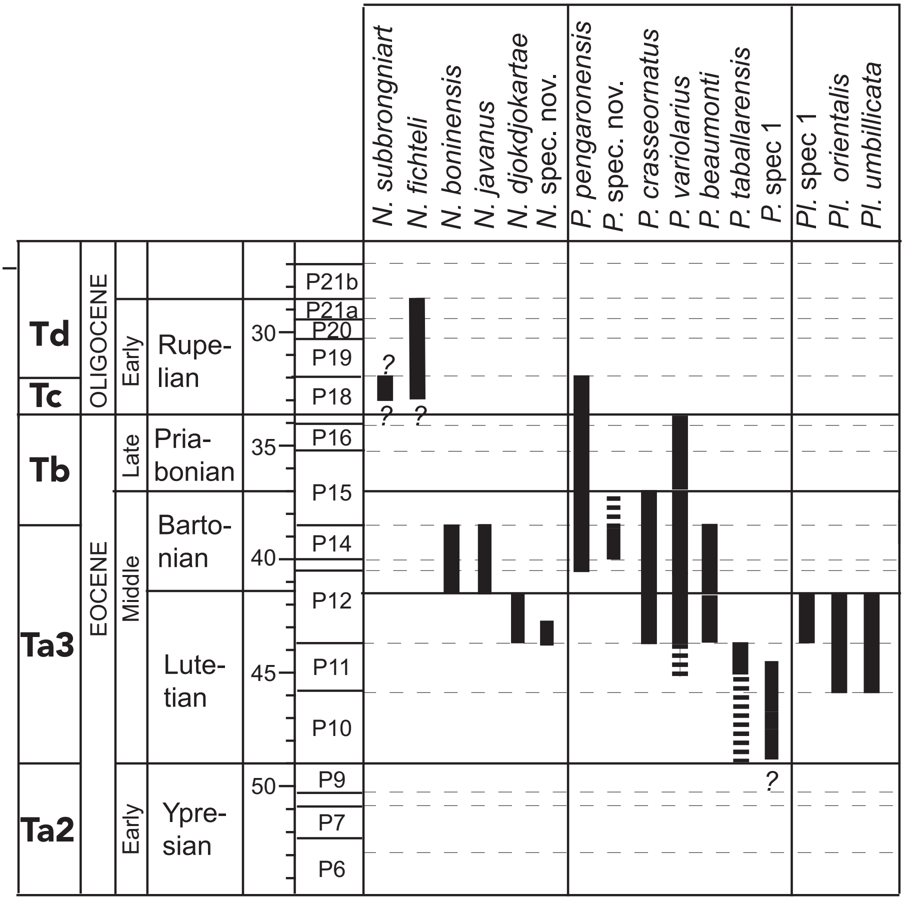


Fig. 6.22. Stratigraphic ranges of the species of the genera *Nummulites, Palaeonummulites* and *Planocamerinoides* in Indonesia.

Conclusions

1. Having reviewed available records of *Nummulites, Assilina* and *Ranikothalia* from the Indonesian Archipelago including the sampling and analysis of several additional localities it is concluded that seven species of *Nummulites*, seven of *Palaeonummulites* and three of *Planocamerinoides* are valid. These are redescribed and illustrated, many for the first time.

2. Many of the taxa described and illustrated herein have their age ranges significantly refined through the integration of new data from associated planktonic foraminifera, nannofossils, dinoflagellates and Sr-isotopes (in the Oligocene only). These data have been integrated to produce a revised zonation which is shown in Fig. 6.22.

3. Far fewer Paleogene nummulitids are known from the Indonesian Archipelago than from the western Tethys. Moreover, unlike the western Tethyan region, there are no verifiable records of nummulitids older than Middle Eocene in the Indonesian Archipelago. Published records of *Nummulites*, *Assilina* and *Ranikothalia* suggested that up to 70 species may be present. After reviewing the records, we conclude that only about 16 of these are valid and we have tabulated the various reinterpretations of the "original" 70 taxa by geographic area in Tables 6.1-6.8.

4. The Indonesian *Nummulites* and *Palaeonummulites* show more limited morphological variation than their coeval forms from the western Tethys. For example, the maximum size of the Middle Eocene Indonesian forms is about 45 mm, whilst in the western Tethys some species attain test diameters of up to 120 mm (Schaub, 1981). Tripartition of the spire and reversals in the direction of coiling, features which are relatively common in western Tethyan Middle Eocene species, have not been observed in the material studied. Intercalatory whorls (common in Middle Eocene Tethyan species) were only rarely observed in Indonesian material, being noted in *N. djokdjokartae*, *N.* nov. spec. and *N. boninensis*. Likewise, the species of *Planocamerinoides* recorded from the region show far lower diversity and morphological variation than their western Tethyan counterparts.

5. Several species previously described as *Nummulites* are reassigned to *Palaeonummulites.* These include *N. beaumonti, N. crasseornatus*, *N. pengaronensis* and *N. variolarius. Palaeonummulites taballarensis* was previously assigned to *Ranikothalia,* whilst one new species of *Palaeonummulites* is described. The first record of *Nummulites sensu stricto* in Indonesia is in the mid Middle Eocene, equivalent to the middle Lutetian stage.

6. All Indonesian species previously assigned to the genus *Assilina* from the Indonesian Archipelago, for which material and/or illustrations were available, are reassigned to *Planocamerinoides*. It is tentatively concluded that *Assilina sensu stricto* (as defined in Haynes *et al*., in press) is not therefore present in the Indonesian Archipelago and is therefore restricted to the Mediterranean, Middle East and Indian subcontinent. This may reflect absence of strata of pre-mid Middle Eocene age in the region, as mentioned above.

7. Records of *Ranikothalia,* especially of the species "*nuttalli*" from the Indonesian Archipelago are considered suspect and it is suggested that the genus is not in fact present in the region; previous records are reassigned to *Palaeonummulites*. *Ranikothalia* is therefore considered, restricted, to the Indian subcontinent and the Middle East (see Haynes *et al*., in press), for stratigraphic rather than palaeogeographic reasons.

7. Palaeogene larger foraminiferal generic diversity in southeast Asia as compared to the western Tethys

Introduction

Scleractinian corals, several families of benthic molluscs and other taxa living in shallow marine, tropical conditions have their highest current diversity in the Indo-West Pacific (IWP) region (Paulay, 1997). Diversity within the IWP region peaks in Indo-Malaysia, is relatively even across the Indian Ocean, and falls gradually eastward across the western and central Pacific (Paulay, 1997). Other, less diverse, faunal provinces are the East Pacific, West Atlantic (including the Caribbean) and the East Atlantic. Of these, the West Atlantic is the most diverse (Paulay, 1997). Larger symbiont-bearing foraminifera also show this biogeographical pattern (Hottinger, 1983; Langer & Hottinger, 2000). The main faunal provinces are the Caribbean and the IWP. Some genera/species have a circum-tropical distribution (e.g., *Heterostegina depressa*, *Sorites orbiculus)*, while others are restricted to the Caribbean (e.g., *Cyclorbiculina compressa*; Langer & Hottinger, 2000). The Caribbean Province houses only about 60% of the number of genera compared to the IWP. Within the IWP, there are faunal differences between the West Pacific (including South Japan, the Philippines and Indonesia) and East Africa (including the Red Sea and the East African coast). For example, the genus *Calcarina* occurs in the IWP, but is absent from East Africa and the Red Sea, whilst for *Heterocyclina tuberculata* holds the opposite.

Three parameters determine the occurrence of larger foraminifera, temperature, oligotrophy and life history. Symbiosis is only profitable (for both host and symbiont) in high temperatures (Hallock, 1987; Hollaus & Hottinger, 1997). The distribution of larger symbiont-bearing foraminifera is restricted to a world-wide climatic belt bordered by the 15-20°C minimum temperature range (Adams *et al.*, 1990; Langer & Hottinger, 2000), similar temperature limits have been observed for zooxanthellate corals (Adams *et al.*, 1990; Veron, 1995). All species have a different sea surface water temperature limit in the coldest winter month, the area showing highest diversity is the area with the highest sea surface temperature (Langer & Hottinger, 2000). *Amphistegina* has the largest tolerance (>14°C in the coldest month), while *Operculina heterosteginoides* and *Alveolinella quoyii* have the most limited temperature tolerance (>26°C in the coldest month).

The biogeographic distribution of living larger foraminifera is controlled by the extent of oligotrophic watermasses (Langer & Hottinger, 2000). The geometric delimitation of faunal provinces does not reflect an important role of the surface currents as the main agents for the distribution and propagation of shallow benthic species. More over, the main faunal provinces are now bounded by the extent of landmasses and upwelling zones (Langer & Hottinger, 2000). On a smaller scale, the input of terrestrial run off affects the distribution patterns of species on a regional or local scale (Langer & Hottinger, 2000; Chapter 3, above).

Larger foraminifera are K-strategists with relatively long life-cycles that favour stable conditions (Hallock, 1987; Hottinger, 1990; Chapter 3, above). Larger foraminiferal species richness is highest in oligotrophic regions of the modern day oceans. However, the largest part of shallow marine seas (<100 m depth) are coastal areas influenced by terrestrial run off. Going offshore there is a gradient from eutrophic to oligotrophic and also a gradient in species diversity of larger foraminifera (Chapter 3, above). The influence of seasonal changes in environmental parameters is also affected by distance to shore. Stable oligotrophic conditions allow larger foraminifera to become highly specialised to specific levels of light availability (Hallock, 1987). In less oligotrophic conditions, these specialised forms disappear due to habitat loss and increased seasonal variability (Hallock, 1987; Chapter 3, above). Larger foraminifera tend to adapt to increasing water depth by increasing their surface area to volume ratio. Large flat, deep living species have very long generation times (Purton & Brasier, 1999) and are therefore extremely vulnerable to periods of adverse environmental conditions. The deep and long living species are generally absent in areas with more seasonal influences in either nutrient availability (transparency) or hydrodynamic energy (Hallock, 1987, 1988; Chapter 3, above).

The broadscale distribution of larger foraminifera is controlled by the same limiting environmental parameters as zooxanthellate corals (Adams *et al.*, 1990) and in modern day distribution patterns can in part be explained by environmental conditions (Paulay, 1997). However, as for the examples of Wilson & Rosen (1998) and Renema (Chapter 4, above) showed in fossil respectively Recent setting, scleractinian corals and larger benthic foraminifera are found in different facies types on reefs and carbonate platforms.

In both groups, the Indo-West Pacific (IWP) is the richest in the world, followed by the Caribbean; hardly any larger benthic foraminifera or zooxanthellate corals are found in the Mediterranean. Within the IWP diversity is highest in the Indo-Malayan area (Paulay, 1997). This diversity pattern can in part be explained by modern day conditions. The surface area of reefs and carbonate platforms, that is the biotope in which larger foraminifera production and preservation potential is highest, in the Indo-Malayan region is the largest in the world. Furthermore, oceanographic conditions differ markedly between the regions, and constrain community structure and habitat diversity (Hallock, 1988; Hubbard, 1997).

However, present day conditions alone can not explain all differences in taxonomic diversity and uniqueness. Biogeographical patterns are the result of three categories of biological processes, related to, respectively, maintenance, distributional change and origination (Rosen, 1988). Maintenance are those processes by which an organism maintains its presence in a particular area. Extinction can be seen as the failure of an organism to maintain itself. Distributional change represents those processes by which an organism survives in response to changing environmental conditions by shifting its geographical range, for example, in following the most suitable habitat. Origination is related to the evolution of new taxa (Rosen, 1988). The larger the geographical and stratigraphical scale, the more influence tectonic, climatologic and oceanographic changes have on the observed patterns. Changing positions of landmasses can create or remove barriers, whilst climatologic changes directly affect the range of latitudes at which larger foraminifera can be expected to occur. However, within this zone differences in seasonality and rainfall (among other parameters) influence the distribution of taxa. Therefore, palaeogeographic and palaeoceanographic changes in the geologic history should be considered as well in order to understand present day biogeographical patterns.

Larger foraminifera, which are essentially circumtropical in distribution, have long played an important role in discussions on Cenozoic climate optima. Changes in latitudinal range are easily recognised. Generic diversity is greatest in the tropics and decreases rapidly when, in the coldest months of the year sea-surface temperature (SST) falls below 25°C; larger foraminifera disappear when temperatures drop below 16°C (Adams *et al.*, 1990; Adams, 1992; Langer & Hottinger, 2000). Analogous to the Recent distribution, expansions and contractions in the latitudinal range of larger benthic foraminifera, have been used to indicate epochs with relatively high (sub)tropical SST (Adams *et al.*, 1990; Adams, 1992; McGowran & Li, 2000). For regional comparison of diversity patterns, however, Palaeocene-Eocene records are relatively rare from Indo-Malaysia, and the Neogene, especially the Middle-Late Miocene has been understudied in previous work (Adams *et al.*, 1990; Adams, 1992).

The configuration of reefs as found in the present-day ocean did not start to develop before the Oligocene. During most of the Palaeogene, reefs mainly occupied shallow epi-continental seas, whilst today they are concentrated along the western side of oceanic basins along continental margins (Kiessling *et al.*, 1999). Larger benthic foraminifera occur both on the reef *sensu stricto* and in fore and back reef settings, as well as on carbonate shelves lacking reefal structures (Arni, 1965; Reiss & Hottinger, 1984; Chapter 3, above). Preservation potential is higher for species living around the reefs on carbonate platforms (or even carbonate platforms without reefs) than for larger foraminifera living on the reef. Reefs, as biologically produced rigid structures that stand topographically high above their surroundings, increase the habitat diversity and thus the number of species (genera) occurring in the area. On the Recent Spermonde shelf (southwest Sulawesi), seven out of 19 species, occur only on the reefs (Chapter 2, above). In the empty larger foraminiferal tests found on the basin floor surrounding the reefs, all species that live only attached to solid substratum were present. However, some were very rare and were only found next to the reefs (Chapter 4, above). Thus, to get a realistic view of the foraminiferal diversity in an area it is important to study as many habitats as possible.

The Cenozoic history of the diversity patterns seen in the Recent fauna is poorly known for the IWP. Wilson & Rosen (1998) have shown that high diversity assemblages of zooxanthellate corals, did not appear in the Indo-Malayan region until the start of the Neogene. During most of the Palaeogene, zooxanthellate coral diversity was much higher in the western Tethys, especially in Europe. However, Palaeogene, and especially pre-Chattian, corals are rare in the IWP and unevenly spread through time. They are found in several (Middle) Eocene assemblages, but the Late Eocene to Early Oligocene is poorly represented in their data set. Wilson & Rosen (1998) argued that the IWP was not a centre of diversity for zooxanthellate corals during the Palaeogene. Instead, this centre was positioned within the western Tethyan realm in Europe. With the Australian plate moving northward into warmer areas during the Oligocene to Miocene, the isolation of the Indo-Pacific area decreased and diversity of zooxanthellate corals increased (Wilson & Rosen 1998). In the meantime in Europe, zooxanthellate coral diversity increased until the Burdigalian, and then gradually decreased. At the end of the Messinian zooxanthellate corals went extinct in the Mediterranean (Wilson & Rosen, 1998; Rosen, 1999)

For most of the Cenozoic, and especially the Palaeogene, the larger foraminiferal fauna from the Caribbean (Fig. 7.1) differed markedly from the European and Southeast Asian faunas (Adams, 1973, 1983, 1992; Adams *et al.*, 1990), the latter being very similar at generic level during the Palaeogene. After the collision of Africa with Eurasia, marking the closure of the Tethys Ocean during the Miocene, the Indo-Pacific faunal elements were no longer able to reach Europe (Adams, 1973).

Southeast Asian Palaeogene carbonates are dominated by larger foraminifera and coralline algae. The foraminiferal genera *Nummulites* and *Palaeonummulites* occurred abundantly within the western Tethyan realm. In the present study, diversity patterns and species occurrences of these genera from the Palaeogene of Europe, Oman and Southeast Asia are compared. The patterns of species distribution within these genera are then compared with the generic diversity pattern of larger foraminifera in the Cenozoic of Southeast Asia and Europe, so as to evaluate Palaeogene geologic events in relation to (geographical) diversity patterns.

Palaeogeographic events influencing the distribution of larger foraminifera

The distribution of larger foraminifera is influenced by changes in the geography and distribution of habitats in time. In the Cenozoic the following major changes in the palaeogeography occurred.

During the Palaeocene and Eocene the Tethys Ocean still existed and formed a more or less continuous passageway at low latitudes (Fig. 7.1). Extensive shallow marine areas, including large carbonate platforms existed in the central Tethys and flanked the northern coast of the African continent.

The Indo-Malayan region is comprised of a complex pattern of several subduction zones (Hall, 1996; Fig. 7.1). Carbonate platforms did not cover large areas and shelf

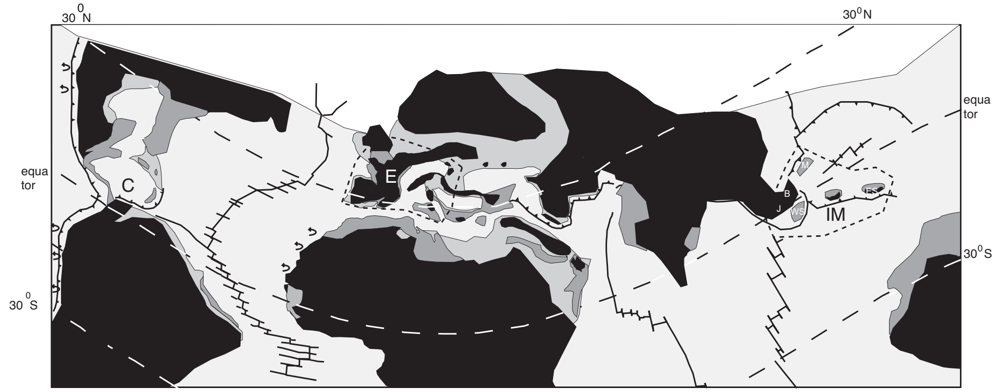


Fig. 7.1. Palaeogeography of the Tethys Ocean during the Lutetian. The map is mainly based on reconstructions by Dercourt *et al.* (1993), with additional information from Hall (1996) concerning the Eastern Tethys. The position of India is arbitrary, other reconstructions (e.g. Kiesling *et al.*, 1999 and Parrish & Curtis, 1982) show a smaller or larger gap in between India and Eurasia. The areas of upwelling (curved arrows) are indicated after Parrish & Curtis (1982). IM = Indo Malaysia, E = Europe, C = Caribean, J = Java, B = Borneo, WS = West Sulawesi, ES = East Sulawesi, M = Mindoro.
Black = land, dark grey = shallow marine carbonates, light grey = shallow marine clastics.

edges were comparatively steep, leaving only few shallow margins. The largest shallow water areas were positioned between southwest Sulawesi and Kalimantan in Indonesia and at Mindoro in the Philippines. Between Australia and the Indo-Malaysian region a large oceanic basin existed. Around the equator some shallow seas and islands existed on crustal fragments that nowadays belong to the Philippines. The position of these shallow carbonate platforms in Fig. 7.1 is inferred from the relative position of parts of the Philippines and palaeoenvironmental information (Hall, 1996, 1998; Wilson & Rosen, 1998), and my own observations on southern Luzon, Mindoro and Mindanao in the Philippines.

With the continuing rotation of Africa, and the northward movement of India and Australia the palaeogeographic conuration changed markedly. The most important change was the final collision of Africa with Eurasia, resulting in the definite closure of the connection between the Indian Ocean and the Mediterranean in the Serravallian, but the first moment of closure was during the Burdigalian (Rögl, 1998).

During the Chattian to Burdigalian, the extent of shallow seas (and carbonate platforms) in the western Tethys decreased. The reverse was the case for the IWP. Australia moved northwards and started to collide with Indo-Malaysia in the Chattian (Fig. 7.2). The extent of shallow seas, and especially carbonate platforms, increased markedly during the Chattian and Early Miocene (Wilson & Rosen, 1998), providing more suitable habitats for larger foraminifera. Deposits bearing larger foraminifera from this time interval are found over large parts of Java, Borneo and Sulawesi, in the southern Philippines and over large areas on the Australian block in New Guinea.

Methods

To compare the diversity in Europe and Indo-Malaysia, comparisons were made at two taxonomic levels. Firstly, species diversity of the genus *Nummulites* in Europe, Oman, and Indonesia and the Philippines have been used. The *Nummulites* data from Europe and Oman are obtained from reviews of *Nummulites* by Schaub (1981) and

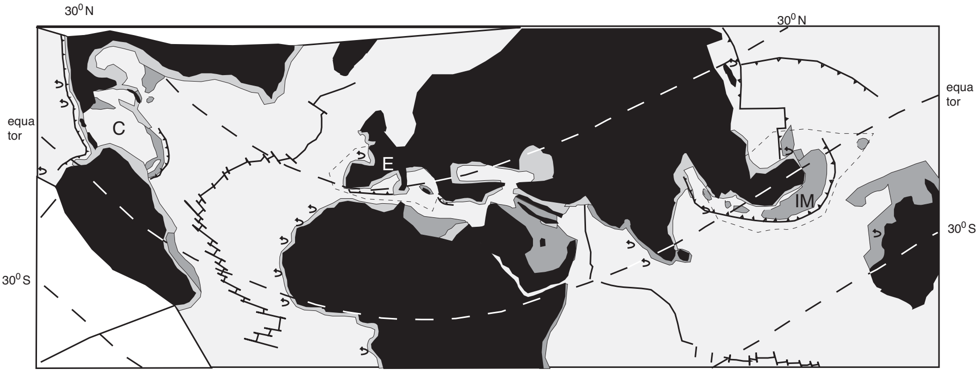


Fig. 7.2. Post-Tethyan palaeogeography during the Burdigalian. The map is mainly based on reconstructions by Dercourt *et al.* (1993), with additional information from Hall (1996) concerning the Eastern Tethys. See Fig. 7.1 for legend.

Racey (1995) supplemented byl stratigraphic information from Sierra-Kiel *et al.* (1998). The data on Southeast Asian nummulitids are from Renema *et al*. (Chapter 6) who gathered and critically reviewed earlier records and collections. In Schaub (1981) and Racey (1995), all involute numulitids with undivided chamberlets were placed in the genus *Nummulites*, but Haynes (1988), Haynes *et al.* (in press) and Renema *et al.* (Chapter 6) have shown that the forms with simple radiate septa should be assigned to *Palaeonummulites*. In the present study species counts include all species of both *Nummulites* and *Palaeonummulites* in an area per time-slice, as given in the above mentioned publications. Additional data from later publications were not taken into account, in order to prevent a bias to better studied areas, and differing species and taxonomic concepts between authors.

Secondly, the generic diversity of 11 time slices through the Cenozoic has been compared between these areas. To evaluate diversity at the generic level, a database was constructed including as much published data on larger foraminifera as possible, focussing solely on illustrated records which could be verified. If generic affiliation of a specimen could not be determined the record was not included. For example, when only the microspheric generation of *Lepidocyclina s.l.* was found it is not possible to establish whether this represented *Eulepidina*, *Lepidocyclina* or *Nephrolepidina,* and the record was omitted.

Larger foraminifera are a polyphyletic group, recognised mainly by their size and complex internal structure. Only families showing characters indicative of algal symbiosis were included. Such characteristics include stolon systems to facilitate the transportation of symbionts responding to irradiation levels; flosculisation of the lateral wall; the development of cups and chamberlets within the chambers, and the development of lateral chamberlets and pillars to regulate the amount of light getting to the symbionts.

In general, all genera belonging to the superfamilies (Table 7.1) Nummulitoidea, Soritoidea and Alveolinoidea are included. It is more difficult within the superfamilies Rotaloidea, Asterigerinoidea and Orbitoidoidea (Table 7.1), where not all families clearly had symbionts. Austrotrillinidae (Milioloidea) are included because of their alveolate walls indicating a zooxanthellate life habit (Adams, 1968).

Though there still are many problems of classification associated with the definition of these taxa, no systematic revision has been attempted. This reduces the applicability on the database for the study of provinciality and migrational pathways.

The generic definitions of Loeblich & Tappan (1987) have been used, except where a more recent revision of a family, subfamily or group of genera was available. Exceptions are the genera *Lepidocyclina*, *Nephrolepidina* and *Eulepidina*. Although Boudagher-Fadel & Banner (1997) proposed a new genus-group classification, the generic subdivision of the Lepidocyclinidae proposed by Sirotti (1982) is used, in which *Nephrolepidina* and *Lepidocyclina* are considered to have evolved in separate lineages from a common ancestor, and therefore are separate genera, with *Eulepidina* evolving from *Lepidocyclina* (Sirotti, 1982). The differences can only be observed in A-forms, and thus all B-forms cannot be identified at the generic level.

The taxonomy of the Soritoidea is not yet resolved. Hottinger (2001) (re)described several Caribbean genera based on several (mainly) internal morphological characters. That study showed that generic and higher taxonomy in this group is far from

Table 7.1. Superfamilies and families included in the database on larger foraminifera occurrences. Note that the nominate taxa of the families Lepidocyclinidae, Meandropsinidae and Lepidorbitoididae are not included in this table since they have not been recorded in the studied area.

Superfamily	**Families included**	**Genera included**
Milioloidea Ehrenberg	Austrotrillinidae Loeblich & Tappan	*Austrotrillina* Parr
Alveolinoidea Ehrenberg	Alveolinidae Ehrenberg	*Alveolinella* Douvillé
		Rhabdorites Fleury
		Glomalveolina Hottinger
		Flosculinella Schubert
		Bullalveolina Reichel
		Borelis de Montfort
		Alveolina d'Orbigny
		Praebullalveolina Sirel & Acar
	Fabulariidae Ehrenberg	*Pseudolacazina* Caus
		Periloculina Munier-Chalmas & Schlumberger
		Lacazina Munier-Chalmas
		Fabularia Defrance
		Lacazinella Crespin
Soritoidea Ehrenberg	Meandropsinidae Henson	*Hottingerina* Drobne
	Peneroplidae Schultze	*Reulina* Lamarck
		Archiacina Munier-Chalmas
		Spirolina Lamarck
		Dendritina d'Orbigny
		Peneroplis de Montfort
	Soritidae Ehrenberg	*Opertorbitolites* Nutall
		Orbitolites Lamarck
		Praerhapydionina van Wessem
		Pseudotaberina Eames
		Archaias de Montfort
		Sorites Ehrenberg
		Globoflarina Fleury
		Marginopora Quoy & Gaimard
		Cyclorbiculina Silvestri
		Parasorites Seiglie & Rivera
		Amphisorus Ehrenberg
Asterigerinoidea d'Orbigny	Amphisteginidae Cushman	*Amphistegina* d'Orbigny
	Boreloididae Reiss	*Boreloides* Cole & Bermudez
	Lepidocyclinidae Scheffen	*Nephrolepidina* Douvillé
		Eulepidina, Douvillé
Rotaloidea Ehrenberg	Calcarinidae Schwager	*Silvestriella* Hanzawa
		Calcarina d'Orbigny
		Baculogypsina Sacco
		Baculogypsinoides Yabe & Hanzawa
	Miogypsinidae Vaughan	*Miogypsina* Sacco
		Miogypsinoides Yabe & Hanzawa
		Miolepidocyclina Silvestri
		Miogypsinoidella Boudagher-Fadel, Lord & Banner
		Lepidosemicyclina Rutten
	Rotaliidae Ehrenberg (pars)*	*Neorotalia* Bermudez
		Pararotalia Le Calvez

Orbitoidoidea Schwager	Linderinidae Loeblich & Tappan	*Linderina* Schlumberger
	Eoannularidae Ferràndez-Cañadell & Serra-Kiel	*Eoannularia* Cole & Bermudez
	Lepidorbitoididae Vaughan	*Actinosiphon* Vaughan
		Daviesina Smout
Nummulitoidea de Blainville	Asterocyclinidae Brönnimann	*Orbitoclypeus* Silvestri
		Asterocyclina Gümbel
	Discocyclinidae Galloway	*Discocyclina* Gümbel
		Nemkovella Less
	Miscellaneidae Sigal	*Miscellanea* Pflender
	Nummulitidae de Blainville	*Assilina* d'Orbigny
		Cycloclypeus Carpenter
		Grzybowskia Bieda
		Heterostegina d'Orbigny
		Katacycloclypeus Tan
		Nummulites Lamarck
		Nummulitoides Abrard
		Operculina d'Orbigny
		Palaeonummulites Schubert
		Planocamerinoides Cole
		Radiocycloclypeus Tan
		Ranikothalia Caudri
		Spiroclypeus Douvillé
		Tansinhokella Banner & Hodgkinson
	Pellatispiridae Hanzawa	*Pellatispira* Boussac
		Biplanispira Umbgrove

* Only the subfamily Pararotalinae, with the genera *Neorotalia* and *Pararotalia*. The extant genus *Neorotalia* houses symbionts. Loeblich & Tappan (1987) regarded these genera as synonymous, but Hottinger *et al.* (1991) have shown sufficient morphological difference to warrant generic distinction.

resolved in the Tethys region, for a large part because of lack of well preserved free-specimens. Furthermore, specimens of the Soritoidea usually make up only a very small fraction of the total assemblage and occur patchily.

Although the use of higher level taxonomy increases the problems of interpretation (Hottinger, 1990), the generic level is used since the taxonomy at species level is poor within the regions used, as shown by the decrease in species recorded in Indonesia from 60 to 14 species in the genera *Nummulites* and *Palaeonummulites* following a revision of existing records in Indonesia (Chapter 2, above).

Hottinger (1990) found that there was a non-linear relationship between generic and species diversity, observing that the lower the number of species in a sample, the higher the proportion of genera. However, in nearly all samples generic diversity increased with an increasing number of species. According to these findings, comparisons of diversity between different areas are only useful within the same taxonomic level.

The most basic taxonomical problem is that even within the same family, different concepts of generic classification have been used by different authors. This problem cannot be resolved completely. For example, historically there have been researchers using mainly numerical data for taxonomy (e.g., in Lepidocyclinidae, Discocyclinidae and Miogypsinidae), while others used typological defined species (in, e.g., Nummulitidae and Alveolinidae). Also, there is no consensus about the value of coiling patterns for generic classification.

Another problem to deal with is that of stratigraphy. Overviews of the Palaeogene larger foraminiferal fauna of the Western Tethys (Serra-Kiel *et al.*, 1998) have been combined with data on planktonic and larger benthic foraminiferal ages. Cahuzac & Poignant (1997) have done the same for the Oligocene to Miocene of the European basins, whilst Boudagher-Fadel & Banner (1999) have revised the Oligocene to Miocene part of the East Indian Letter Classification for the Cenozoic of the Indo-Pacific. Together with the revision of nummulitids, the stratigraphy of the Palaeogene in the Indo-Malayan region has been revised (Chapter 6, above.). For localities on Java, Sulawesi and Luzon, additional stratigraphic data were gathered using planktonic foraminifera and nannoplankton, and all sections have been calibrated to the chronostratigraphy published by Berggren *et al.* (1995).

Pliocene data are rare, so the diversity for this period might be lower than represented in the faunal diagrams. Little attention has been paid to long ranging taxa in publications dealing with stratigraphy. European faunas include localities from Spain, France, Italy, former Yugoslavia, and Greece, but exclude Turkey (Fig. 7.1). Indo-Malaysia (IM) consists of records from Indonesia (without Irian Jaya), Malaysia and the Philippines (Fig. 7.1), but does not include New Guinea or other areas on the Australian plate. The denomination Indo-Malaysia is chosen in preference to Southeast Asia, since the region studied is smaller than that used by Wilson & Rosen (1998). However, it is emphasised that it is used as a geographical term and that no biogeographical implications are intended.

The geochronology used in this paper is based on Berggren *et al.* (1995). Serra-Kiel *et al.* (1998) divided the Palaeocene to Eocene in 20 biozones, based on data from the Western Tethys (Shallow Benthic Zones, SBZ1-20). The Ypresian comprises SBZ 6-12, the Lutetian SBZ 13-16 and the Bartonian SBZ 17 and 18. The divisions used in the present paper have been chosen in a way that most time-slices are of similar length and that correlation between Europe and the Southeast Asian region is still possible. The shortest unit used is the Priabonian (3.2 Ma), the longest the Lutetian (7.6 Ma). For the species level, the Ypresian was divided into three parts, early (SBZ7-9, approximately P6), middle (SBZ9-10, P7-8) and late (SBZ11-12, P9), as was the Lutetian in which early Lutetian comprises P10 (SBZ13), middle Lutetian comprises P11 (SBZ14) and late Lutetian comprises most of P12 (SBZ15, 16).

Southeast Asian Palaeogene nummulitid-bearing deposits

During most of the Cenozoic, Southeast Asia consisted of several small, tectonically controlled basins. Many of these basins experienced rapid subsidence or uplift. Often, the occurrence of larger foraminiferal species is not determined by replacement with younger species, but by facies changes (Racey, 1995). Composite sections and isolated samples cover most of the Ypresian to Priabonian in Southeast Asia.

Unfortunately, no reliable Palaeocene to earliest Ypresian records deposits yielding of larger foraminifera bearing deposits are known from Indo-Malaysia. At the Kudat Peninsula (Sabah), a mixed assemblage of reworked Late Palaeocene and *in situ* Early Miocene foraminifera has been found (van der Vlerk, 1951). Hashimoto & Matsumaru (1981a) interpreted the interval without Miocene foraminifera as *in situ* Upper Palaeocene sedimentary rocks. Although undoubtedly Thanetian (or possibly Ypresian) sedimentary rocks were deposited in this area, these have now been reworked into younger deposits and an exact stratigraphic age for them can not be determined (van der Vlerk, 1951).

Ypresian deposits are also quite rare, and can only be confirmed from Sumba and Halmahera. On Halmahera these consist of deep marine sedimentary rocks, whilst on Sumba it is not clear which part of the Ypresian is present. An age could not be assigned to the oldest Cenozoic deposits found on Sumba, since no age-diagnostic fossils have been found in these strata. The basal Lutetian is rare, and has only been found on Timor, Sumba, East Sulawesi, Mindoro and Luzon. For a more complete discussion see Chapter 6.

Middle Lutetian to Bartonian sedimentary rock are the most widespread Eocene deposits in Indo-Malaysia. These having been found at 10-14 localities throughout the archipelago (Chapter 6, above).

Deposits of Early Priabonian age are quite common as well. On Java and Southwest Sulawesi these are of similar marly facies and contain numerous large (up to 3 cm diameter) *Discocyclina*, *Operculina* and small *Palaeonummulites*. Sedimentary rocks of Late Priabonian age are, however, rare and have only been found in the Melinau

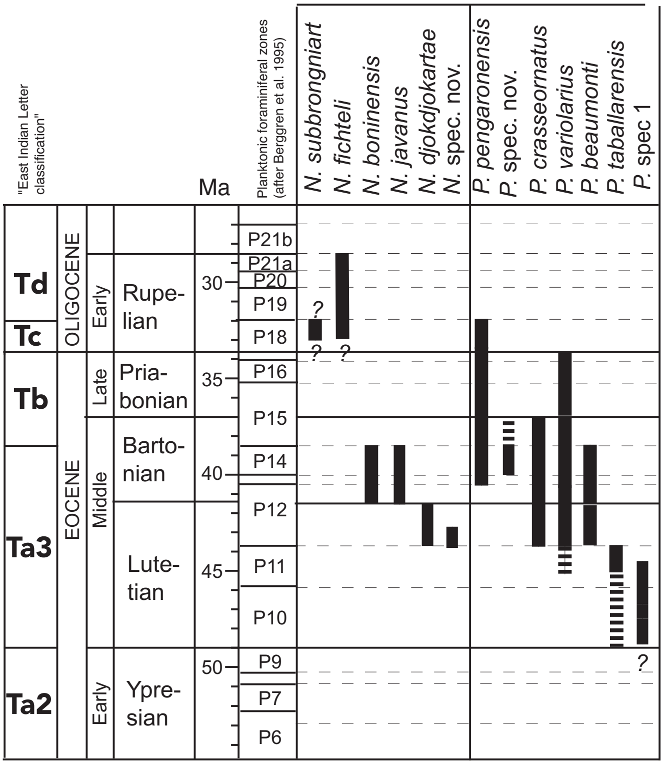


Fig. 7.3. Stratigraphic ranges of the species of *Nummulites* (N.) and *Palaeonummulites* (*P.*) in Indo-Malaysia (after Renema *et al.* (Chapter 6, this thesis).

Limestone (Sarawak), a carbonate platform deposited from the Bartonian to Early Miocene (Adams, 1965). The boundary interval between the uppermost Priabonian and Rupelian is present, but does not contain larger bentic foraminifera. Other deposits of late Priabonian age have been recorded from Sumba (Caudri, 1934), Sulawesi (Osimo, 1908) and Luzon (personal observation) and a reworked boulder on Java. For a more extensive discussion of Indonesian Eocene deposits see Chapter 6.

Species of *Nummulites*

Pringgoprawiro *et al.* (1998) reported about 60 species of *Nummulites s.l.* from Indonesia. After eliminating synonyms, only seven species of *Nummulites* are believed to be valid (Fig. 7.3; Chapter 6, above). Seven additional Indo-Malayan species that have previously been included in *Nummulites* should be reassigned to *Palaeonummulites (*Chapter 6, above.).

The number of nummulitid species per time slice in Indo-Malaysia increased from two in the late Ypresian to six in the late Lutetian and Bartonian, and dropped back to two in the Priabonian. In the Rupelian three species were present (Fig. 7.4).

In Europe, North Africa and Oman (data from Schaub, 1981 and Racey, 1995), the number of species in the Ypresian was higher, in the early Ypresian varying from 2-15,

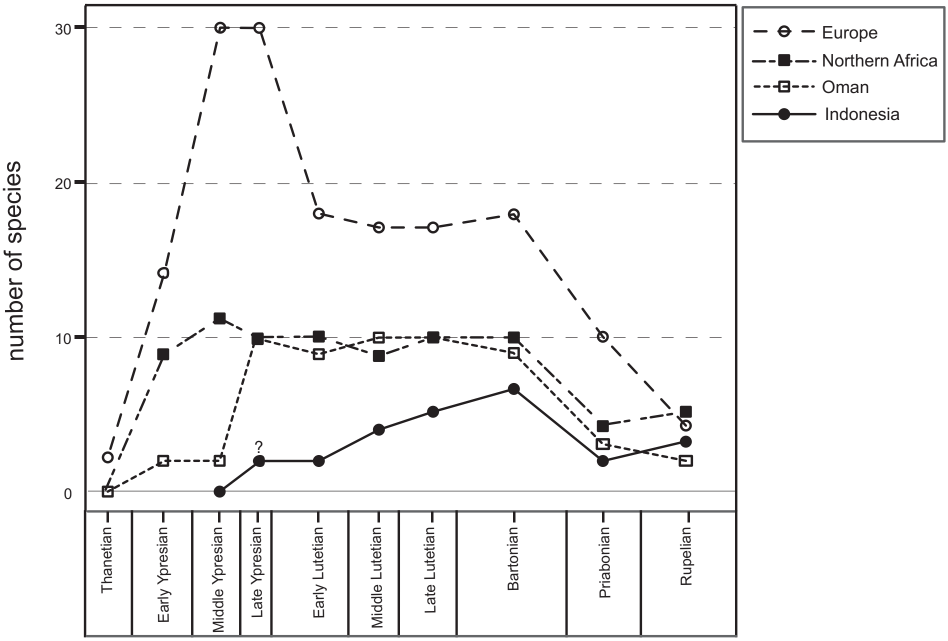


Fig. 7.4. Number of species of the genera *Nummulites* and *Palaeonummulites* per time slice in four regions of the Tethys. Data for Europe and Northern Africa are from Schaub (1981), those for Oman from Racey (1995) and those for Indo-Malaysia from Renema *et al.* (Chapter 6, this thesis). High species numbers in the Ypresian are artificial because of accumulation of short ranging species.

in the late Ypresian from 10-30. During the Lutetian to Bartonian, species richness in Europe, North Africa and Oman are fairly constant, around 17-18 in Europe, and 9-10 in North Africa and Oman. In the Priabonian species number reduced to 10 in Europe, and 3-4 in North Africa and Oman. The very high species richness in Europe, especially in the Ypresian, is due to a very detailed zonation and thus an artificially high diversity achieved by oversplitting. Furthermore, the relatively high numbers in the Lutetian and Bartonian can in part be explained by biogeographic provinces within Europe (West Europe, South Central Europe, East Europe; Hottinger, 1990). Thus, the species richness patterns are very similar between the four areas, but the number of species is much lower in the Indo-Malaysian region, especially in the Ypresian and Lutetian.

In Indo-Malaysia test size was largest in the Bartonian, with a maximum test-diameter of 37 mm. The large species all went extinct at or before the Bartonian-Pri-

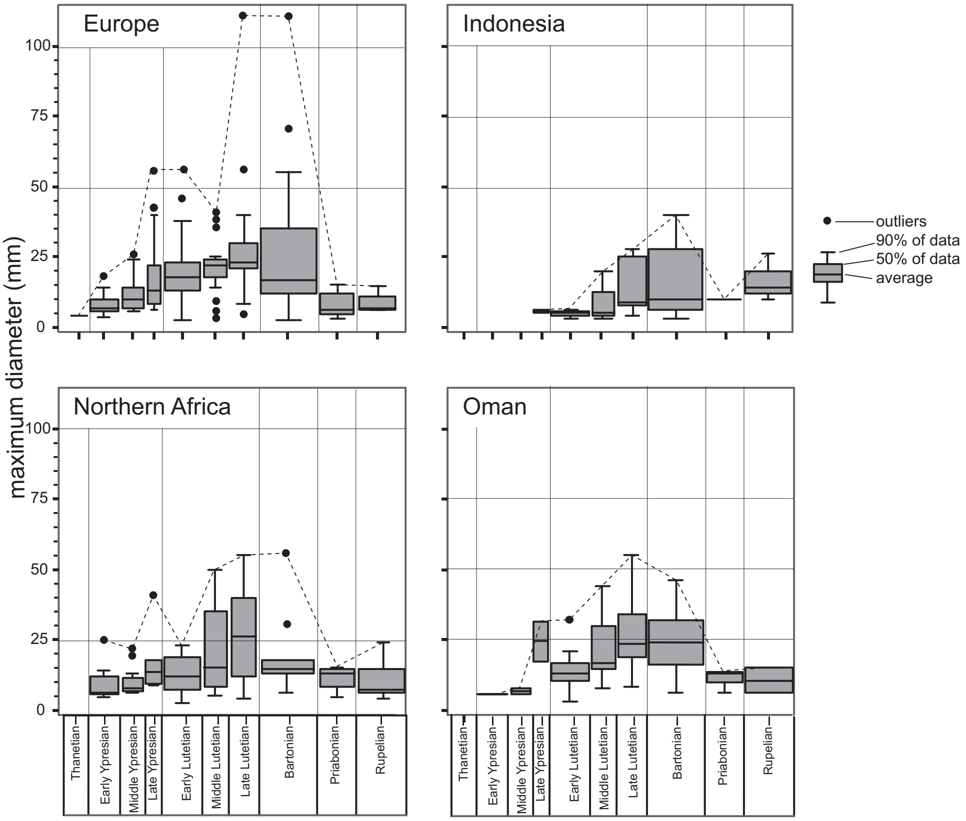
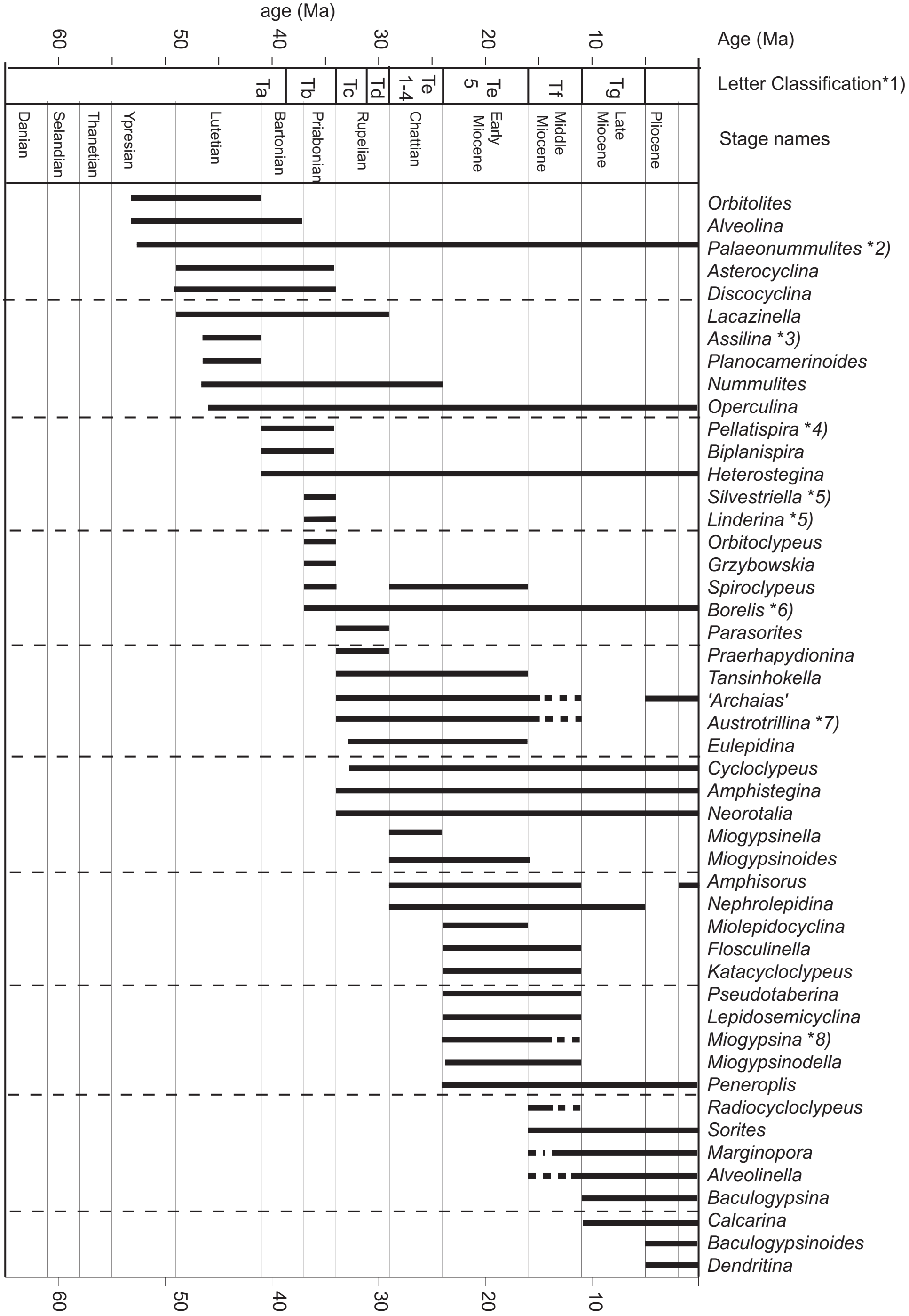


Fig. 7.5. Median diameter of the test of B-forms of species of the genera *Nummulites* and *Palaeonummulites* in four regions of the Tethys. Data for Europe and Northern Africa are from Schaub (1981), those for Oman from Racey (1995) and those for Indo-Malaysia from Renema *et al.* (Chapter 6, this thesis). Boxes contain 50% of the genera, error bars contain 90% of the genera, and dots are outliers. For time scale see Fig. 7.3.


age (Ma)
60
50
40
30
20
10
Age (Ma)
Ta
Tb
Tc
Td
Te 1-4
Te 5
Tf
Tg
Letter Classification*1)
Danian
Selandian
Thanetian
Ypresian
Lutetian
Bartonian
Priabonian
Rupelian
Chattian
Early Miocene
Middle Miocene
Late Miocene
Pliocene
Stage names
Orbitolites
Alveolina
*Palaeonummulites *2)*
Asterocyclina
Discocyclina
Lacazinella
*Assilina *3)*
Planocamerinoides
Nummulites
Operculina
*Pellatispira *4)*
Biplanispira
Heterostegina
*Silvestriella *5)*
*Linderina *5)*
Orbitoclypeus
Grzybowskia
Spiroclypeus
*Borelis *6)*
Parasorites
Praerhapydionina
Tansinhokella
'Archaias'
*Austrotrillina *7)*
Eulepidina
Cycloclypeus
Amphistegina
Neorotalia
Miogypsinella
Miogypsinoides
Amphisorus
Nephrolepidina
Miolepidocyclina
Flosculinella
Katacycloclypeus
Pseudotaberina
Lepidosemicyclina
*Miogypsina *8)*
Miogypsinodella
Peneroplis
Radiocycloclypeus
Sorites
Marginopora
Alveolinella
Baculogypsina
Calcarina
Baculogypsinoides
Dendritina
60
50
40
30
20
10

abonian boundary. In the Priabonian maximum size is 10 mm, but in the Rupelian the maximum diameter increased to 25 mm (Fig. 7.5).

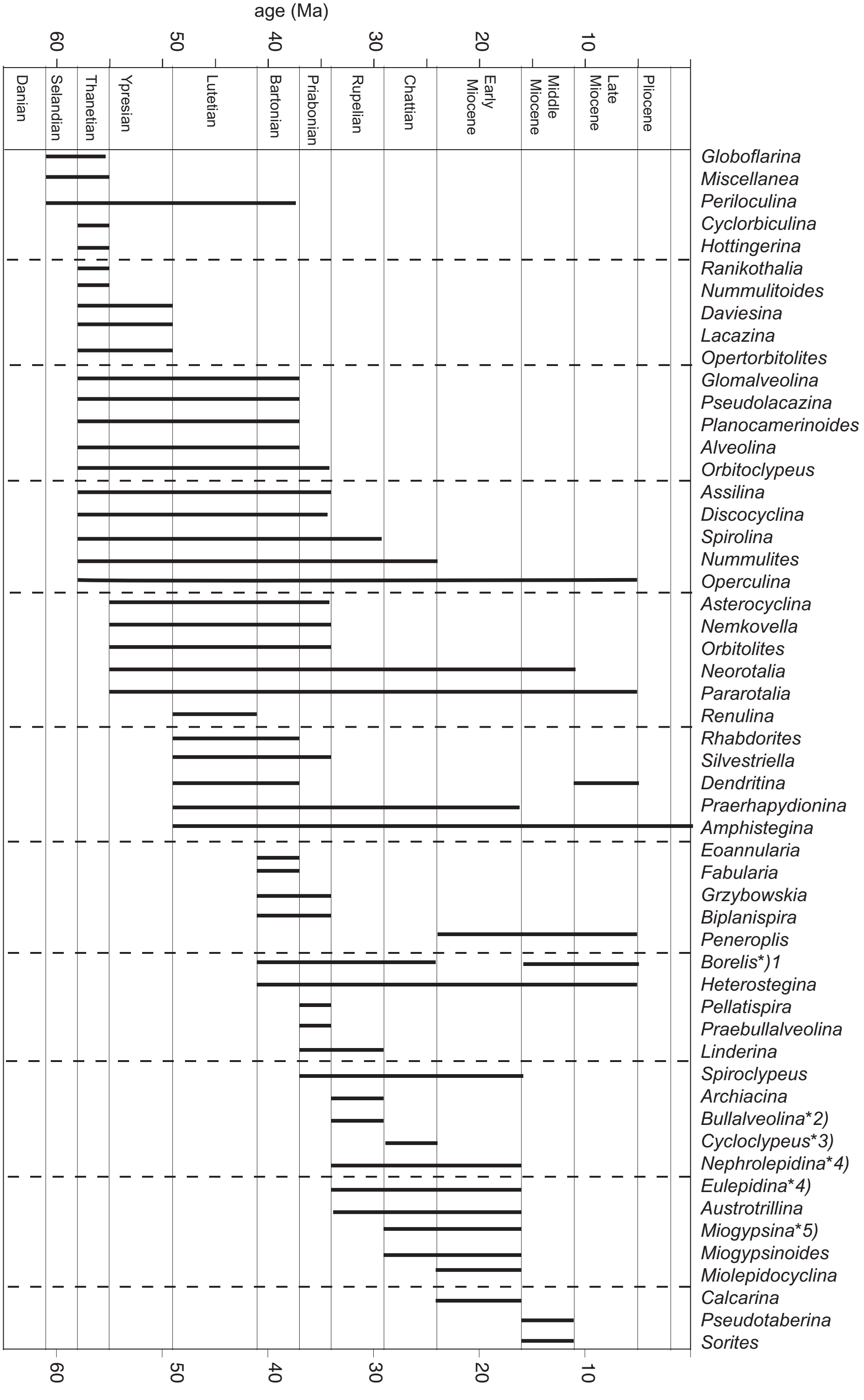
In the three western Tethyan areas the largest species occurred in the Lutetian, but the average test size increased.

The size distribution through the Palaeocene and Eocene is very similar between the four areas (Fig. 7.5). The average test diameter in the B-forms of *Nummulites* increased from the Palaeocene to late Lutetian. The maximum size decreased after the Bartonian, except for a slight decrease at the end of the late Lutetian in Oman. In the Bartonian the maximum size was still large, but the average decreased into the lower part of the box containing 50% of the data, indicating a relative higher abundance of small sized species. In Northern Africa, as in Indonesia, maximum diameter of *Nummulites* increased again in the Rupelian, with *N. sublaevigatus* reaching a diameter of 25 mm.

Cenozoic generic diversity

During the Eocene, larger foraminifera were important contributors to carbonate production in the shallow marine realm of Indo-Malaysia (Wilson & Rosen, 1998). Yet, compared to Europe, the species diversity within the most important genera of larger foraminifera is lower. But is the generic diversity also lower in the Indo-Malaysian

◀ Fig. 7.6. Range chart of Indo-Malayan larger foraminifera. *1) 'East Indian Letter Classification' as used in the present study. Within Southeast Asia it is possible to, for example, subdivide Tf into Tf1-3 (or even more) subunits, but it is not yet possible to correlate these datum planes to the Cenozoic timescale of Berggren *et al.* (1995). *2) see Chapter 6. *Palaeonummulites* is an extant genus, limited to the West Pacific and easternmost Indian Ocean. Although not often reported, *Palaeonummulites* is regularly recorded in Miocene to Pliocene sediments (e.g. Whitakker & Hodgkinson, 1979; pers. obs. Bulu Lst, Middle Miocene, Central Java). *3) *Assilina* has not been observed from Indonesia, and thus not included in Renema *et al.* (Chapter 6, this thesis). There is a published record of a specimen that probably should be assigned to *Assilina* from the Philippines (Hashimoto *et al.*, 1979). *4) The earliest record of *Pellatispira* is several localities were it co-occurs with *N. javanus* and planktonic foraminifera indicative of P12-P14 (see Renema *et al.*, Chapter 6, this thesis). *5) There are two documented records of *Linderia* and one of *Silvestriella* from the region. Osimo (1908) and Provale (1909) provide two records (Central Sulawesi and East Borneo) for both genera, but all figured specimens of *Silvestriella* are from Sulawesi. In a sample from Sangiran (Central Java) collected by Peter Lunt numerous *Silvestriella* and *Linderina* were observed. This sample was collected from a boulder with abundant *Pellatispira* sp., *Discocyclina* sp. and *Orbitoclypeus* sp., all indicative of a Tb , Late Eocene age. *6) Records older than Tb, Priabonian of *Borelis* (e.g. Bakx, 1932; Henrici, 1934) have all been reassigned to other alveolinid genera. *Borelis* is most common in the Upper Oligocene to Lower Miocene strata, with rare records in the Upper Miocene and Pliocene. *7) see Adams (1968) and Adams (1970). Co-occurring with *Orbulina universa* in the youngest records, thus of Middle Miocene age (Adams, 1970). Youngest record in Tf1, equivalent to the Langhian. *8) Adams (1992) doubted the validity of records of *Miogypsina* in the Middle Miocene, since all records he knew of either could be proven to be reworked or wrongly dated, or "there was no evidence that they had not been reworked". Boudagher-Fadel & Banner (1999) place the extinction of *Miogypsina* in N12. In Leupold & van der Vlerk (1931) the top Tf2 (about middle Middle Miocene) was defined by the extinction of, among others, *Miogypsina*. In the Bulu Limestone (Central Java), *Miogypsina* co-occurs with *Katacycloclypeus annulatus*, a species typical for Tf2. The youngest records of *Miogypsina* are with *Globorotalia fohsi*, in N11-12 (Peter Lunt, pers. com.), thus confirming the extinction age of Boudagher-Fadel & Banner (1999).


age (Ma)
60
50
40
30
20
10
Danian
Selandian
Thanetian
Ypresian
Lutetian
Bartonian
Priabonian
Rupelian
Chattian
Early Miocene
Middle Miocene
Late Miocene
Pliocene
Globoflarina
Miscellanea
Periloculina
Cyclorbiculina
Hottingerina
Ranikothalia
Nummulitoides
Daviesina
Lacazina
Opertorbitolites
Glomalveolina
Pseudolacazina
Planocamerinoides
Alveolina
Orbitoclypeus
Assilina
Discocyclina
Spirolina
Nummulites
Operculina
Asterocyclina
Nemkovella
Orbitolites
Neorotalia
Pararotalia
Renulina
Rhabdorites
Silvestriella
Dendritina
Praerhapydionina
Amphistegina
Eoannularia
Fabularia
Grzybowskia
Biplanispira
Peneroplis
Borelis*)1
Heterostegina
Pellatispira
Praebullalveolina
Linderina
Spiroclypeus
Archiacina
Bullalveolina*2)
Cycloclypeus*3)
Nephrolepidina*4)
Eulepidina*4)
Austrotrillina
Miogypsina*5)
Miogypsinoides
Miolepidocyclina
Calcarina
Pseudotaberina
Sorites
60
50
40
30
20
10

region?

In the Indo-Malayan Ypresian only three genera have been recorded, increasing to ten in the Lutetian and Bartonian and fifteen in the Priabonian (Figs. 7.6, 7.8). The generic diversity continued to increase until a maximum was reached in the Early and Middle Miocene (24 genera). At the end of the Middle Miocene the number of genera decreased rapidly from 24 to 14 genera in the Late Miocene (Fig. 7.6). The generic diversity per million year shows a similar pattern (Fig. 7.7), only the Priabonian is relatively rich in genera, compared with the other Eocene periods.

The oldest Cenozoic occurrences of larger symbiont-bearing foraminifera in Europe are from the Selandian, in which three genera occur (Figs. 7.7; 7.8). Thanetian generic diversity was already much higher with 20 genera. Nineteen and 22 genera have been recorded from the Ypresian and Lutetian respectively, while the diversity maximum was reached in the Bartonian with 27 genera. From the Bartonian onwards generic diversity decreased in Europe. In the Priabonian 22 genera were found. Other large drops in generic diversity were at the end of the Early Miocene (15 to 9 genera) and at the end of the Late Miocene (7 to 1 genera). Generic diversity per million year shows a very similar trend, although the Ypresian and Lutetian are less diverse than the Thanetian and Bartonian/Priabonian.

Even rarefaction of the data set by random elimination of approximately 10% of the genera from the database (5 out of 53 respectively 48) does not change the general pattern, but only decreases the generic diversity per time slice (Fig. 7.8).

Most of the genera that have been found in the Indo-Malaysian Ypresian to Lutetian interval are the genera represented by the largest number of species in Europe in the same period (*Assilina, Nummulites, Alveolina, Orbitolites, Planocamerinoides, Discocyclina* and *Asterocyclina*). *Lacazinella* (with records from Mindoro and Timor) is the only genus that has not been found in Europe. This genus occurs only on remnants of the Australian craton in Indonesia (Lunt, 2000b), but has also been found in Oman and other parts of the Middle East (White, 1994)

The faunal character changed markedly at the Eocene-Oligocene transition (Adams, 1973). The genera mentioned above were the most important genera during the Eocene, while from the Oligocene onwards *Nephrolepidina*, *Eulepidina*, *Cycloclypeus* and to a lesser extent miogypsinids dominated the fauna. The extinction at the end of the Eocene was not a rapid one, but took place in several steps, starting in the Bartonian and with the last extinctions at the Priabonian-Rupelian boundary.

◀ Fig. 7.7. Range chart of larger foraminifera genera in Europa. *1) see Romero *et al*., 1999. *2) Although known from the entire Oligocene, I known of no Early Miocene records of *Borelis* in Europe. In Indo-Malaysia, the Early Miocene is the interval in which *Borelis* is most abundant. *3) *Bullalveolina* characterises the Rupelian (Cahuzac & Poignant, 1997). *4) Although known from the Rupelian to Recent in Indo-Malaysia, *Cycloclypeus* is restricted to the Chattian in Europe. *5) Like in Indo-Malaysia, *Eulepidina* has not been recorded from the earliest part of the Rupelian. Cahuzac & Poignant (1997) define their zone boundary SB21- SB22 on the first occurrence of the *Eulepidina* and *Nephrolepedina*. Unlike Indo-Malaysia, *Nephrolepidina* has been recorded in the European Rupelian, while in Indo-Malaysia the oldest record is from the Chattian. *6) The last occurrence of *Miogypsina* in Europe is within the Early Miocene (Cahuzac & Poignant, 1997), while in Indo-Malaysia it extends into the Middle Miocene.

In Europe, at both the Bartonian-Priabonian and the Priabonian-Rupelian boundaries, about half of the existing genera went extinct (fig. 7.9) and the number of first occurrences (FO) in the succeeding period is similar to those in earlier stages, resulting in a net loss in generic diversity. In Indo-Malaysia the extinction at the Bartonian-Priabonian boundary was less pronounced. In the Bartonian one out of ten genera went extinct, but five genera had their FO in the Priabonian, resulting in a net increase in generic diversity over the Bartonian-Priabonian boundary (Figs. 7.9, 7.10). At the end of the Priabonian the nine genera went extinct, but in the Rupelian ten genera had their first occurrence, again resulting in a net gain over the Priabonian-Rupelian boundary. Some contributing patterns should be noted, however:

1. Four genera are restricted to the Priabonian, whilst *Spiroclypeus* had its FO in the Pribonian, went locally extinct at the end of the Priabonian and did not return until the Chattian. This increased the number of FOs and LOs in the Priabonian by five.

2. Although the generic diversity increased in the Bartonian to Rupelian, the faunal composition had completely changed. In the Thanetian-Bartonian, Priabonian and Rupelian- Late Miocene the most important genera were the same in Europe and Southeast Asia.

3. Since it is not possible yet to correlate the FOs of newcomers in the Rupelian of Indo-Malaysia and Europe, no distinction is made between Tc and Td faunas in the present study. When this had been done, the Tb-Tc (Priabonian-Rupelian) boundary would also have shown a drop in generic diversity, since most of the FOs in the Rupelian of Indonesia occur in Td (or at the Tc-Td boundary), a couple of million years later than the Tb-Tc boundary, which is defined as the FO of *Eulepidina*.

After the Priabonian-Rupelian boundary, the differences in the patterns of first occurrences and last occurrences (LO) between Europe and Indo-Malaysia increased even more. In Europe, there were many FOs in the Rupelian and less in the Chattian. In the Early, Middle and Late Miocene there was only 2, 2 and 0 FO respectively (Fig. 7.10). The number of LOs was relatively high during most of the Oligocene to Miocene, with maxima at the end of the Early and Late Miocene (Fig. 7.10). The pattern in the number of FO and LO per million year does not deviate from the pattern in the absolute numbers (Figs. 7.9, 7.10).

In Indo-Malaysia, there are many FOs in the Rupelian to Early Miocene (9 in the Rupelian, 8 in the Early Miocene, 5 in the Chattian, Fig. 7.10). In the Middle Miocene to Pliocene, there were not as many FOs. The number of LOs increased gradually from the Rupelian (3) to the Middle Miocene (11).

Nummulites species diversity

Before discussing the diversity at both genus and species level, it is necessary to exclude the possibility that the observed differences are only an artefact of different fauna compositions and/or of the amount of strata outcropping. Nummulite-bearing deposits are much more abundant in Europe and North Africa than in Indo-Malaysia. Since nummulitids show hardly any endemism within the Indo-Malayan basins, the number of species found is believed to be a true reflection of the diversity within the Palaeogene rather than a sampling artefact.

Stratigraphic resolution is more refined in the Western Tethys and, especially in

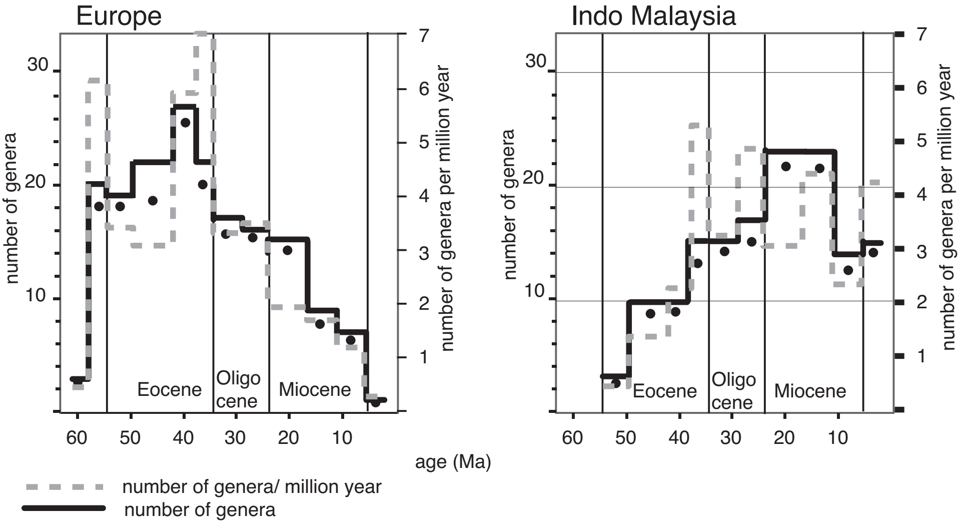


Fig. 7.8. Number of genera per time slice. Line shows the observed number of genera, the dots show the average number of genera after 5 genera have been removed from the data set at random.

the Ypresian, many short ranging species are present. The stratigraphy in Indonesia is not so well resolved and, because species counts have been used, these are artificially high in the three Tethyan regions, especially in the Ypresian. Typical species numbers in a SBZ zone are about 15 in Europe and 10 in North Africa and Oman (all early-middle Lutetian), which is still considerably higher than the maximum of six species in one (longer) time slice in Indonesia.

In Europe, Indo-Malaysia, North Africa and Oman the Lutetian-Bartonian-Priabonian transitional period is not only characterised by a marked decrease in number of species (fig. 7.4), but also by a decrease in the maximum diameter in the species present (see also Hottinger, 1960; Schaub, 1981; Brasier, 1995; Racey; 1995; Fig. 7.5). The Indo-Malayan *Nummulites* fauna is much less diverse (Fig. 7.4), but showed a similar pattern, although the maximum diameter was much smaller than in the western Tethys. Since morphologic diversity is directly related to taxonomic diversity in Recent faunas (Hallock, 1988; Chapter 2, above), it seems unlikely that the low species richness is an artefact of the limited attention that has been paid to Indo-Malayan nummulitids.

The number and extent of Palaeogene outcrops in Europe is much greater than in Indo-Malaysia. A more appropriate comparison between species numbers can be made with the Palaeogene of Oman, where a similar amount of Palaeogene strata is outcropping (Racey, 1995). Oman has a much smaller area than the Indo-Malaysian region. A larger area enhances the chance of endemism, thus with all things being equal, in a large area more species would be expected to occur. The Ypresian is better represented in Oman, though in the Lutetian and Bartonian almost twice as many species have been found in Oman than in Indo-Malaysia.

The problem of the area of outcrop can be circumvented by looking at species diversity by localities, which shows the same pattern as that noted at the regional level. In a typical Eocene locality in Indonesia, two or three species of *Nummulites* are found, while in Europe and Oman up to 10 species can co-occur (Schaub, 1981; Racey, 1995). This is in accordance with diversity patterns seen at the regional level.

In brief, despite the limited amount of attention paid to the Indonesian Middle Eocene *Nummulites* fauna, it can be concluded that this fauna is less diverse than contemporaneous faunas in the Western Tethys. Both in Indonesia and the other regions, the largest species did not survive the Lutetian-Bartonian-Priabonian transitional period. Indonesian diversity decreases less dramatically than in other regions over the Priabonian-Rupelian boundary.

Tethyan generic diversity

Much more effort has been put into studying the European fossil record than any other place. Also, the number of especially Palaeogene outcrops is much larger in Europe than in Indo-Malysia. The combination of these facts can have a marked effect on the diversity patterns found. To test for this sampling bias, several tests were performed. The amount of strata (deposited in a suitable habitat for larger benthics) outcropping in the Neogene is comparable between the two areas.

First, the number of records per genus is similar between Europe and Indo-Malaysia, apart from the Eocene. In the Eocene the number of records per genus is higher in Indo-Malaysia by almost by a factor 2. The larger benthic foraminifera fauna in Indo-Malaysia is characterised by few, but abundant genera, while in Europe also rare genera occur. During the Neogene the number of records per genus is similar between Europe and Indo-Malaysia.

The last evidence that the observed patterns are not resulted from research intensity of amount of strata comes from the average generic diversity per locality. Although it is not always possible to extract locality data from all references, the available data could be evaluated. The number of genera per locality is significantly higher in the European Eocene than in the Indo-Malaysian Eocene ($p<0.01$, Kolmogorov-Smirnov two sample test).

All these data show that the Cenozoic generic diversity can be compared between the two areas and that the observed results are unlikely to be an artefact of sampling and research intensity.

Palaeocene- Eocene

Whether the Indo-Malayan fauna was more or less diverse in the Palaeogene does not depend on the number of species per genus. The faunal assemblages could be entirely different in Western and Eastern Tethys. The generic composition of the assemblages from the Palaeogene of Europe and Indo-Malaysia is very similar (Adams, 1992; Renema, unpublished data). The dominant taxa in both regions are *Nummulites*, *Palaeonummulites* and *Alveolina*, together with rarer orthophragminids, *Orbitolites* and *Planocamerinoides* and other even less frequent genera. *Assilina* and *Planocamerinoides* are more abundant in Europe than in Indo-Malaysia.

In the Priabonian, orthophragminids constituted a more important part of the fauna. *Nummulites* and *Palaeonummulites* were less abundant in the Priabonian than in the

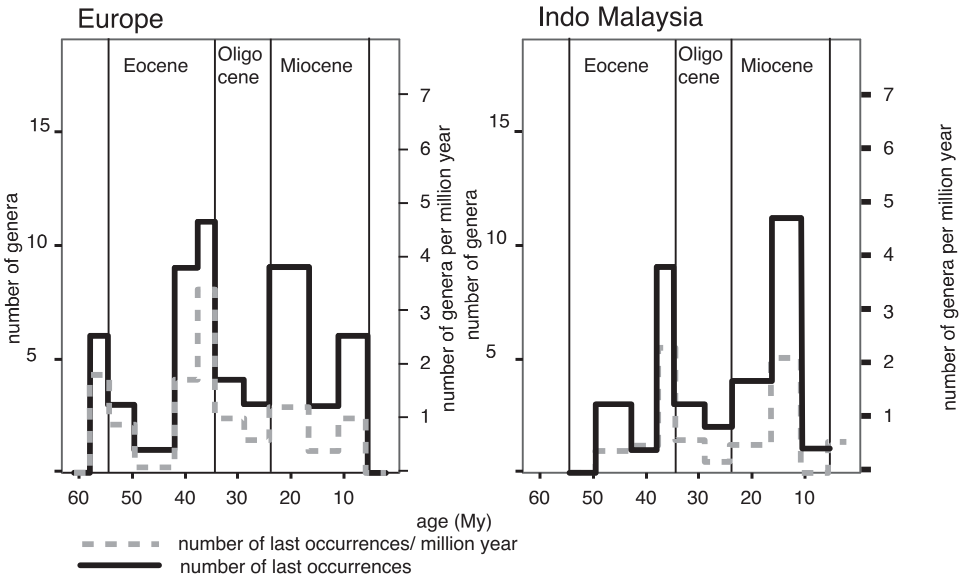


Fig 7.9 Last occurrences per time slice in Europe and Indo-Malaysia

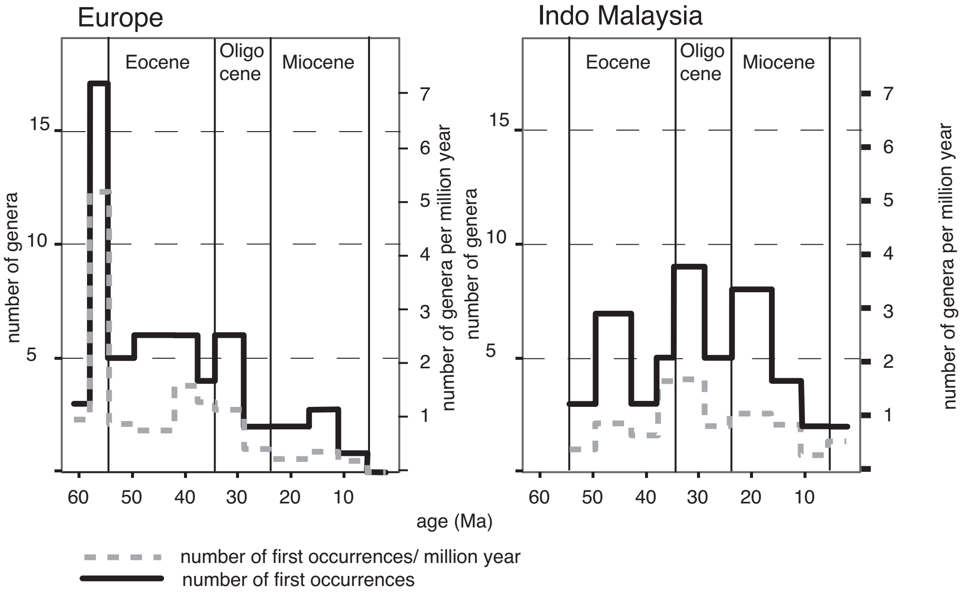


Fig 7.10 First occurrences per time slice in Europe and Indo-Malaysia

other part of the Eocene. Furthermore, there are some genera restricted or nearly restricted to the Priabonian, such as *Silvestriella* and *Linderina*.

Eocene diversity at the genus level is much lower in Indo-Malaysia than in Europe. All but one genus is found in Indo-Malaysia have been found in Europe as well and the most important genera are more speciose in Europe. Wilson & Rosen (1998) found similar results for the diversity of zooxanthellate corals in Europe and southeast Asia.

Oligocene-Recent

In the Rupelian and Chattian the faunas in Indo-Malaysia and Europe both show many FOs (Fig. 7.10) after the extinctions during the Priabonian. Fauna composition and generic diversity is similar between Europe and Indo-Malaysia (Fig. 7.8). The generic diversity of Indo-Malaysia and Europe start to differ in the Chattian to Early Miocene, and this difference increased in the Middle Miocene. Looking at the FO/LO pattern, Europe and Indo-Malaysia show a marked difference. In Europe, a high extinction rate is observed at the end of the Early Miocene and at the end of the Late Miocene, while in Indo-Malaysia there is a large extinction (12 out of 24 genera) at the end of the Middle Miocene.

The number of European FOs is much lower during the Neogene, and especially during the Miocene, than in Indo-Malaysia. Increased isolation because of the closure of the Tethyan seaway might have prevented immigration of genera from the eastern Tethys to Europe, and thus have a significant effect on the diversity of European larger benthic foraminifera.

A similar pattern is found in zooxanthellate corals (Wilson & Rosen, 1998; Rosen, 1999). Rosen (1999) found that zooxanthellate coral diversity in the Mediterranean region matched fairly well with the isotope temperature curve in the early and late Miocene, but not in the middle Miocene. This anomaly might at least partly be caused by an increasing isolation of the Mediterranean in this time. Like generic diversity, occurrences of species of larger benthic foraminifera also show a decrease in diversity (species number) from the Rupelian to Langhian in nearly all regions, except southeast Asia and the Pacific (Jones, 1999). The generic diversity drops in Indo-Malaysia at the end of the Middle Miocene, at a time that average global temperature decreased as well.

Morphology

In Recent larger foraminifera morphologic variability is directly related to environmental parameters (Hallock *et al.*, 1991b; Hottinger, 2001). Areas with a deep photic zone and stable conditions have a higher diversity of euphotic habitats, allowing foraminifera to diversify and specialise in these conditions (Hallock, 1987).

The pattern of morphologic variability in the Eocene suggests that more oligotrophic, shallow marine habitats were present in Europe than in Indo-Malaysia. Not only species numbers were lower in Indo-Malaysian nummulitids, but morphologic variability was less than in the European faunas as well. In the Ypresian the B-forms are generally small, then an increase occurred with the largest species occurring in the late Lutetian and early Bartonian (*N. maximus, N. millecaput*), and a distinct drop around the Bartonian-Priabonian boundary. This is in accordance with the findings in Indo-Malaysia. Brasier (1988, 1995) showed that, using the data of Blondeau (1972), the largest diameter of *Nummulites*

(140 mm) is reached at the end of the Lutetian, after which a marked size decrease occurs to less than 10 mm in the Bartonian and Priabonian.

Alveolinidae and orthophragminidae are two other families that are very abundant in Eocene shallow water limestones. Generally, they are considered to have lived in environments different to those of *Nummulites*. Whereas *Nummulites* is associated with shallow water fore reef habitats, alveolinids are more often found in back reef to even restricted settings whilst orthophragminids are more typical of deep-water fore-reef settings (van Gorsel, 1988). Larger foraminifera are not necessarily associated with reef habitats, however, and can occur in high density on shallow marine carbonate platforms. On carbonate platforms, alveolinids live in the shallow and coastal parts, nummulitids in intermediate depth ranges, while orthophragminids occupy the deepest areas, as long as they remian in the photic zone.

The orthophragminids become extinct at the Eocene-Oligocene boundary, whilst *Alveolina, Planocamerinoides* and *Assilina* become extinct at the end of the Bartonian. *Borelis*, another alveolinid genus, first occurred in the Priabonian and is still extant (Hottinger, 1960; Fleury & Fourcade, 1990).

Both alveolinids and orthophragminids have a higher species diversity within the European realm than in Indo-Malaysia. At least seven species of alveolinids have been reported ranging from Ypresian to Bartonian in Indonesia (Pringgoprawiro *et al.*, 1998), but the occurrence of this genus in southeast Asia needs revision (Adams, 1970). In a revision of the Indonesian alveolininds, Bakx (1932) reported only five species in the Ypresian to Lutetian.

In the European realm more than 80 species of the genus *Alveolina* have been reported ranging from Middle Palaeocene to Bartonian (Hottinger, 1960). The alveolinids reached their largest diameter in the middle Lutetian, but their elongation (diameter/axial length) increased until the end of the Lutetian (up to 20; Brasier, 1988; 1995). The size of the Indonesian species reported by Bakx (1932) range between 7 and 10 mm and their elongation is between 2.5 and 3. Also, Indonesian species show less internal morphological variation; all five species reported by Bakx (1932) belong to the *Alveolina oblonga* group of Hottinger (1960).

Orthophragminids have been reported in a similar number of species to the alveolinids from Indo-Malaysia, while more than 60 occurred in Europe (Less, 1987, 1998; Serra-Kiel *et al.*, 1998). However, no reasonably complete review has been published on the Indo-Malayan orthophragminids, making a comparison between the regions very difficult. The maximum diameter of Indonesian Bartonian *Discocyclina* is about 3 cm, and up to 1.5 cm in the Priabonian.

No complete compilations of morphological diversity in the post-Eocene Cenozoic is available. Large sized lepidocyclinids occur in the Chattian of Europe and Indo-Malaysia, and at least the Early Miocene and possibly the Middle Miocene of Indo-Malaysia.

Habitat structure and trends in other taxa

Palaeogeographic reconstructions incorporating palaeoenvironmental data show that the amount and nature of shallow marine deposits changed markedly during the Cenozoic in southeast Asia (Hall, 1998; Wilson & Rosen, 1998). During the Eocene shallow water carbonates were not widespread. Their geographic extent increased gradually so that they covered a large area by the end of the Oligocene and beginning of the Miocene. During this time the composition of their dominant faunal assemblages changed from larger foraminifera and algae in the Eocene to zooxanthellate corals associated with algae and larger foraminifera n the Miocene (Wilson & Rosen, 1998). Carbonates dominated by larger foraminifera and algae also continued to occur in the Oligocene-Miocene. Wilson & Rosen (1998) suggested that the fragmentation of Southeast Asia, because of the collision with (fragments of) the Australian plate increased the available habitat for zooxanthellate corals. The number of reefal structures also increased during this period (Kiessling *et al.*, 1999). The presence of reefs also increased the habitat diversity for larger foraminifera and thus has a positive effect on larger benthic foraminifera diversity. However, the most abundant larger foraminifera of the entire Cenozoic did not live on the reefs *sensu stricto*, but on the sediment around reefs or on carbonate platforms devoid of reefs. As shown by Hottinger (1990), these are the most stable environments in shallow carbonate shelf systems. Genera whose preferred habitat comprised solid substrates show a more localised distribution (Reis & Hottinger, 1984; Chapter 4, above).

In larger benthic foraminifera, test shape is partly related to the habitat availability. Species with a high diameter/thickness ratio are characteristic of areas with a deep euphotic zone and generally are absent from areas with a shallower euphotic zone (Hallock, 1987, 1988; Chapter 3, above). In *Nummulites* the morphological variability is higher in Europe than in southeast Asia. Moreover, the highest diversity of *Nummulites* in the Eocene of Europe is found within the oligotrophic subtropical gyre of the central Western Tethys (Hottinger, 1990), illustrating the relationship between diversity and nutrient availability.

The higher morphological diversity observed in Europe during the Eocene suggests that the coeval low diversity in southeast Asia was not only caused by its isolated position, but also by environmental factors restricting the number of available habitats, especially an increased differentiation in the photic gradient. The combined shift in both generic and morphologic diversity hints at a change in oceanographic currents (related to changes in palaeogeography). Analogous to the modern day biogeographic patterns, the Eocene larger benthic foraminifera diversity patterns suggest that the Western Tethys was more oligotrophic and warmer than the Eastern Tethys. With changing palaeogeography and palaeoceanography, the Western Tethys became isolated, cooled and may have become more eutrophic than the Eastern Tethys.

The Indo-Malaysian increase in the number of genera may already have started in the Priabonian, but is obscured by the Priabonian-Rupelian faunal turnover. Changing ocean currents and tectonic conuration facilitated migration into the region and create more available habitats for larger foraminifera in Southeast Asia. The fauna turnover at the Eocene-Oligocene boundary was not very rapid, but a gradual process spanning the Lutetian to Priabonian.

Conclusions

1. In the Palaeogene, the larger foraminifera genus *Nummulites* developed more species and larger in the Western than in the Eastern Tethys.
2. This pattern is not unique for *Nummulites,* with *Alveolina* and orthophragminids being less diverse in the Eastern Tethys as well.
3. Morphological data for these three groups shows that variability is smaller in Indo-Malaysia than in Europe. Diversity during the Eocene, at both species and genus level, was higher in the European realm, in prallel to patterns found by Wilson & Rosen (1998) for zooxanthellate scleractinian corals.
4. The Bartonian-Priabonian-Rupelian period of global cooling affected the European fauna more severely than the Indo-Malaysian. In both areas the identity of the faunas changed completely, but the generic diversity increased over this period in Indo-Malaysia, while the maximum diversity in Europe was in the Bartonian, and decreased ever since.
5. Generic diversity already started to increase during the Priabonian in Indo-Malaysia, but the Priabonian- Rupelian extinction obscured this pattern.
6. The number of genera decreased rapidly in Europe during the Miocene, due to the collision between Arabia and Eurasia, which closed the connection with the tropical eastern Tethys, and also caused a decrease in area with a suitable habitat, due to tectonics and climate cooling in Europe.

8. Synthesis

In this chapter I will summarise the current knowledge of environmental parameters affecting the distribution of larger foraminifera in tropical seas. I further discuss the recognition and nature as well as biogeographic relevance of diversity in the fossil record. Finally, the diversity patterns in the Cenozoic fossil record are discussed and related to climatic and tectonic events on global and regional scale.

The Recent situation

The main environmental parameters that discriminate between habitats of species of larger benthic foraminifera are light intensity, hydrodynamic energy, substrate type and nutrient availability. All these parameters are related in a complex way (Fig. 1.1). The distribution of species along a depth gradient is determined by their differing tolerance in illumination levels and hydrodynamic energy. Based on this principle Hohenegger (1995) proposed to use transfer functions for depth estimation based on the density of larger foraminifera species.

The same species occur in much shallower water in the Spermonde Archipelago than in Okinawa, since the transparency of the water is higher in Okinawa than in the Spermonde. For example, the depth range at which *Operculina ammonoides* has been recorded in Okinawa is 30-100 m depth, with a maximum abundance at 60 m (Hohenegger, 1994; 1995), whilst in the Spermonde *O. ammonoides* occurs at 6-12 m in zone 1B and its depth range increases to 21-33 m (40 m in grabsamples) in zone 3+4.

Furthermore, some of the species living at greater depth in Okinawa have not been found in the Spermonde Archipelago.

In Chapter 3 (see above) a model was presented based on the life history of species and seasonally varying conditions in the Spermonde Archipelago (Fig. 3.4). Species that can survive in low irradiation levels are more susceptible to seasonal variation than shallow living species because of the logarithmic decrease in light intensities. In this model the first assumption is that all species have the same range in tolerance to irradiation level. For example, a shallow living, species tolerant to high irradiation levels has a range of 10-50% of the surface irradiation level, whilst a deeper living species, not tolerating high irradiation levels has a range of 1-5%. Data presented by Hohenegger *et al.* (1999) are congruent with this assumption. The second assumption is that species are not able to move into deeper/ shallower habitats seasonally.

Larger foraminifera can only maintain their large cell mass because of the energy provided by their light dependant symbionts. During longer periods of adverse conditions, maintaining symbionts will not be profitable anymore and even cost extra energy because of the higher nutrient demands for the entire cell. In seasonal conditions, transparency is reduced during part of the year. The hypothetical depth at which the foraminifer species can live thus becomes shallower (Fig. 3.4a, b). A species can only survive at a locality, otherwise favourable, when the irradiation level is within its critical limits during its entire life. This condition is more likely to be met in species that live in high light levels than in species living in low light levels (Fig. 3.4a).

Environmental predictability is an important factor controlling the distribution especially of longer living species. Because of their large size, larger foraminifera often have long generation times. In Recent larger foraminifera, it takes the agamont of *Cycloclypeus carpenteri* six months to reproduce; thus the much larger sized gamont

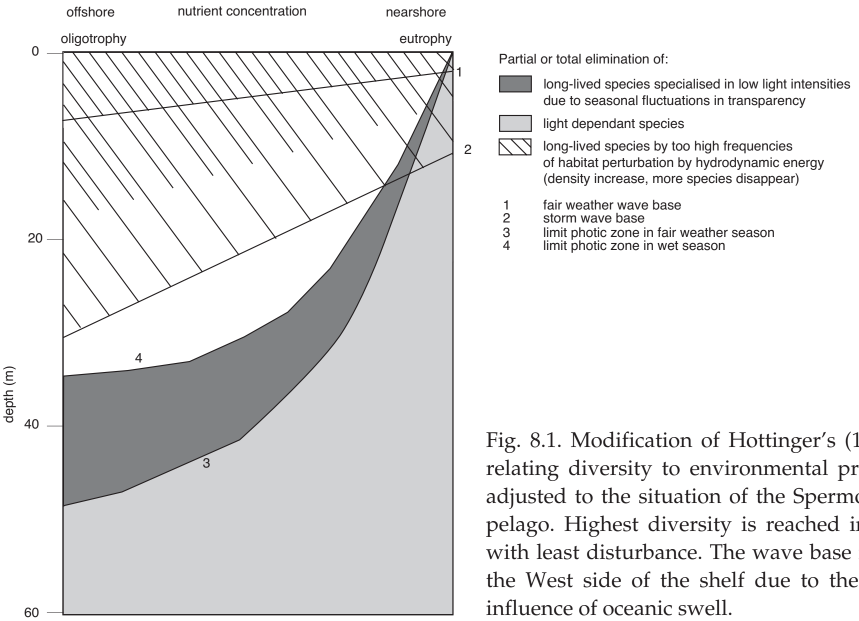


Fig. 8.1. Modification of Hottinger's (1990) model relating diversity to environmental predictability, adjusted to the situation of the Spermonde Archipelago. Highest diversity is reached in the range with least disturbance. The wave base is deeper at the West side of the shelf due to the decreasing influence of oceanic swell.

will reproduce after a much longer period (Krüger *et al.*, 1996). Purton & Brasier (1999) showed that the B-forms of Eocene *Nummulites planulatus* could live for up to six years before reproducing. If during this period the conditions move outside the critical limits for the species for too long a period (the length of this time is not yet known), it will die before reproduction. If this happens on a more or less regular basis, the species will not be able to maintain itself in the area.

Hottinger (1990) also made a large-scale model concerning the interaction between habitats, life history and cyclical dynamics in environmental parameters. He made a cartoon showing factors affecting benthic foraminifera diversity in the upper part of the water column. This cartoon I modified into Figure 8.1, by adding a zone in which species preferring low light intensities cannot occur. To apply this figure to the occurrence of (larger) benthic foraminifera in the Spermonde, it should be slightly modified. The (storm) wave base is shallower in the eutrophic part of the Spermonde Shelf, because of the effect of oceanic swell on the seaward (west) side of the shelf. The depth should be re-scaled as well.

The occurrence of a species within a biotope does not necessarily mean that the environmental conditions are optimal at that specific locality, but that the environmental parameters are within the critical limits for that species. Since all species in a comunity have different tolerance to relevant environmental parameters, it is not necessary that in all regions or reefs species occur in the same assemblage. Changing combinations of environmental parameters between areas can result in a biotope shift. In Table 8.1 the distribution of species found in the Spermonde Archipelago (Chapters 2,3, above) and Cabilao (Chapter 5, above) are summarised, and compared to observations in other areas within the Indo-West Pacific, from which only in a limited number of areas are comparable data available. Sesoko Island is the most extensively studied area, with studies by Hohenegger (1994, 1995, 2000) and Hohenegger *et al.* (1999). The study by Hohenegger *et al.* (1999) is most comparable to the studies in this thesis, since only the upper reef slope (<50 m depth) was investigated. Hallock (1984) and Hohenegger (1996) published on the occurrence of larger foraminifera from Palau. Several other studies dealth with a limited number of taxa only.

The distribution of Nummulitidae over the Spermonde Shelf best fits the proposed models, in both the living fauna and the thanatocoenosis. *Operculina ammonoides* is the most tolerant species, followed by *Palaeonummulites venosus*, *Operculina complanata* and *Operculina heterosteginoides*. Species which have been found at even larger depths outside the Spermonde (e.g., *Cycloclypeus carpenteri* and *Heterostegina operculinoides*) have not been found on the Spermonde Shelf.

The largest difference in faunal characteristic between the Spermonde Archipelago and Cebu Island is the almost total absence of *Elphidium craticulatum* in the >0.5 mm size fraction at the latter, whilst in the Spermonde Archipelago *E. craticulatum* is the second most abundant species in terms of sample number and the most abundant in terms of number of individuals. The most important ecological trait that distinguishes *Elphidium craticulatum* from larger symbiont-bearing foraminifera is that it shows chloroplast retention and is not an obligate algal-host system. Chloroplast retention is not a symbiotic relationship, since it is lethal to the algae: *E. craticulatum* feeds on and digests the diatoms, but the chloroplasts are left intact and functioning (Correia & Lee, 2000). A model of nutrient flows in a host-symbiont system for chloroplast-husbandry shows that in the latter the nutrient supplies of the foraminifera and the chloroplast are decoupled, whilst in symbiont-bearing foraminifera this flow is coupled. Chloroplast retention is profitable for the foraminifera in systems where dissolved nutrients are abundant and light is still available. It is observed in a much wider range of conditions, from cold fjords in Norway to tropical reefs in Indonesia, than symbiosis. The algae (symbionts) do not need the hosts to make nutrients available for their metabolism. There are no experimental data available whether or not chloroplast husbandry is obligate in *Elphidium.* Possibly the energy provided by the chloroplasts is not essential, but photosynthesis might enhance calcification and thus be profitable to the foraminifera.

Particularly if chloroplast husbandry is not obligate, *Elphidium* will be able to cope better with changing conditions than species that are obligate symbiotic. Living at a depth where conditions allow photosynthesis for only a couple of weeks a year, the opportunistic *Elphidium* takes benefit from this by not completely digesting the chloroplasts, whilst the obligate symbiotic species cannot maintain itself long enough for reproduction. The increase in abundance of *Elphidium* towards the depth limit of the photosymbiotic species as seen in the Spermonde Archipelago favours this explanation, but testing in a laboratory is required.

Nutrient availability, sea surface temperature and diversity

Shallow tropical marine ecosystems are characterised by high diversity and low net productivity (Hallock & Schlager, 1986). This paradox can be better understood by distinguishing different aspects of biological productivity (Hallock & Schlager, 1986). The term “nutrients” refer to fixed nitrogen or phosphate ions required by all organisms to synthesize proteins and nuclear material cell maintenance, growth, and reproduction. In shallow oligotrophic ecosystems primary productivity (the rate at which energy is fixed into organic carbon) can be very high, but the fixed energy is mainly used for respiration, thus net productivity is low (Hallock & Schlager, 1986) and limited by the availability of nutrients. The high respiration rates promote symbiotic associations between primary producers (algae, photosynthetic bacteria) with ‘predators’ capable of capturing particulate organic matter (mixotrophs; Hallock, 1985). In very oligotrophic environments the primary production is by animal-plant symbionts (Birkeland, 1985; Hallock, 1987). Furthermore, the length of the food web increases in oligotrophic environments. In oligotrophic environments water transparency is higher, allowing a larger depth range at which symbiont-host systems can photosynthesise (Hallock, 1987). Oligotrophic areas occur in regions with no or very limited terrestrial influx, thus transparency is entirely determined by the plankton concentration, which is inturn determined by nutrient availability (Hallock, 1987).

In contrast, in eutrophic conditions short living r-selected organisms support a short food chain (Hallock, 1987). In less eutrophic environments, the food chain starts to get increasingly complex.

Hallock (1987, 1988) proposed a model that described the potential utilisation of the photic zone by symbiotic larger benthic foraminifera as a function of nutrient availability. This model predicted that in relatively eutrophic environments, taxa occur unspecialised in respect to light. In more oligotrophic conditions these unspecialised taxa, given enough time, are replaced by more specialised species with respect to light intensity, resulting in less interspecific competition (Fig. 3.4b; Hallock, 1987). Zonations of many specialised species only occur in highly transparent areas that are sufficiently stable. One of the conditions that determine where the most specialised species cannot occur is in more variable conditions in areas richer in nutrients (Hallock, 1987).

The distribution of all high-temperature dependent, shallow water organisms should be governed by climate and ocean currents, with the strongest response to temperature, nutrient availability and variability (Adams *et al.*, 1990; Hallock, 1987; this thesis). Using global distribution maps, Langer & Hottinger (2000) found lower temperature limits for many species, but they did not find an upper temperature limit

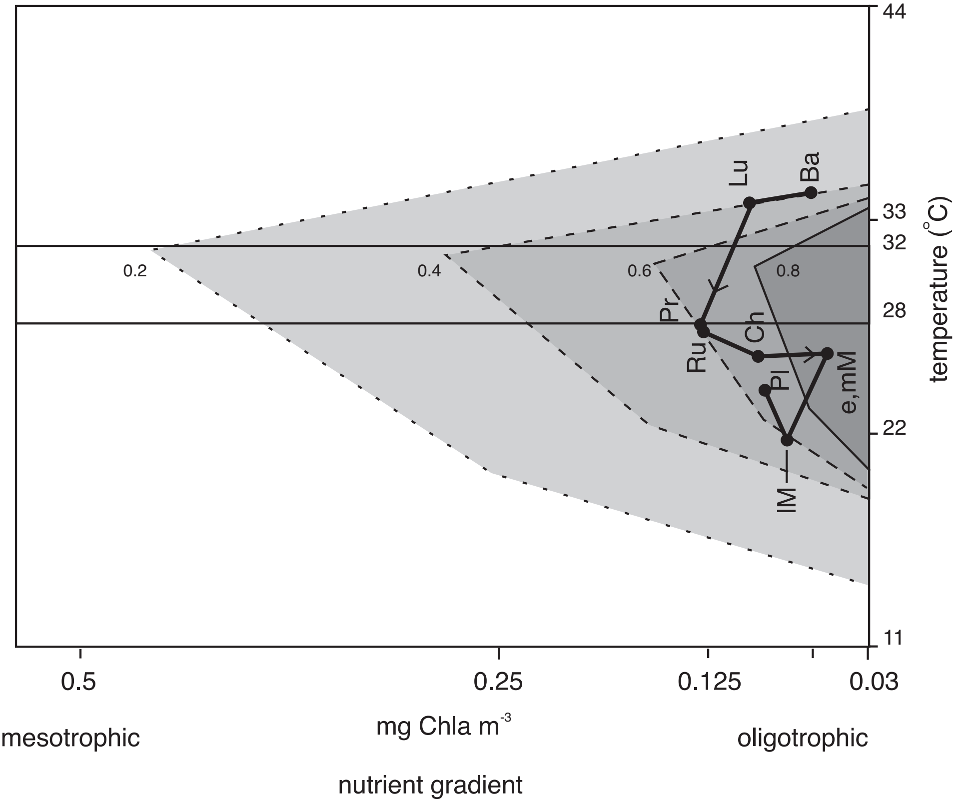


Fig. 8.2. Diversity as a function of sea surface temperature and productivity. For this graph, maximum diversity was reached at 28-32°C. The areas are bordered by lines connecting similar fractions of maximum diversity that can be reached (in this graph highest diversity is reached at 30°C and very oligotrophic conditions).

The nutrient gradient is adapted from Hallock (2001). In oligotrophic conditions the dominant macro-benthos are corals, going to macroalgae in a mesotrophic system. The exact place of the values along the x-axis is arbitrary. The trace in the graph are the values found for the Indo-Malaysian time slices (see text for explanation). Lu = Lutetian, Ba = Bartonian, Pr = Priabonian, Rupelian, Ch = Chattian, e,m M = early-Middle Miocene, lM = late Miocene, Pl = Pliocene.

for any larger foraminifera. However, in local situations high water temperature can be limiting to the distribution of larger foraminifera. For instance, on the shallow reef flat behind the rampart in the Spermonde during several months each year with extreme low tide, water temperature rise to >32°C and no larger benthic foraminifera are found here. Yet, larger benthic foraminifera occur on the reef flat of Lankai, which is as shallow and at least as highly energetic as the other reef flats of the Spermonde Archipelago, but the temperature of the water is lower because it is regularly flushed by water from the cooler Makassar Strait. *Laevipeneroplis proteus*, restricted to this very shallow environment, is only found here.

On the other hand, the poikiliothermal larger benthic foraminiferal metabolic rate doubles with a 10°C temperature rise. Thus, with the same nutrient concentration, twice as many nutrients are needed to maintain the foraminifera. Temperature decreases with depth, and thus it is more likely that the bottom temperature at deep places is below the upper temperature limit of deep dwelling species in high SST areas.

Taking these considerations in mind, I developed a theoretical productivity-temperature graph, predicting diversity (Fig. 8.2). For this graph I constructed a productivity- temperature function, in which diversity (D) is the product of predicted diversity based on productivity ($D_{(p)}$) and predicted diversity based on temperature ($D_{(t)}$). In this function both $D_{(p)}$ and $D_{(t)}$ are expressed as a fraction of maximum diversity, i.e. $D_{(p)} = D_{obs(p)}/D_{max}$ and $D_{(t)} = D_{obs(t)}/D_{max}$, in which $D_{obs(p)}$ is the observed diversity at nutrient availabilty p within the range of maximum diversity with respect to temperature, $D_{obs(t)}$ is the observed diversity at temperature t in the most oligotrophic condition, and D_{max} is the maximum observed diversity. In the shown graph, I used maximum diversity at 28-32°C and a linear relationship between nutrient availability and diversity. For example, at a locality halfway the nutrient availability spectrum and with a SST of 24°C, $D_{(p)} = 4/8 = 0.5$, $D_{(t)} = 5/8 = 0.63$ and $D_{(0.5,\,24)} = 0.5 \times 0.63 = 0.3$.

Which areas are most diverse?

With all these requirements and restrictions on the distribution of (larger) benthic foraminifera we would like to know which areas have the highest potential diversity. Before we can proceed with this question we should decide how diversity best can be expressed. The easiest way is 'simple diversity' or species richness, the number of species recorded in a sample or area. Though it is tried to sort out a similar number of specimens from a sample (200-300), sample sizes do differ. Species do not occur in similar abundance in samples as well, and, for example a sample with eight species in similar abundance can be regarded as more diverse than a sample containing predominantly one species and rare specimens of seven others.

I have used the Spermonde data set to get an impression of the dependence of diversity on sample size. Species number (S), Shannon diversity ($H = \ln p/p_i$) and evenness ($E = H/\ln S$) show a similar relationship with sample size. Large samples never have a low value for either S, H, or E, but the highest measures of S, H, and E are found in intermediate sample sizes (Figs. 8.3a-c). Thus, the largest samples are not necessarily the richest samples. Also, S and H are positively correlated (Anova, $F = 225$, $p < 0.005$).

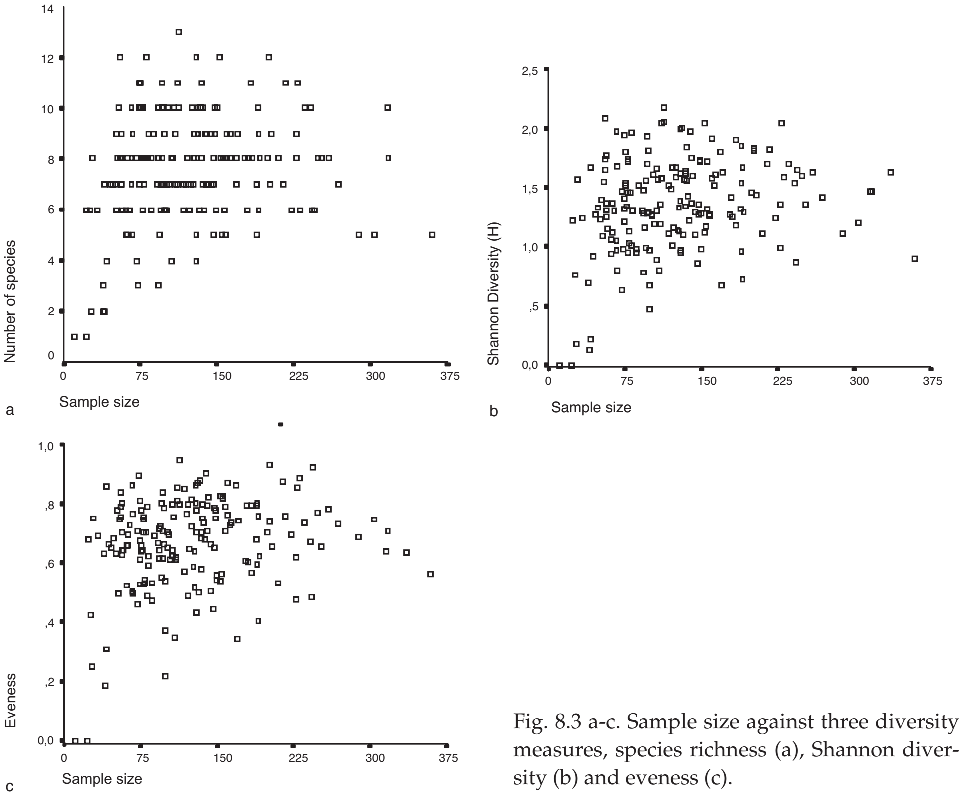


Fig. 8.3 a-c. Sample size against three diversity measures, species richness (a), Shannon diversity (b) and eveness (c).

Since larger benthic foraminifera genera contain only a limited number of species and can be actively searched during field research, the best (and easiest) way to express their diversity is by species number. Also, using standardisation would not alter the patterns found.

Taking into account the larger benthic foraminifera only, the Indo-West Pacific, and especially East Indonesia, the Philippines and Japan, are the richest areas (Hallock, 1988; Langer & Hottinger, 2000). Calcarinids, except for *Neorotalia calcar*, are restricted to the Indo-West Pacific, and also more species of nummulitids have been recorded here. Not all sites in this area are equally diverse. Areas with a deep photic zone and moderate hydrodynamic energy have the highest potential for housing high numbers of species, since along the depth gradient (light intensity) species specialised to narrow ranges of light intensities can occur. A deep photic zone may protrude well beyond the storm wave base where species with very friable and easily transported tests can safely occur.

Battering of waves regularly disturbs the coral cover on the upper reef slope providing habitat for species preferring solid substrate. However, too frequent storms disturb the substrate too often for species with a long generation time to reproduce and those will be absent there.

A wide reef flat also promotes diversity. From the reef edge onwards the reef flat first has an area showing very low larger foraminifera density, because of continuous high wave energy. Sand in this region shows wave ripples and larger foraminifera will not be able to stay on top of the sediment to take advantage of their symbionts. Further from the reef edge, the reef flat is sheltered from swell originating from outside the system, and is only affected by high hydrodynamic energy caused by local storms. Here enough suitable habitat is present to find shelter against too high illumination levels and hydrodynamic energy. Crest pools and deeper areas also diversify the number of available biotopes, and, thus, the number of species on the reef flat.

The Spermonde Archipelago can serve as the test case for a model that explains what happens when conditions deteriorate for larger benthic foraminifera. Along a gradient with decreasing terrestrial influence, species number increased from 7 in the most nearshore area (SNZ, Chapters 2 and 3) to 15, 17 and 18 in the Northern Nearshore, Mid Shelf and Outer Shelf Zones, respectively, at increasing distance from the shore. Including species of which only empty shells have been found enhances this pattern, since two species are added in the outer shelf zone. This pattern compares very well with the model proposed by Hallock (1987, 1988; Fig. 3.4a). Also on a regional scale, nutrient availability affects diversity directly.

The tropical realm is discontinuous because of some barriers that prevent or at least limit communication between areas (Langer & Hottinger, 2000). The faunal provinces are confined to trophic gradients in longitudinal regions. In the present day, three faunal provinces can be recognised.

The Indo-West Pacific Province reaching from the Maldives to Hawaii, with a central region (East Indonesia, Philippines and South Japan) that has some additional species.

The Western Indian Ocean Province which is limited by the east coast of Africa to the West and the circum India high nutrient zones to the East. This province has many similar species as the Indo-Pacific province, but is characterised by the occurrence of *Heterocyclina tuberculata* as a substitute for *Cycloclypeus carpenteri* and the absence of calcarinids (Langer & Hottinger, 2000).

The Caribbean Province has an entirely different fauna and is isolated from the Indian and Pacific Ocean by the landmasses of Africa and America (Langer & Hottinger, 2000; Paulay, 1997).

Diversity in the fossil record

Larger benthic foraminifera show a strong correlation between morphology and environmental parameters (Figure 1.1; Hallock *et al.*, 1991; Hottinger, 1997; 2000). In the fossil record, similar test architecture occurs repeatedly in phylogenetically unrelated taxa (Hottinger, 1997). As a result of extant taxa constituting only a limited part of Cenozoic assemblages, and a large faunal turnover at the Eocene-Oligocene boundary, the depth gradient is occupied by a set of different species during the Palaeocene-Eocene, the Oligo-Miocene and the Pliocene-Recent. In the modern day ocean, the highest diversity can be related to the most oligotrophic areas, limited by oceanographic boundaries. Diverse areas are characterised by a long light gradient and stable conditions, so that species can differentiate along this gradient. This differentiation is not only in species, but also in morphology. For instance, in the Indo West-Pacific faunal province the deepest living species are (on soft substrate) *Palaeonummulites venosus*, *Operculina ammonoides*, *Cycloclypeus carpenteri*, *Heterostegina operculinoides* and *Operculina heterosteginoides* (Hohenegger *et al.*, 1999). The last two species only occur in the most diverse part of the faunal province. These nummulitids all show a phenotypic increase in diameter/thickness ratio.

The most diverse samples in the thanatocoenosis of the Spermonde are found around the reefs (Chapter 4). Here species living on the reef slope and at the reef base are mixed. Because of the high-energy environment, preservation potential on the reef slope and reef flat is low, and empty tests of species living there were only found displaced in the reef base samples. This does not directly affect estimates of diversity, but should be taken into account during palaeoenvironmental reconstructions.

Parameters affecting the diversity distribution act on temporal and spatial levels. First there is the worldwide recognizable subdivision of the Cenozoic into three or four faunas, the Palaeocene-Middle Eocene, the Late Eocene, the Late Oligocene to Middle Miocene, and the post-Miocene fauna, which occur as interactions with global events (Hottinger, 1997). Secondly, there is interaction with regional and local parameters that attenuates these global patterns into local and regional patterns.

Large scale palaeoenvironmental processes influencing the palaeobiogeography of larger foraminifera

Sea surface temperature (SST)

Geologic plate configurations, and the presence and absence of either Antarctic or Arctic polar ice-caps, resulted in changing ocean circulation patterns and global climatic conditions, i.e., in latitudinal contractions and expansions of the high sea surface temperature (SST) belt (e.g., Adams *et al.*, 1990). Throughout the Cenozoic, ocean circulation patterns and basin configurations lead to high temperatures at the western sides of oceans. Indo-Malaysia was always positioned on or near the equator, within the warmest regions on earth. Due to the collision of Australia with Eurasia and the narrowing of the Indo-Pacific gateway, the Pacific Warmpool moved gradually eastward during the Miocene (Wang, 1994; Hall, 1998). Europe, positioned at the northern margin of the Western Tethys, laid at considerably higher latitude, around 30°N, and was thus more affected by changes in the temperature gradient.

All other parameters remaining constant, a prediction based on SST would show a high diversity in Indonesia throughout the Cenozoic, and at all times a lower and decreasing diversity from the early Eocene onwards in Europe.

Palaeoceanography and ocean circulation rates

Several studies have linked larger foraminifera diversity to planktonic foraminiferal diversity by the trophic resource continuum model. The Trophic Resource Continuum (TRC) in euphotic waters of the world's ocean is the spectrum of conditions from the richest runoff and upwelling to the most nutrient deficient subtropical seas (Hallock, 1987). Though at first developed to predict larger foraminiferal diversity and distribution in Recent oceans, the model can also be used to explain diversity trends through time (Hallock, 1987, 1988; Hallock *et al.*, 1991; Boersma *et al.*, 1998; McGowran & Li, 2000).

Changes in ocean circulation rates influence the global nutrient gradient in surface waters. Reduced rates of circulation result in an expanded nutrient gradient and a higher potential diversity, while higher mixing rates contract the nutrient gradient and has a lower potential diversity (Hallock, 1987; Hallock *et al.*, 1991a). During periods of strong oceanic mixing the deep photic zone assemblage, with species adapted to living in very low light levels, disappear resulting in both a taxonomic and morphologic lower diversity (see also Fig. 3.1).

Eustacy

Apart from the effect of direct causes of eustatic sealevel change (predominantly produced by the waxing and waning of ice caps and changes in rate of sea floor spreading), an obvious result of high sealevels is the flooding of continental margins leaving more potential habitats for shallow marine fauna like larger foraminifera. During periods with low sealevels the base level of erosion is lowered and, accordingly, erosion rates will be higher, thus supplying more nutrients and sediment to the coastal zone, further deteriorating the environment for larger benthic foraminfera.

Faunal characteristic

The distribution and diversity of Recent larger foraminifera is, apart from historical factors, also determined by abiotic parameters in the surrounding ocean and terrestrial realm. On a global scale, the Indo-West-Pacific faunal province is divided into two parts by the outflow of the Indus and Ganges rivers from the Indian continent, supplying abundant nutrients and mud to the marine environment (Langer & Hottinger, 2000). Obvious parameters affecting larger foraminiferal distribution are the presence and extent of tropical shallow marine seas. Other important parameters are interactions with the terrestrial realm, especially the amount of run off. This is affected by precipitation rate, topography, vegetation cover and drainage systems.

In order to compare these parameters, palaeoenvironmental maps provided by Hall (1998) have been used (reproduced here as Fig. 8.4). Mapping terrestrial environment and physiography of former land area is difficult because periods of uplift, erosion and emergence are mainly recorded by negative evidence, such as unconformities and stratigraphic incompleteness (Hall, 1998). However, it should be kept in mind that especially the position of mountainous areas are indirectly inferred and that estimates of surface area of mountainous terrains are typically quite rough.

The Cenozoic can be divided into three or four periods with high diversities, the Early-Middle Eocene, the Late Eocene, the Miocene and the Pliocene to Recent separated by three periods of larger foraminiferal turnover, the Thanetian (LFT1), the Late Eocene-Early Oligocene (LFT2) and the Middle-Late Miocene (Hottinger, 1997).

The Eocene

In the Ypressian to Lutetian models predict a 20-24°C temperature at 37 m depth (Bice, pers. com). The highest temperature in this model was found off the east coast of Africa, around the Palaeoequator (Bice, pers. com.). The most recent combined cli-

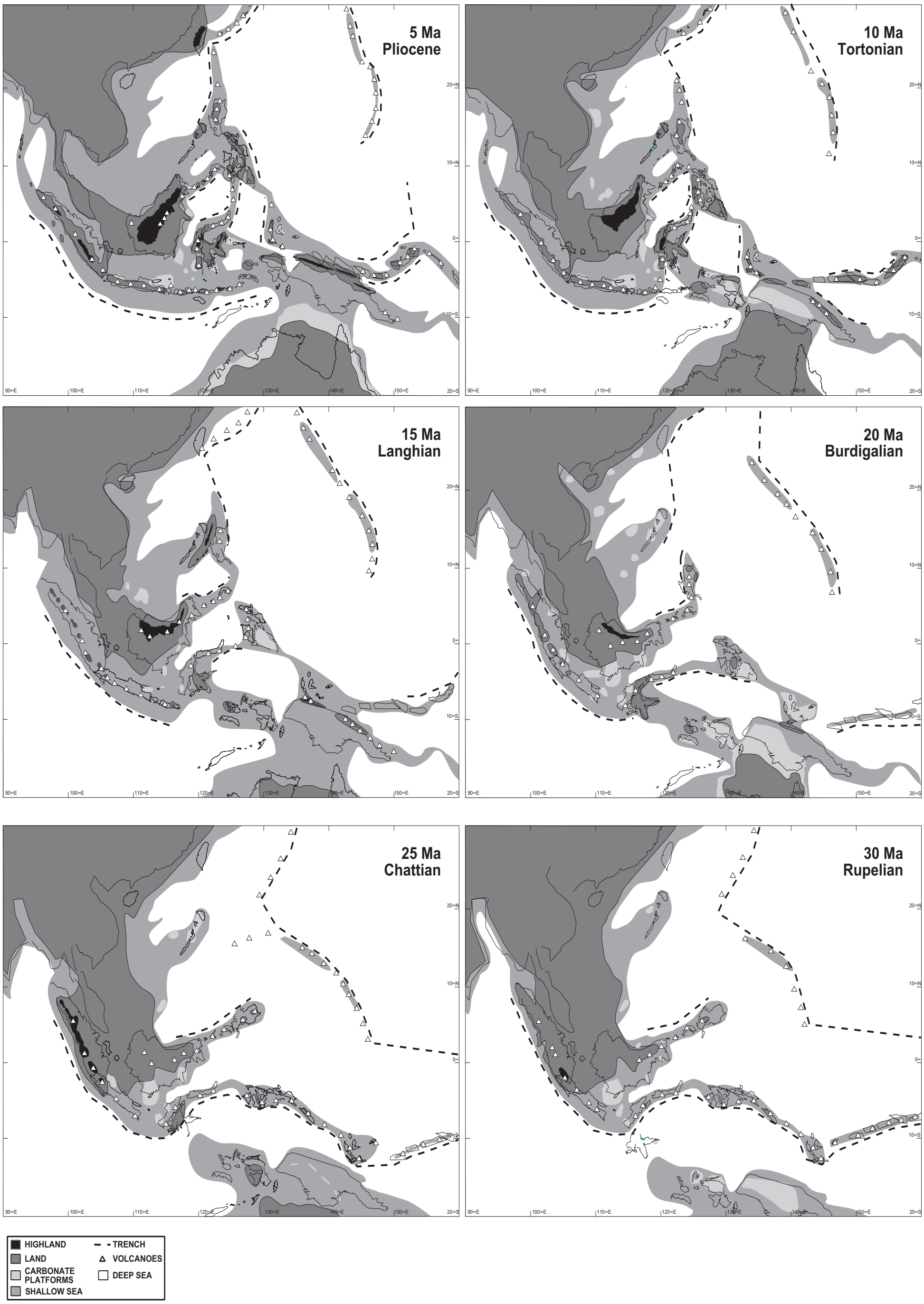


Fig. 8.4. Paleogeographic maps, showing mountainous areas, land, shallow seas and deep sea during the Rupelian, Chattian, Burdigalian, Langhian, Tortonian and Pliocene (after Hall, 1998).

mate and ocean circulation models show tropical SSTs that are somewhat higher than present day values (30-36°C) in the Ypresian, with highest temperatures on the western sides of the ocean basins (Bice, Norris, Pearson, pers. com.).

The situation within the Lutetian and Bartonian is less clear. Deep waters in the world's ocean and surface water at high latitude cooled strongly after the very warm early Eocene. Early Eocene surface waters at the poles were estimated to have 15-17°C, while at some time during the Bartonian or Priabonian at least partial ice sheets developed on Eastern Antarctica (Prentice & Matthews, 1988; Thomas, 1992 and references therein). This suggests a stronger equator to pole temperature gradient and less effective transport of heat from the equator to the pole, which suggests higher equatorial temperatures. The latitudinal gradient increased during the Late Eocene and Early Oligocene, while tropical temperatures remained similar to today's values (Zachos *et al.*, 1994).

In a review of biotic evidence, Adams *et al.* (1990) showed that the fossil record of mangroves, zooxanthellate corals and larger foraminifera suggests that a considerable part of the world oceans has experienced tropical (>25°C) sea surface temperatures and that a larger area surrounding the tropical zone had experienced subtropical (20°C-25°C) sea-surface temperatures; this area expanded and contracted during periods of global climatic warming and cooling since the late Cretaceous. Subsequent compilations of $\delta^{18}O$ data from planktonic foraminifera more or less confirmed this pattern for the Palaeogene (Zachos *et al.*, 1994; Pearson *et al.*, 2001).

In general, the onset of glaciation in Antarctica marked a period of changing ocean circulation patterns. Circum-tropical transport became increasingly difficult with the collision of India to Eurasia, and even more so because of Africa approaching Arabia. Throughout Palaeogene times, continental connections progressively loosened between Antarctica and Australia, although the presence of small units in the Tasman Sea area prevented the establishment of a deep water gateway until ~40 Ma (Lawver *et al.*, 1992). Similarly, between South America and the Anarctic Peninsula, the Drake Passage remained closed to deep circulation until slightly later; but by ~30 Ma, deep and shallow circumpolar circulation had been established and the thermal isolation of Antarctica was complete (Lawver *et al.*, 1992; Dingle & Lavelle, 2000). The most important effect of this change was that ocean circulation was driven by differences in temperature and to a lesser extent by salinity during the Palaeocene, whilst in the new (post-Oligocene) situation salinity became more important, resulting in larger density differences between watermasses and thus faster circulation, at least in the Southern Ocean (Diester-Haass, 1995; Salamy & Zachos, 1999).

Faster ocean circulation rates result in increased upwelling, thus increasing surface water productivity (Salamy & Zachos, 1999). The Palaeogene thermal isolation of Antarctica and mountain building in the Himalayas also resulted in seasonally more variable conditions; the first evidence for a monsoonal climate around the equator came from this time (Morley, 2000). In a monsoonal climate the seasonality increased, decreasing predictability of the environment and reducing the availability of suitable conditions for long living specialists. In the dry period of monsoons dust is blown over coastal seas. Nowadays this is the most important source (together with ice-rafted debris) of limiting micro-nutrients (e.g., Fe) to the Southern Ocean (Salamy & Zachos, 1999). Together, these changes will have noticeably increased the productivity of the world oceans (Salamy & Zachos, 1999). This increase in productivity occurred stepwise, with three periods of marked increase in productivity at 41.6-43.1 Ma, 36.9-35 Ma and 35-33 Ma (Diester-Haass, 1995).

At the close of the Palaeocene the first larger foraminifera turnover (LFT1) took place, characterized by a considerable differentiation at the species level and an increased adult dimorphism, i.e., a difference in size between the microspheric and macrospheric generation (Hottinger, 1998; Orue-Etxebarria *et al.*, 2001; Fig. 8.5). In the Western Tethys (Europe to Pakistan) LFT1 is readily recognizable at one level (SBZ5 in Serra-Kiel *et al.*, 1998). In Indonesia LFT1 is not recognized at the same level, but occurred in the Middle Lutetian (Fig. 8.5). The Ypresian and early Lutetian fauna is still characterized by small forms, few genera and low adult dimorphism; adult dimorphism and generic as well as species diversity increased from the middle Lutetian onwards.

The highest diversity of larger foraminifera was reached within the Lutetian to Bartonian (Adams *et al.*, 1990; Brasier, 1995; above). At this time not only specific and generic, but also morphologic diversity, was highest (with a possible exception for the Oligocene to Early Miocene). Langer & Hottinger (2000) showed that modern day diversity coincided with regions of high SST.

Although only limited data are available for Early Eocene larger foraminiferal diversity in the East Tethys, it was much higher in the Western Tethys than in Indo-Malaysia (IM). Morphological data confirm this observation. In the IM only (relatively) small larger foraminifera occur, while in Europe and northern Africa large specimens occur commonly. A very large sized *Nummulites* (*N. luterbachi* Boukhary, Bassiouni & Hussein-Kamel*)* in the Early Eocene of Egypt occurred on the edge of the zone of highest SST, while maximum diameter elsewhere in the West Tethys was much lower (Wielandt, 1999).

As is shown in figure 8.2, there are two explanations to this incongruence between the fossil and Recent pattern possible, which do not exclude each other:

- there is an upper limit to larger benthic temperature tolerance.
- there are no sites with upwelling in the Western Tethys or Caribbean (Bice *et al.*, 2000). Furthermore, mountainous vegetation types made up a large part of the Sundaland flora and, together with the humid climate, terrestrial run off is probably high (Morley, 2000). Both factors lead to high productivity and few opportunities for larger foraminifera. High productivity is confirmed by the planktonic foraminifera assemblage from the Nanggulan Formation (Java: Pearson, pers. com.). Hottinger (1990) showed that the highest diversity in the Western Tethys was reached in a subtropical gyre, isolated from nutrient input from land and from upwelling.

The Eocene-Oligocene transition

The larger foraminiferal turnover around the Eocene-Oligocene transition (LFT2) occurred simultaneously, and in the same sequence all over Tethys (Fig. 8.5). Genera containing species that obtain large diameters disappeared stepwise. *Assilina* and *Pseudocamerinoides* had obtained their largest diameter (though never as large as *Nummulites*) already at the end of the Lutetian, and disappeared completely in the Bartonian.

In *Nummulites* the largest species disappeared before the Bartonian-Priabonian boundary, and four out of seven species in the latest Bartonian are early species in lineages that diversified in the Priabonian or Rupelian (Schaub, 1981; Serra-Kiel *et al.*,

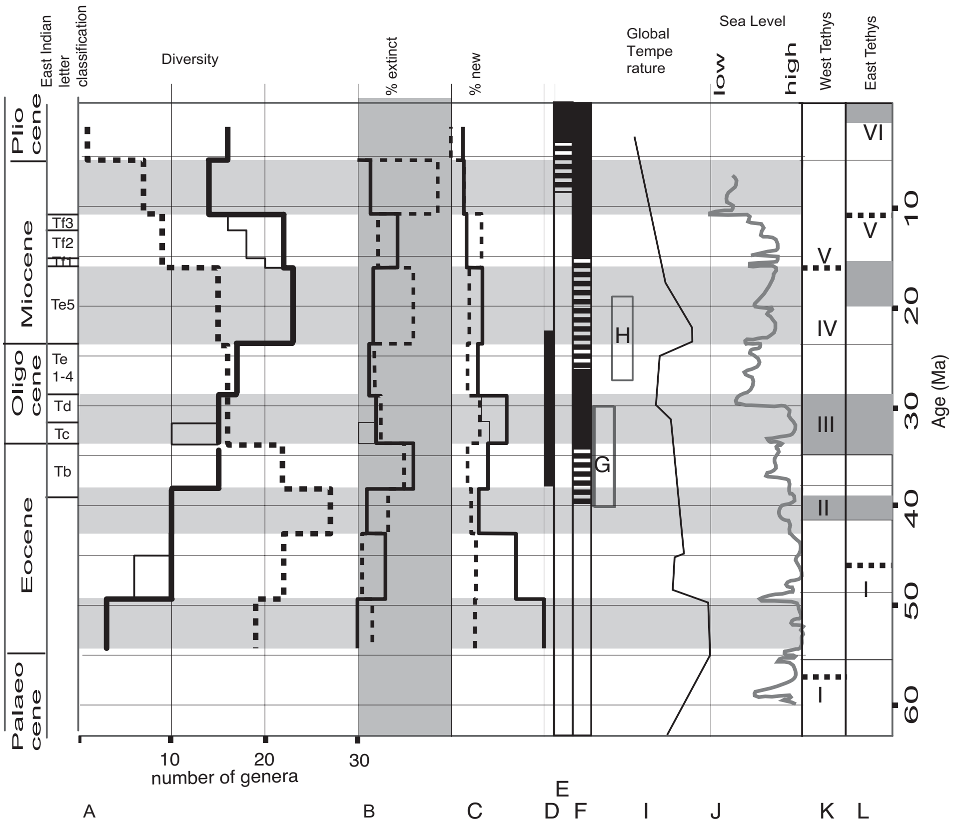


Fig. 8.5. Compilation of diversity measures and palaeogeographic and palaeoenvironmental events.

A: generic diversity in Europe (broken line) and Indo- Malaysia (solid line). The thin line indicates diversity in letter stages that can be recognised in Indo-Malaysia, but so far cannot be correlated to recognisable units in Europe.

B: percentage of genera in time slice that has its (local) last occurrence at the end of that time slice. lines as above.

C: percentage of genera in time slice that has its (local) fist occurrence at the beginning of that time slice. lines as above.

D: dark line indicates the absence of ever wet forests in Southeast Asia (from Morley, 2000, and Morley pers com).

E: presence of Arctic icesheets (solid: permanent, broken ephemeral) (Zachos *et al.*, 2001).

F: presence of Antarctic icesheets (solid: permanent, broken ephemeral) (Zachos *et al.*, 2001).

G: opening of the circum Antarctic current system (Dingle & Lavelle, 2000).

H: collision of Africa to Eurasia.

I: Global average temperature during the Cenozoic, simplified after Zachos *et al*. (1994).

J: Third order sea level curve of Haq *et al.* (1987)

K: larger foraminiferal events in the West Tethys: I first occurrence of species with pronounced adult dimorphism (LFT1), II: interval of maximum adult dimorphism and global diversity, III: transitional period with low diversity faunas with reduced adult dimorphism (LFT2), IV: interval of maximum diversity and adult dimorphism, V: Miocene extinctions (LFT3), VI: recovery in the Pleistocene to Recent of Indo-Malaysia.

L: larger foraminiferal events in the East Tethys (for explanation of numbers, see K).

1998). Note that many of the species occurring in the early part of the Bartonian had a large geographic range, that provincialism was reduced at that time. In Indonesia stratigraphic resolution is not yet detailed enough to see whether the largest forms disappeared at or before the Bartonian-Priabonian boundary.

Priabonian 'chronofauna'

The Priabonian fauna, characterized by the occurrence of large *Discocylina*, and *Pellatispira*, in the absence of typical Middle Eocene genera like *Assilina* and *Alveolina* and large representatives of *Nummulites*, has been recognized as a separate chronofauna (Hottinger, 1997). Most assemblages from this age are characterized by relatively large orthophragminids and *Operculina*. However, instead of being a separate chronofauna, the distinct nature of the Priabonian fauna could also be a response to environmental conditions causing the presence of more algal overgrowth on the substrate.

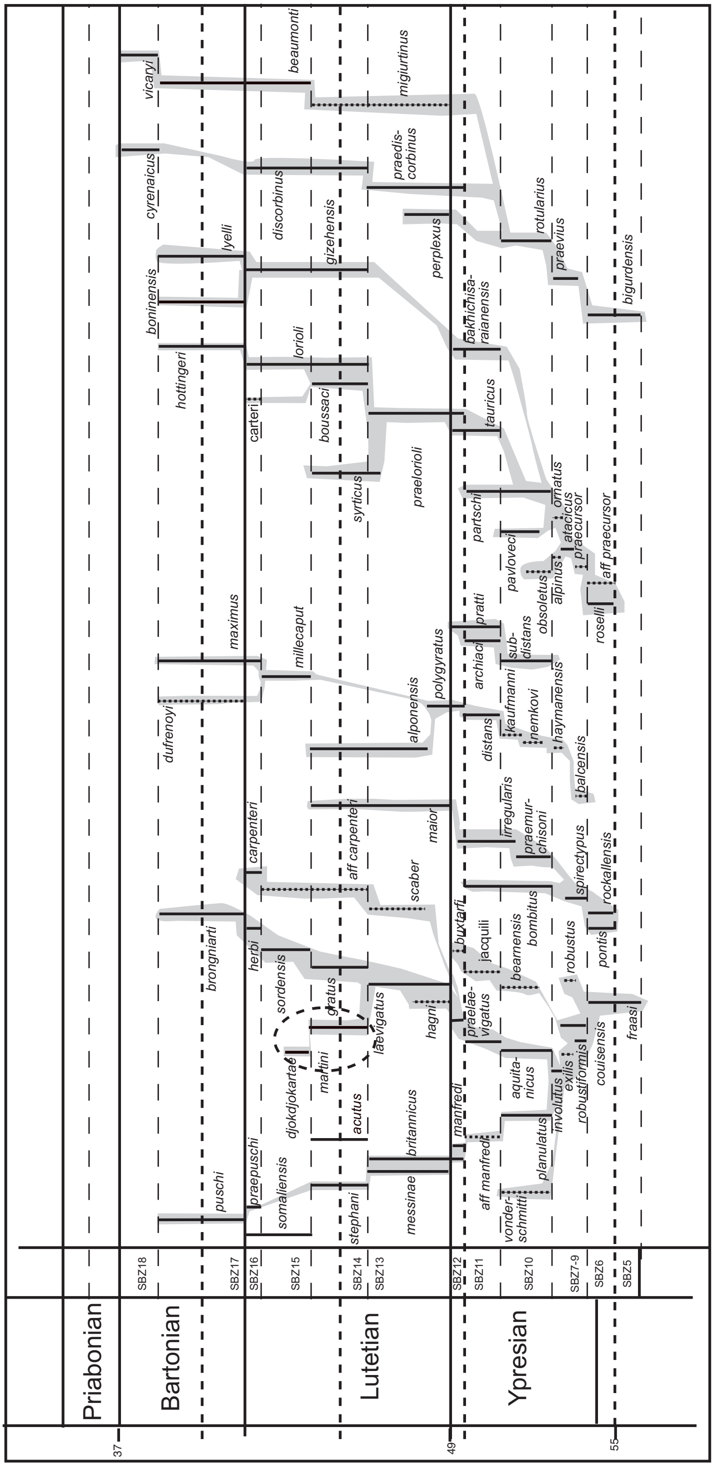
Genera that are typical for this 'chronofauna' have their first occurrence in the Lutetian or Bartonian. Four genera have their only occurrence in this time slice, *Grzybowskia*, *Sylvestriella*, *Linderina* and *Orbitoclypeus*. The morphology of these genera is very similar to the exposed slope assemblages at the Spermonde Archipelago (*Grzybowskia* vs *Heterostegina depressa*, *Sylvestriella* vs *Baculogypsinoides* and *Linderina* vs *Amphisorus*).

Unlike in Europe, diversity increased over the Bartonian- Priabonian boundary in Indo-Malaysia. According to Figure 8.2, diversity decreases either when productivity increases or when temperature rises, if we do not take high temperature as a limiting factor for diversity. Oceanographic evidence given above, however, shows that the Priabonian was colder and richer in nutrients than the Lutetian-Bartonian. The local rock record also does not provide evidence that the Indo-Malaysian environment deviated from the global trend. This provides circumstantial evidence that the diversity in the Lutetian and Bartonian is limited by too high a temperature. Speculating even further, the Priabonian fauna need not be a k-selected fauna, despite some characters of a specialized, k-selected fauna. The presence and extinction of large discocyclinids (with a marked adult dimorphism) should be seen in the line of 'progressive' extinctions of the largest species of genera (or complete genera) at the end of the Lutetian (*Assilina* and *Pseudocamerinoides*) and the Bartonian (*Nummulites*). The other genera, such as *Spiroclypeus* and *Heterostegina,* are typically forms living on a solid substrate instead of a soft substrate like the previously mentioned genera. Solid substrate inhabited by larger foraminifera is usually covered by algae, and an increase in genera preferring solid substrate in the Priabonian thus hints at an increased nutrient level.

Range extension versus phyletic speciation

Schaub (1981) proposed a phylogenetic relationship for most of the species treated in his overview, reproduced here (Fig. 8.6) against linear time using the stratigraphic ranges provided by Serra-Kiel *et al.* (1998). The species from Oman and Indonesia not yet known to Schaub (1981) have been included where possible.

The interpretation of the genus *Palaeonummulites* in this thesis, results in a polyphyletic genus *Nummulites*, since only the ancestral species of the *burdigalensis*, *laeviga-*


Priabonian
Bartonian
Lutetian
Ypresian
37
49
55
SBZ18
SBZ17
SBZ16
SBZ15
SBZ14
SBZ13
SBZ12
SBZ11
SBZ10
SBZ7-9
SBZ6
SBZ5
vicaryi
beaumonti
migiurtinus
cyrenaicus
discorbinus
praedis-corbinus
gizehensis
perplexus
rotularius
praevius
bigurdensis
boninensis
lyelli
hottingeri
lorioli
bakhchisa-raianensis
carteri
boussaci
tauricus
syrticus
praelorioli
partschi
ornatus
atacicus
praecursor
aff praecursor
pavloveci
alpinus
obsoletus
roselli
pratti
archiaci
sub-distans
maximus
millecaput
polygyratus
alponensis
kaufmanni
nemkovi
haymanensis
dufrenoyi
distans
balcensis
carpenteri
aff carpenteri
maior
irregularis
praemur-chisoni
scaber
spirectypus
rockallensis
brongniarti
herbi
sordensis
gratus
buxtorfi
jacquilii
bearnensis
bombitus
robustus
pontis
laevigatus
hagni
praelae-vigatus
martini
djokdjokartae
aquita-nicus
exilis
involutus
robustiformis
couisensis
fraasi
acutus
manfredi
britannicus
planulatus
puschi
praepuschi
somaliensis
stephani
messinae
aff manfredi
vonder-schmitti

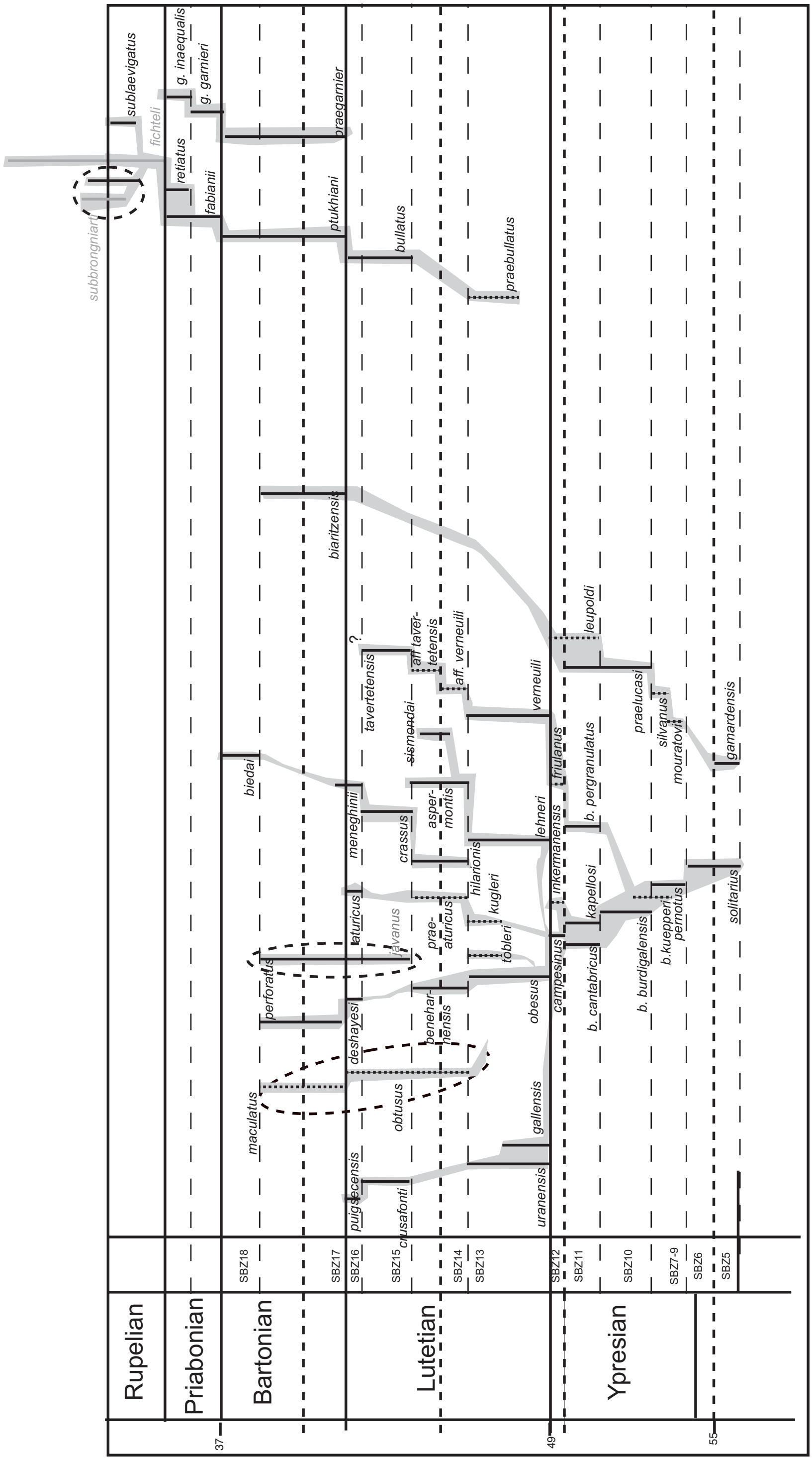
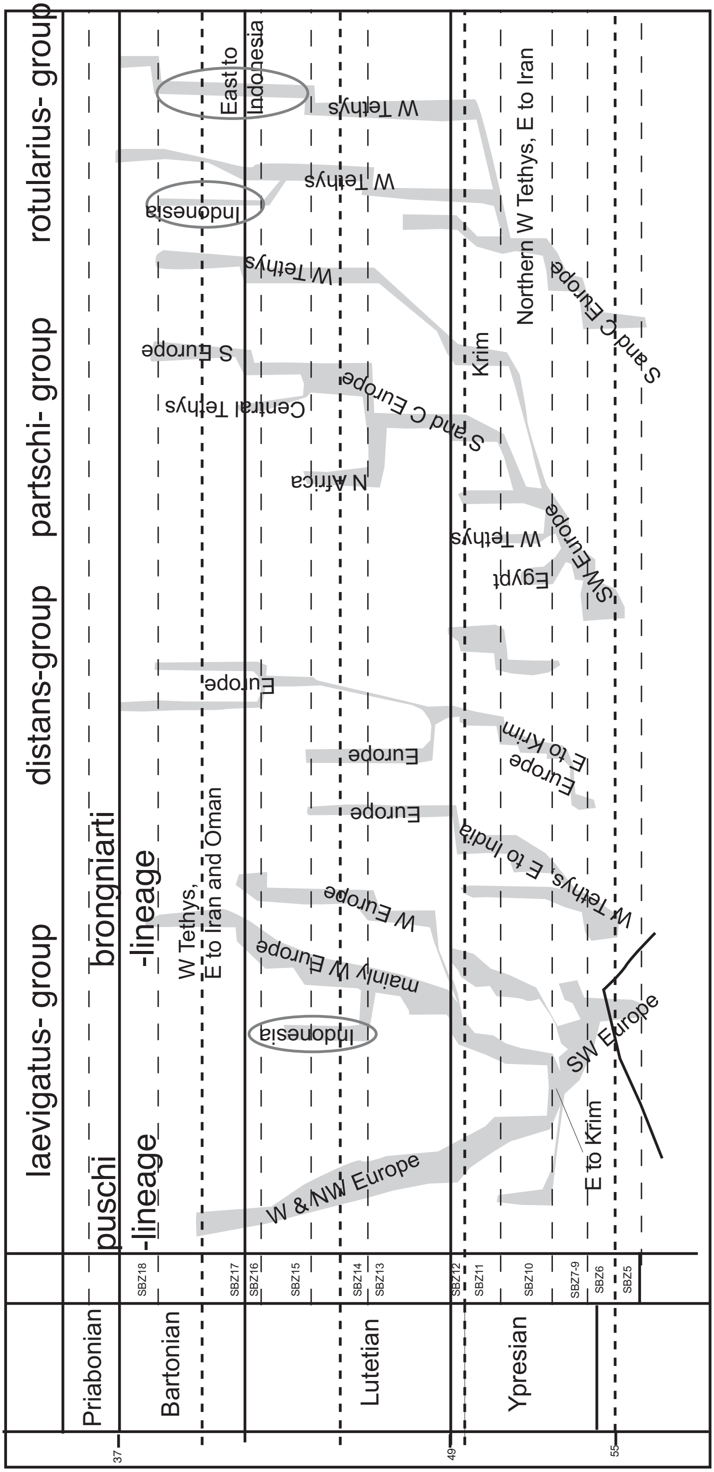


Fig. 8.6. Lineages of Schaub (1981), figured against linear time using stratigraphic ranges given by Serra-Kiel *et al.* (1998). Species that were not included in the latter study are dotted, and the stratigraphic range is inferred from species with the same range in Schaubb's figures.


laevigatus- group
distans-group
partschi- group
rotularius- group
puschi
-lineage
brongniarti
-lineage
W Tethys,
E to Iran and Oman
East to
Indonesia
Indonesia
Indonesia
W & NW Europe
mainly W Europe
W Europe
Europe
Europe
Europe
N Africa
Central Tethys
S Europe
S and C Europe
W Tethys
W Tethys
W Tethys
W Tethys, E to India
E to Krim
Europe
E to Krim
SW Europe
Egypt
W Tethys
SW Europe
Krim
Northern W Tethys, E to Iran
S and C Europe
Priabonian
Bartonian
Lutetian
Ypresian
SBZ18
SBZ17
SBZ16
SBZ15
SBZ14
SBZ13
SBZ12
SBZ11
SBZ10
SBZ7-9
SBZ6
SBZ5
37
49
55

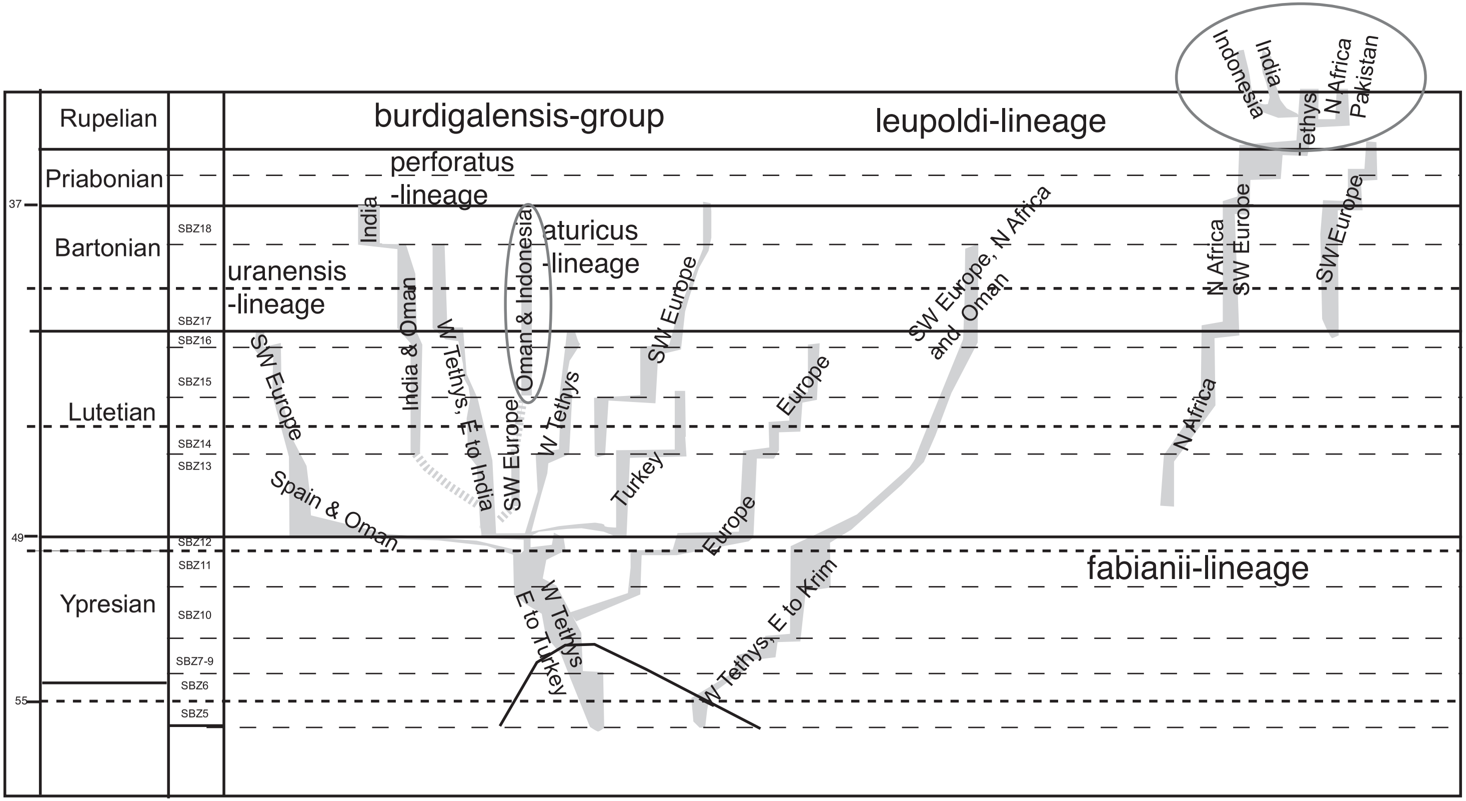


Fig. 8.7. Geographic distribution of the lineages shown in Fig. 8.6. The species occurring in Indonesia are marked.

tus, and the *leupoldi*-groups are included in *Palaeonummlites*. A revision at the generic level of the genus *Nummulites* is outside the scope of this thesis, however.

Most lineages show a very consistent geographic distribution (Fig. 8.7). Many lineages are restricted to west and central Europe, with an occasional species migrating into a larger geographic area. In the contrast, in the east Tethys most species occur as isolated taxa, with some uncommon lineages. In particular, the abundant, long ranging species in Europe have migrated to the East and sometimes evolved into separate species.

From this pattern, it is concluded that speciation occurred mainly in Europe, with species migrating to the east. After arrival in India or Indonesia, some species differentiated into local endemics, which were than replaced by new immigrant species from Europe, an example of range extension speciation. Note, that this migration is counter current, since the main current systems are from east to west.

The reticulate nummilitids were abundant and widespread in the Priabonian of Europe, but absent in Indo-Malaysia, where *N. fichteli* arrived in the Rupelian. During Tc, the early Rupelian, *N. fichteli* evolved into several species in the east Tethys, but these derived species have not been found in Europe. In the Indonesian Rupelian, there are more examples of lineages in the Lepidocyclinidae, Miogypsinidae and other genera within the Nummulitidae. In Europe, similar lineages have been found (e.g., Drooger, 1993). These lineages have not been independently dated yet, so it is impossible to determine whether species evolved at similar rates all over the Tethys or if speciation was limited to a ‘centre of origin’ out of which species migrated.

Other taxa

High latitude deep-sea benthic foraminifera show a similar pattern of stepped extinctions at the end of the Lutetian, the Bartonian and the beginning of the Rupelian (Thomas, 1992). Low-latitude planktonic foraminiferal populations experienced a major faunal turnover between the late Middle Eocene and the early Late Oligocene (Keller *et al.*, 1992). This turnover involved over 80% of planktonic foraminiferal species. The overwhelming majority of species becoming extinct were surface-dwelling forms that were replaced by more cold-tolerant, subsurface dwelling species (Keller *et al.*, 1992). The majority of extinctions took place at the Middle-Late Eocene boundary and Early-Late Oligocene boundary (Keller *et al.*, 1992).

On land, global climate deterioration started at the end of the Eocene and resulted in a change in vegetation throughout the region, and a major retraction of megathermal rain forest (Morley, 2000). Lowland rainforests were largely replaced during the Oligocene and earliest Miocene by seasonal climate (monsoonal) vegetation types. With cooler climates, montane forests with frost tolerant conifers became common in the upland areas (Morley, 2000 and pers. com.). Major events at this transition are global cooling resulting in the development of first small ephemeral ice-sheets and subsequently the first permanent glaciation in the Antarctic region (Fig. 8.5; Salamy & Zachos, 1999; Zachos *et al.*, 2001).

The faunal change did not necessarily reflect cooling, but can also be attributed to a change in zonation of photic biotopes (Hallock *et al.*,1991a). The appearance of full scale continental ice-sheets on east Antarctica intensified ocean circulation and upwelling of nutrients into oceanic surface water, thus shallowing the photic zone and increasing seasonality, both resulting in a decreased diversity of more k-type species.

There are three possible reasons why LFT2 in the Indo-Malayan region was less pronounced than in Europe, each of them not excluding the other:

The equatorial position of Indo-Malaysia, while the northern margin of the west Tethys (Europe) was at about 30°N. Together with the position at the west side of the Pacific Ocean, the late Eocene-Oligocene cooling in Indo-Malaysia was less severe than in Europe. It might even have increased opportunities for larger benthic foraminifera if, during the Middle Eocene, diversity was limited by high temperatures.

The reduction of mountainous area in Indo-Malaysia around the Eocene/Oligocene transition and the dryer climate reduced the terrestrial influx to Indo-Malaysian marginal seas. This resulted in a (relative) increase in the depth of the photic zone and more opportunities for specification in the area.

Changing basin conurations could result in a local decrease in the intensity of upwelling, or in an upwelling zone further away from shallow marine areas. In the Lutetian, southwest Sulawesi started to separate from Borneo, resulting in a carbonate platform that is not directly flanked by an upwelling zone (Moss & Wilson, 1998). This resulted in a smaller regional nutrient stress and lower extinction rates in the Bartonian. The early part of the Priabonian is represented by a characteristic marly facies over much of the region (southwest Sulawesi, north Sulawesi, west Java and several localities on Borneo), indicating that nutrient levels increased at this time. In a large part of Indonesia the Priabonian-Oligocene boundary falls within a hiatus, but where present algae are a dominant component of carbonates, e.g., Borneo (Adams, 1965), Java and Sulawesi (this thesis), indicating nutrient stress increased on the carbonate platforms (Adams, 1965).

Early to Middle Miocene diversity

From the Oligocene onwards, there have been continental ice-sheets on east-Antarctica. In the Rupelian and early Chattian these were permanent, but were ephemeral from the late Chattian to Middle Miocene these were ephemeral (Zachos *et al.*, 2001). The late Chattian to early middle Miocene was a period with warmer conditions, with the highest temperatures at the Middle Miocene climatic optimum (16 Ma; Fig. 8.5). The Middle Miocene saw a major climatic revolution. The early stage of this climatic revolution from ~16 Ma to 14.8 Ma was marked by major short term variations in global climate, East Antarctic Ice Sheet (EAIS) volume, global sealevel and deep ocean circulation (Flower & Kennett, 1994). In the later stage from 14.8-12.9 Ma climatic developments involved major growth of the EAIS, a distinct increase in the meridional temperature gradient, a sealevel fall and increased production of Antarctic bottom water, increasing the ocean circulation rates (Flower & Kennett, 1994). From 10 Ma increasing restriction of surface water flow through the Indonesian seaway led to piling up of warm surface waters in the western equatorial Pacific (Gasperi & Kennett, 1993).

After the low diversity of larger foraminifera in the early Rupelian (East Indian Letter stage Tc; Fig. 8.5), larger foraminifera started to diversify in both Europe and

Indonesia (late Rupelian,Td). No complete compilation of maximum diameter is available at this moment for the Tethys assemblages, but in the Chattian and Early Miocene especially *Nephrolepidina* and *Eulepidina* reached large diameters (up to 12 cm in Indonesia). In the Caribbean largest diameter of lepidocyclinids was reached at the end of the Chattian, and species diversity in larger foraminifera dropped at the Aquitanian-Burdigalian boundary (Brasier, 1995). In Europe a similar diversity drop occurred, but in Indonesia large *Nephrolepidina* was present in the Middle Miocene, together with relatively large *Cycloclypeus*. Also in Australia, large lepidocyclinids have been found in the Middle Miocene (McGowran & Li, 2000).

A more detailed look at the larger foraminiferal diversity drop in the Middle Miocene shows that was not as abrupt as the thick line in Figure 9.5 suggests. Ranges of genera with a first occurrence in Tf_2 or Tf_3 count as being present during the entire Middle Miocene, whilst the same holds for species with a last appearance at the end of Tf_1 or Tf_2. The thin unbroken line in Figure 8.5 represents the generic diversity when these more detailed ranges are used. This shows a continuous decline in diversity throughout the Middle Miocene, following the diversity maximum of the Early Miocene.

The high diversity of larger foraminifera in the Early Miocene in Indo-Malaysia was coincident with optimal conditions in two parameters:

a) The late Early and earliest Middle Miocene was the warmest period of the Miocene (Flower & Kennett, 1994; Zachos *et al.,* 2001). During the Early and Middle Miocene, the widespread expansion of humid climates resulted in the expansion of rain forests across most of the region. Tropical rain forests reached their greatest expansion in the early Middle Miocene (Langhian), because of warm and moist climates in periods of sealevel highstands (Morley, 2000). At the same time mangroves were widespread (Adams *et al.,* 1990). During periods with lower sealevel there was a corresponding expansion of vegetation adapted to seasonal climates (Morley, 2000). After the Langhian climate deteriorated and the latitudinal expansion of tropical rain forest decreased.

b) At the same time as the larger foraminiferal maximum diversity, upland vegetations were much reduced from the Chattian onward (Morley, 2000). At the end of the Rupelian (30 Ma) the only mountainous area was at the southeast tip of Sumatra and northwest of Java, while land was only present on the Sunda block, extending over a large part of Borneo (Hall, 1998). Carbonate platforms were extensive in the Chattian-Burdigalian, covering south Borneo, and a large part of the Java Sea and parts of northeast Borneo, while large carbonate platforms were present on southwest Sulawesi, Mindanao and Palawan- Mindoro (Hall, 1998). This pattern started to change in the Middle Miocene, when a larger part of the Sunda block was flooded and mountain building started in Borneo (Hall & Nichols, 2001)

Unlike the Lutetian-Rupelian events, the Miocene extinctions (LFT3) occurred diachronously, with many last occurrences during the Early Miocene in Europe (and the Caribbean), but many first occurrences in Indo-Malaysia. The increase in diversity in Indo-Malaysia occurred concurrently with a sealevel rise and the start of the collision of the Australian and Eurasian plates, with island arcs in between. Both processes resulted in the increase of shallow marine habitats in Indo-Malaysia. Because of tectonic events no immigration was possible of newly evolved genera to the Mediterranean region. Rosen (1999) found an increasing anomaly between isotope predicted temperatures and diversity of zooxanthellate corals related to the increased isolation of the Mediterranean basin.

After the relatively cold period during most of the Oligocene, in the latest Chattian temperatures rose, and the Early and especially Middle Miocene temperatures were relatively high. With the onset of permanent ice sheets on the Antarctic (around the Middle/Late Miocene boundary) temperatures became lower again. At the same time the collision between Australia and Eurasia intensified, resulting in high mountains on Borneo and much terrestrial run off over the shelves, reducing the area of potential larger benthic foraminiferal habitat (Hall, 1998; Hall & Nichols, 2001). Erosion rates were very high and large deltas started to develop from the drainage systems. These deltas decreased the surface area of carbonate platforms on the Sunda shelf, but extensive carbonate platforms were still present on East Sulawesi, Mindanao and Halmahera (Hall, 1998; Hall & Nichols, 2001; Fig. 8.4).

The effect of these events was enhanced, because of the shallower photic zone and the reduced depth stratification of the habitats. Over large parts of Java (pers. obs. and Lokier and Wilson, pers. com.) carbonate platforms were dominated by onkolitic reefs at the end of the Middle Miocene (planktonic foraminfera zone N12). Other shallow marine, warm water taxa such as corals show a similar pattern (Wilson & Rosen, 1998).

The termination of the Chattian-Miocene larger foraminiferal fauna occurred earlier in Europe than in Indonesia. Possible causes of this pattern could be:

a) The collision of Africa with Eurasia, which shut of the possiblitiy of exchange with areas with a more diverse larger foraminiferal population, limiting the possibilities of repopulation after extinctions, allthough conditions improved.

b) The geographic position of Indo-Malaysia at the equator. With increased glaciation, the latitudinal gradient in the oceans increased, having more effect in the Mediterranean basin than in the equatorial Pacific. The collision of Africa to Eurasia also prevented warm surface waters to enter the Mediterranean, resulting in an increased cooling in the Mediterranean, causing extinction.

The main extinctions in Indo-Malaysia occured several million years after the climatic optimum, at the same time when planktonic foraminifera adapted to living at intermediate depths went extinct as well (Hodell & Vayavanada, 1993). This time was characterized by a shift in dominance of provenance of oceanic deep water from the east Tethys to high latitudes, increasing ocean circulation rates and nutrient flux to the oceanic surface waters (Flower & Kennett, 1994).

This pattern is enhanced by increased terrestrial run off because of mountain building in Borneo and a sealevel fall, the latter two both leading to fewer oligotrophic habitats in the area.

Late Miocene to Recent diversity

Sulawesi emerged from the Late Miocene onwards, and from 5 Ma uplift increased relief and the emergence of many Indonesian islands, like Sumatra, Java, Sulawesi, Papua New Guinea, Timor, and Ceram (de Smet *et al.*, 1989). At this time carbonate platforms occurred mainly around the palaeoequator, off east Java, the southwest, east and northeast arms of Sulawesi and southeast Borneo. The presence of Late

Miocene pollen of alpine trees in Southeast Asia, providing an indication of the mountainous area in the region, shows a similar pattern in the Neogene, with a return of alpine floras from 5 Ma onwards. Thus, at about 5 Ma a second plate tectonic reorganization occurred, mainly related to the onset of collision between the continents of Eurasia and Australia, instead of the island arcs and oceanic crust (Hall, 1998).

In the Late Miocene, although there were periods with widespread representation of rain forests, dry climates coinciding with periods of marked sealevel lowstand were intermittently widespread (Morley, 2000). During the Pliocene moist climates were widespread within Kalimantan, but dry vegetations were established on Java with the development of the monsoonal climate. During this period, montane vegetation types were more extensive and made up a larger part of the pollen association. With the build up of the Indo-Pacific warm pool SST increased in the region, allowing for a larger number of photic habitats in Indo-Malaysia. Global temperature was highest in the early Pliocene (5-4 Ma), and decreased with the onset of glaciation in the Arctic.

Glacial-Interglacial cycles severely affect the habitat of larger benthic foraminifera. Most of the Recent reefs and carbonate platforms are flanked by steep margins, leaving very limited surface area available as a suitable habitat for larger foraminifera (and other reef associated biota) during glacial lowstands. Further, increased terrestrial run off during glacials aggravated this pattern. Especially on the Sunda, but also on the Sahul shelf, rivers with large catchment areas were present during glacial times (Molengraaff & Weber, 1919; Voris, 2000).

Today at least 18 genera occur within the Indo Pacific realm, and diversity is even higher if the species of the Nummulitidae dwelling on unlithified sediment are divided into *Planostegina* and *Planoperculina,* as suggested by Hohenegger *et al.* (2000). The fauna is characterized by several genera that originate in the early Cenozoic. The first occurrence of *Operculina* and *Palaeonummulites* was already within the Early Eocene or even Palaeocene, while *Borelis* originated in the Middle/Late Eocene and *Alveolinella, Cycloclypeus* and *Amphisorus* evolved from ancestors in the Miocene. The five calcarinid genera have a much sparser fossil record and appear mainly in the Pliocene.

Summary of events in the Cenozoic

1. During the Lutetian to Bartonian the diversity of larger benthic foraminiera diversity did not change in southeast Asia, but global temperatures dropped. Diversity might have been more limited by high water temperatures rather than by high nutrient availability.

2. The Bartonian-Priabonian transition was marked by global cooling and higher nutrient availability due to increased ocean circulation rates. Nevertheless, diversity increased in the Indo Malaysian region.

3. During the Chattian to Early Miocene global temperatures rose, and ocean circulation rates were slowed down again. This resulted in an increase in habitats, leading to a diversity maximum, coincident with the late Early Miocene climate optimum.

4. During the middle Miocene ocean circulation rates increased again and temperatures decreased. This resulted in a lower diversity in the Late Miocene, but the Tf_1-Tf_3 diversity also fits in this trend.

5. During the Pliocene diversity slightly increased again, despite globlal cooling. Recent diversity is even higher, but that is probably related to taphonomical factors.

Conclusions

Distribution patterns of larger foraminifera show that diversity and distribution is limited by an interplay of temperature and nutrient availability, fine tuned by sealevel fluctuations. The Eocene-Oligocene faunal turnover can mainly be attributed to oceanographical/climatological related changes (SST, nutrient availability), while with the extinction of the Miocene faunas tectonics related factors (availability of shallow marine habitat and increased terrestrial run off) play a more important role.

The faunal turnover around the Eocene-Oligocene boundary was driven by an increased fertility of surface waters, increased upwelling rates and increased transport of terrestrial dust into surface waters. Both upwelling and the input of wind-blown terrestrial dust have a pronounced seasonal component, resulting in a more variable system, thus limiting the opportunities for K-selected species.

Cenozoic larger foraminifera faunas can be divided into three periods of high diversity, characterized by increased adult dimorphism. The time interval in which these three faunas occur differ between the west and east Tethys. The increase in adult dimorphism and species diversity occurred more than 10 million years earlier (in the Palaeocene) in Europe than in Indonesia. The extinction of the Late Oligocene-Early Miocene fauna happened later in Indonesia than in Europe and the Recent fauna is not present at all in Europe (Fig. 8.5).

In the Eocene, the Indonesian fauna was characterised by immigration of genera from the west, that sometimes locally evolved into new species, but hardly any lineages of species are recognisable.

The opening of the Makassar Strait, starting in the middle Lutetian, was an important event for the evolution of a diverse shallow marine fauna in the Indo-Malayan region. With the opening of the Makassar Strait large shallow marine environments away from upwelling zones became available for colonisation.

9. References

Adams, C.G., 1965. The foraminifera and stratigraphy of the Melinau Limestone, Sarawak, and its importance in Tertiary correlation. *Quarterly Journal of the Geological Society, London* **121**: 283-338.

Adams, C.G., 1968. A revision of the foraminiferal genus *Austrotrillina* Parr. *Bulletin of the British Museum (Natural History)* Geology **16**: 73-97.

Adams, C.G., 1970. A reconsideration of the East Indian letter classification of the Tertiary*. Bulletin of the British Museum (Natural History)* Geology **19**: 1-137.

Adams, C.G., 1973. Some Tertiary foraminifera. *In*: Hallam, A. (ed.), *Atlas of Palaeobiology*. Amsterdam, Elsevier: 453-471.

Adams, C.G., 1983. Speciation, phylogenesis, tectonism, climate and eustasy: factors in the evolution of Cenozoic larger foraminiferal bioprovinces. *In*: Sims, R.W., Price, J.H. & Whalley, P.E.S. (eds), Evolution, Time and Space: the Emergenceof the Biosphere. *Systematics Association Special Volume* **23**: 255-289.

Adams, C.G., 1984. Neogene larger foraminifera, evolutionary and geological events in the context of datum planes. *In*: Ikebe, N. & Tsuchi, R. (eds), *Pacific Neogene Datum Planes*. University of Tokyo Press, Tokyo: 47-67.

Adams, C.G., 1988. Septa, septal traces and septal filaments in the foraminiferal genus *Nummulites* Lamarck. *Journal of Micropalaeontology* **7**: 89-102.

Adams, C.G., 1992. Larger foraminifera and the dating of Neogene events. *In*: Tsuchi, R. & Ingle, J.C. Jr. (eds), *Pacific Neogene: Environment, Evolution and Events*. University of Tokyo Press, Tokyo: 221-236.

Adams, C.G., Lee, D.E. *&* Rosen, B.R., 1990. Conflicting isotopic and biotic evidence for tropical sea-surface temperatures during the Tertiary. *Palaegeography, Palaeoclimatology, Palaeoecology* **77**: 289-313.

Akhtar, M. & Butt, A.A., 1999. Lower Tertiary biostratigraphy of the Kala Chitta Range, northern Pakistan. *Revue de Paléobiologie* **18**: 123-146.

Alexander, R.M., 1983. *Animal Mechanics*. Blackwell Scientific, Oxford: 301 pp.

Andel, T. van, 1948. Some remarks on *Nummulites javanus* Verb. and *Nummulites perforat*us de Montf. *Proceedings of the Koninklijke Nederlandsche Academie van Wetenschappen* **51**: 1013-1023.

Archiac, A. d', 1846. Description des fossiles recueillis par M. Thorent, dans les couches à Nummulitique recueillis par M.S. P. Pratt et M.J. Delbos aux environs de Bayonne et de Dax. *Mémoire de la Société géologique de France* **2** (7): 157-192.

Archiac, A.d', 1846. Description des fossiles recueillis par M. Thorent dans les couches à Nummulines des enivirons de Bayonne. Mémoires de la Societé Géologique France (2) **2**: 189-217

Archiac, A. d' & Haime, J., 1853. *Description des Animaux Fossiles du Groupe Numulitique de l'Inde. Précedé d'un Resumé Géologique et d'une Monographie des Nummulites*. Paris. [Not seen.]

Arni, P., 1965. L'evolution des Nummulitinae en tant que facteur de modification des depots littoraux. France. *Bureau de Recherches Géologique et Minéralogique, Mémoir* **32**: 7-20.

Bain, J.H.C. & Binnekamp, J.G., 1973. The foraminifera and Stratigraphy of the Chimbu Limestone, New Guinea. *Bureau of Mineral Resources and Mines Geological Papers Bulletin* **139**: 1-12.

Bakx, L.A.J., 1932. De genera *Fasciolites* en *Neoalveolina* in het Indo-Pacifische gebied. *Verhandelingen van het Koninklijk Nederlandsch Geologisch en Mijnbouwkundig Genootschap voor Nederland en Koloniën* **9**: 205-267.

Banner, F.T. & Hodgkinson, R.L., 1991. A revision of the foraminiferal subfamily Heterosteginae. *Revista Española de Micropaleontología* **23**: 101-140.

Bemmelen, R.W. van, 1949. *Geology of Indonesia*. Government Printing Office, The Hague: 732 pp.

Benoist, A.H., 1889. Etude sur les Nummulites et les Assilines du Sud Ouest de la France. Recueillis dans divers gisements tertiaires de la Chalosse et du Bordelais. Bulletin de la Societe des Sciences Borda **14**: 3-22

Berggren, W.A., Kent, D.V., Swisher III, C.C.& Aubry, M.-P., 1995. A revised Cenozoic geochronology and chronostratigraphy. *SEPM Special Publication* **54**: 129-212.

Bice, K.L., Sloan, L.C. & Baron, E.J., 2000. Comparison of early Eocene isotopic paleotemperatures and the three dimensional OGCM temperature field: the potential for use of model-derived surface water δ^{18}O. *In:* Huber, B.T., MacLeod, K. G. & Wing, S.L. (eds*), Warm Climates in Earth History.* Cambride University Press, Cambridge: 79-131.

Binnekamp, J.G., 1973. Tertiary larger foraminifera from New Britain, PNG. *Bureau of Mineral Resources and Mines Geological Papers, Bulletin* **140**: 1-27.

Birkeland, C., 1985. Ecological interactions between mangroves, seagrass beds and coral reefs. *UNEP Regional Seas Reports and Studies*: **73**: 1-26.

Blondeau, A., 1972. *Les Nummulites*. Vuibert, Paris: 255 pp.

Boersma, A., Premoli Silva, I. & Hallock, P., 1998. Trophic models for the well-mixed and poorly mixed warm oceans across the Paleocene/Eocene Epoch boundary. *In:* Aubry, M.-P., Lucas, S.G. & Berggren, W.A. (eds), *Late Paleocene- Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records.* Columbia University Press, New York: 204-213.

Boichard, R., Burollet, P.F., Lambert, B. *&* Villain, J.-M., 1985. La Plateforme carbonatée du Pater Noster. *Notes et Mémoires Total CFP* **20**: 104 pp.

Boudagher-Fadel, M.K. & Banner, F., 1997. The revision of some genus-group names in Tethyan Lepidocyclininae. *Paleopelagos* **7**: 3-16.

Boudagher-Fadel, M.K. & Banner, F., 1999. Revision of the stratigraphic significance of the

Oligocene-Miocene “Letter-Stages”. *Revue de Micropaléontologie* **42**: 93-97.

Boussac, J., 1911. Études paléontologiques sur le Nummulitique alpin. *Mémoires pour servir à l’Explication de la Carte Géologique détaillée de la France:* 439 pp.

Brady, H.B., On a true Carboniferous nummulite. *Annals and Magazine of Natural History (4)* **13**: 222-231.

Brady, H.B., 1876. On some foraminifera from the Loo Choo islands. *Proceedings of the Royal Irish Academy 2nd series* **2**: 600 pp.

Brasier, M.D., 1988. Foraminiferid extinction and ecological collapse during global biological events. *In:* Larwood, G.P. (ed.). *Extinction and Survival in the Fossil Record. The Systematics Association Special Volume* **34**: 37-66.

Brasier, M.D., 1995. Fossil indicators of nutrient levels 2: evolution and extinction in relation to oligotrophy. *Geological Society Special Publication* **83**: 133-150.

Bruguière, J.G., 1792. Histoire naturelle des Vers. *In: Encyclopédie Méthodique 1*. Paris: 345-757. [Not seen.]

Cahuzac, B. & Poignant, A., 1997. Essai de biozonation de l’Oligo-Miocene dans les bassins Europeens a l’aide des grands foraminifères neritiques. *Bulletin de la Société Géologique de France* **168**: 155-169.

Carter, H.J., 1861. Further observations on the structure of foraminifera and on the larger fossilized forms of Sind, including a new genus and species. *Annals and Magazine of Natural History* **11** (2): 1-161.

Caudri, C.M.B., 1934. *Tertiary Deposits of Sumba*. Amsterdam, H.J. Paris, 223 pp.

Cizancourt, Mme de, 1938. *Nummulites* et Assilines du flysch de Gardez et du Khost, Afghanistan Oriental. *Mémoire Société Géologique de France (n.s.)* **17** (39): 1-28.

Cole, W.S., 1954. Larger foraminifera and smaller diagnostic foraminifera from Bikini drill holes. *U.S. Geological Survey Professional Paper* **260-O**: 569-608.

Cole, W.S., 1956. Larger foraminifera [of Saipan Mariana Islands]. *U.S. Geological Survey Profesional Paper* **280**-I: 321-357.

Cole, W.S., 1957. Larger foraminifera from Eniwetok drill holes. *U.S. Geological Survey professional paper* **260**-V: 743-784.

Cole, W.S., 1963. Tertiary foraminifera from Guam. *U.S. Geological Survey Professional Paper* **403**-E: 1-28.

Cole, W.S. & Bridges, J., 1953. Geology and larger foraminifera from Saipan Island. *U.S. Geological Survey Professional Paper* **253**: 1-45.

Correia, M.J. & Lee, J.J., 2000. Chloroplast retention by *Elphidium excavatum* (Terquem). Is it a selective process? *Symbiosis* **29** (4): 343-355.

Cosico, R., Gramann, F. & Porth, H., 1989. Larger Foraminifera from the Visayan Basin and adjacent areas of the Philippines (Eocene through Miocene). *Geologisches Jahrbuch* **B70**: 147-205.

Crotty, K.J. & Engelhardt, D.W., 1993. Larger foraminifera and palynomorphs of the upper Malawa and lower Tonasa Formations, southwestern Sulawesi island, Indonesia. *Proceedings of the International Symposium on Biostratigraphy of mainland Southeast Asia: Facies and Paleontology*. Indonesian Petroleum Association, Jakarta: 71-82.

Cushman, J.A., 1924. Samoan foraminifera. *Publications of the Carnegie Institution of Washington 342 Department of Marine Biology Papers* **21**: 1-75.

Davies, A.M., 1927. The Ranikot beds of Thal (north-west frontier provinces of India*). Quarterly Journal of the Geological Society, London* **83**: 260-290.

Davies, A.M., 1940. The upper Kirthar beds of North-West India. *Quarterly Journal of the Geological Society, London* **96**: 199-230.

De la Harpe, P., 1877. Notes sur les *Nummulites* des Alpes occidentales*. Actes de la Société Helvétique des Sciences Naturelles* **60**: 227-323.

De la Harpe, P., 1883. Étude sur les *Nummulite*s de la Suisse et révision des espèces éocènes des genres *Nummulites* et *Assilina*. *Mémoire de la Société Paléontologique de la Suisse* **10**: 4-180.

De la Harpe, 1926. Matériaux pour servir à une monographie des Nummulites et Assilines. *A Magyar Allami Földtani Intézet évi jelentése* **27**: 1-102.

Denys de Montfort, P., 1808. *Conchyliologie Systématique et classification Méthodologique des Coquilles*, 1. F. Schoell, Paris.

Deprat, J., 1905. Les depots éocènes néo-caledoniens; leur analogie avec ceux de la région de la Sonde. *Bulletin de la Société Géologique de France* **5**: 485-516.

Dercourt, J., Ricou, L.E. & Vrielynck, B. (eds), 1993. *Atlas Tethys Palaeoenvironmental maps*. Gauthier-Villars, Paris, 307 pp.

Deshayes, G.P., 1838. Description des coquilles fossilles recueillis en Crimée par M. de Verneuill. *In*: de Vernieull, E. (ed.) *Mémoire Géologique sur la Crimée*. *Mémoire Société de la Géologique de France* **3**(1): 37-69.

Diester-Haass, L., 1995. Middle Eocene to early Oligocene paleooceanography of the Antarctic Ocean (Maud Rise, ODP leg 113, site 689): change from a low to a high productivity ocean. *Palaegeography, Palaeoclimatology, Palaeoecology* **113**: 311-334.

Dingle, R.V. & Lavelle, M., 2000. Antarctic peninsula Late Cretaceous- Early Cenozoic palaeoenvironments and Gondwana palaeogeographies. *Journal of African Earth Sciences* **31**: 91-105.

Dollfus, G.F., 1917. Paléontologie du voyage à l'île de Celebes de M.E.C. Abendanon. *In*: Abendanon, E.C. (ed.), *Geologische en Geografische Doorkruisingen van Midden Celebes III*. Koninklijk Nederlandsch Aardrijkskundig Genootschap, Den Haag: 959-1016.

Doornink, H.W., 1932. Tertiary Nummulitidae from Java. *Verhandelingen van het Geologisch en Mijnbouwkundig Genootschap voor Nederland en Koloniën* **9**: 267-315.

Douvillé, H. 1905. Les foraminifères dans la Tertiaire de Bornéo. *Bulletin de la Société Géologique de France* **5** (4): 434-464.

Douvillé, H., 1911. Les foraminifères dans la Tertiare des Philippines. *Philippines Journal of Science* **D6**: 53-80.

Douvillé, H., 1912a. Quelques foraminifères de Java. *Sammlungen des Geologischen Reichsmuseums in Leiden* **8**: 279-294.

Douvillé, H., 1912b. Les foraminifères de l'île de Nias. *Sammlungen des Geologischen Reichsmuseums in Leiden* **8**: 253-278.

Douvillé, H., 1919. l'Eocène inferieur en Aquitaine et dans le Pyrénèes. *Mémoire pour servir a l'Explication de la Carte Géologique Détaillee de la France*, Paris: 84 pp.

Drooger, C.W., 1993. Radial foraminifera; morphometrics and evolution. *Proceedings of the Royal Academy of Sciences and Arts of the Netherlands, Science series* **41**: 242 pp.

Drooger, C.W., Marks, P. & Papp, A., 1971. Smaller radiate *Nummulites* of Northwestern Europe. *Utrecht Micropaleontological Bulletins* 5: 1-137.

Dufrêne, M. & Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible assymmetrical approach. *Ecological Monographs* **67** (3): 345-366.

Ehrenberg, C.G., 1839. Uber die Bildung der Kreidefelsen und des Kreidemergels durch unsichtbare Organismen. *Physikalische Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin* **1839**: 81-174.

Erftemeijer, P.L.A., 1993. *Factors Limiting Growth and Production of Tropical Seagrasses: Nutrient Dynamics in Indonesian Seagrass Beds*. Ph.D. Thesis, Nijmegen University, Nijmegen: 171 pp.

Fichtel, L.von & Moll, J.P.C.von, 1798. *Testacea Microscopia Aliaque Minuta ex Generibus Argonauta et Nautilus*. Anton Pichler, Vienna.

Fleury, J.J.& Fourcade, E., 1990. The Alveolinacea super-family (Foraminifera): taxonomy and tentative phylogenetic interpretation. *Revue de Micropaléontologique* **33**: 241-268.

Flower, B. P.& Kennett, J.P., 1994. The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaegeography, Palaeoclimatology, Palaeoecology* **108**: 537-555.

Forskål, L.P., 1775. *Descriptions Animalium, quae in Itinere Oriental Osseravit Petrus Forskål.* Haumiae, Copenhagen: 164 pp.

Fujita, K. & Hallock, P., 1999. A comparison of phytal substrate preferences of *Archaias angulatus* and *Sorites orbiculus* in mixed macroalgal-seagrass beds in Florida bay. *Journal of Foraminiferal Research* **29**: 143-151.

Gasperi, J.T. & Kennett, J.P., 1993. Vertical thermal evolution of Miocene surface waters: Western equatorial Pacific DSDP Site 289. *Marine Micropaleontology* **22**: 235-254.

Gerth, H., 1929. The stratigraphical distribution of the larger Foraminifera in the Tertiary of Java. *Proceedings 4th Pacific Science Congress,* Jakarta: 591-599.

Gill, W.D., 1953. The genus *Assilina* in the Laki (Lower Eocene) of the Kohat-Potwar Basin, northwest

Pakistan. *Contributions of the Cushman Foundation for Foraminiferal Research* **4**: 76-86.

Gmelin, J.F., 1791. *Systema Naturae Linnaei.* G.E. Beer, Germania.

Gorsel, J.T. van, 1988. Biostratigraphy in Indonesia: methods, pitfalls and new directions. *Proceedings of the Indonesian Petroleum Association, 16th Annual Convention*. IPA, Jakarta: 275-300.

Gronovius, L.T., 1781. *Zoolphylacii Gronoviani*, vol 3. Theodorus Haak et Soc .Leyden: 241-380.

Guilcher, A., 1988. *Coral Reef Geomorphology*. John Wiley and Sons, Chichester: 228 pp.

Haak, R. & Postuma, J.A., 1975. The relation between the tropical planktonic foraminiferal zonation and the Tertiary Far East Letter classification. *Geologie en Mijnbouw* **54**: 195-198.

Hall, R., 1996. Reconstructing Cenozoic SE Asia. *In:* Hall, R. & Blundell, D. (eds), *Tectonic Evolution of Southeast Asia*. *Geological Society Special Publication* **106**: 153-185.

Hall, R., 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. *In:* Hall, R. & Holloway, J.D. (eds), *Biogeography and Geological Evolution of Southeast Asia.* Backhuys, Leiden: 99-131.

Hall, R. & Nichols, G., 2001. Cenozoic sedimentation and tectonics in Borneo: climatic influences on orogenesis. *In:* Jones, S.J. & Frostick, L (eds). *Sediment Flux to Basins: Causes, Controls and Consequences*. *Geological Society Special Publication* **191**: 522-547.

Hallock, P., 1981a. Light dependence in *Amphistegina*. *Journal of Foraminiferal Research* **11**: 40-46.

Hallock, P., 1981b. Production of carbonate sediments by selected large benthic foraminifera on two Pacific coral reefs. *Journal of Sedimentary Petrology* **51** (2): 467-474.

Hallock, P., 1981c. Algal symbiosis: a mathematical analysis. *Marine Biology* **62**: 249-255.

Hallock, P., 1984. Distribution of selected species of living algal symbiont-bearing Foraminifera on two Pacific coral reefs. *Journal of Foraminiferal Research* **14**: 250-261.

Hallock, P., 1985. Why are larger Foraminifera large? *Paleobiology* **11**: 195-208.

Hallock, P., 1987. Fluctuations in the trophic resource continuum: a factor in global diversity cycles? *Paleoceanography* **2**: 457-471.

Hallock, P., 1988. Interoceanic differences in Foraminifera with symbiotic algae: a result of nutrient supplies? *Proceedings Sixth International Coral Reef Symposium*, *Volume 3*: 251-255.

Hallock, P., 1997. Reefs and reef limestones in earth history. *In*: Birkeland, C. (ed*.), Life and Death of Coral Reefs.* Chapman & Hall, New York: 13-42.

Hallock, P., 1999. Symbiont-bearing foraminifera. *In:* B.K.S. Gupta (ed.), *Modern Foraminifera*. Kluwer Academic, Dordrecht:123-139.

Hallock, P., 2000. Symbiont-bearing foraminifera: harbingers of global change. *Micropaleontology* **46** (supplement 1): 95-104.

Hallock, P., 2001. Coral reefs, carbonate sediments, nutrients and global change. *In:* Stanley, G.D. Jr (ed.) *The History and Sedimentology of Ancient Reef Systems*. *Topics in Geobiology* **17**: 388-422.

Hallock, P., Forward, L.B. *&* Hansen, H.J., 1986. Influence of environment on the test shape of *Amphistegina*. *Journal of Foraminiferal Research* **16** (3): 224-231.

Hallock, P. & Peebles, M.W., 1993. Foraminifera with chlorophyte endosymbionts: habitats of six species in the Florida Keys. *Marine Micopaleontology* **20**: 277-292.

Hallock, P., Premoli Silva, I. & Boersma, A., 1991a. Similarities between planktonic and larger foraminiferal evolutionary trends through Paleogene paleoceanographic changes. *Palaegeography, Palaeoclimatology, Palaeoecology* **83**: 49-64.

Hallock, P., Röttger, R.& Wetmore, K., 1991b. Hypothesis on form and function in Foraminifera. *In*: J.J. Lee & O.R. Anderson, O.R. (eds), *Biology of Foraminifera*. Academic Press, London: 41-72.

Hallock, P. & Schlager, W., 1986. Nutrient excess and the demise of coral reefs and carbonate platforms. *Palaios* **1** (4): 389-398

Hansen, H.J. *&* Buchardt, B., 1977. Depth distribution of *Amphistegina* in the Gulf of Elat, Israel. *Utrecht Micropaleontological Bulletins* **15**: 205-224.

Hanzawa, S., 1947. Eocene Foraminifera from Haha-Jima (Hillsborough Island). *Journal of Paleontology* **21**: 254-259.

Hanzawa, S., 1957. Cenozoic foraminifera from Micronesia. *Geological Society of America Memoir* **66**: 163 pp.

Haq, B.U., Hardenbol, J. & Vail, P.R., 1987. Chronology of fluctuating sealevels since the Triassic. *Science* **235**: 1156-1167.

Hashimoto, W., Alcantara, P.M., Aoki, N., Balce, G.R. & David, P.P., 1978a. *Nummulites* from the Lubingan Crystalline Schist of Bongabon, Nueva Ecija and their significance on the geologic development of the Philippines. *Proceedings of the Japanese Academy* **B54(**1): 1-4.

Hashimoto, W., Aoki, N., David, P.P., Balce, G.G. & Alcantara, P.M., 1978b. Discovery of *Nummulites* from the Lubingan crystalline schist exposed east of Bongabon, Nueva Ecija, Philippines and its significance on the geologic development of the Philippines. *Geology and Palaeontology of Southeast Asia* **19**: 57-63.

Hashimoto, W., Kitamura, N., Balce, G.R., Matsumaru, K., Kurihara, K. & Aliate, Z., 1979. Larger foraminifera from the Philippines, part X. Stratigraphic and faunal breaks between the Maybangain and Kinabuan Formations in the Tanay Region, Rixal, Phillipines. *Geology and Paleontology of Southeast Asia* **20**: 143-157.

Hashimoto, W., Kurihara, K. & Masuda, F., 1973. A study on some reticulate *Nummulites* from Kalimantan Selatan, Indonesia. *Geology and Palaeontology of Southeast Asia* **13**: 73-90.

Hashimoto, W. & Matsumaru, K., 1978. Larger Foraminifera from the Philippines 9. Larger Foraminifera found from the Zigzag Limestone, south of Baguio, Benguet, Luzon, Philippines. *Geology and Palaeontology of Southeast Asia* **19**: 89-96.

Hashimoto, W. & Matsumaru, K., 1981a. Larger Foraminifera from Sabah, Malaysia, part 1. Larger Foraminifera from the Kudat Peninsula, the Gomanton Area, and the Semporna Peninsula. *Geology and Palaeontology of Southeast Asia* **22**: 49-54.

Hashimoto, W. & Matsumaru, K., 1981b. Larger Foraminifera from the Philippines, 12. Eocene Limestone from southeastern Luzon. *Geology and Palaeontology of Southeast Asia* **22**: 63-73.

Hashimoto, W. & Matsumaru, K., 1981c. Geological significance of the discovery of *Nummulites fichteli* (Michelotti) from the Sagada plateaux, Bontoc, Mountain Province, Northern Luzon, Philippines. *Geology and Palaeontology of Southeast Asia* **22:** 75-82.

Hashimoto, W. & Matsumaru, K., 1984. Mesozoic and Cenozoic Larger Foraminifera of the Philippines and a references to those found from Borneo by the APRSA's palaeontological reconnaissance. *Geology and Palaeontology of Southeast Asia* **25**: 147-166.

Hashimoto, W., Matsumaru, K. & Kurihara, K., 1978c. Larger Foraminifera from the Philippines. 6. Larger Foraminifera found from the Pinugay Hill Limestone, Tanay, Rizal, central Luzon. *Geology and Palaeontology of Southeast Asia* **19**: 65-72.

Haynes, J.R., 1965. Symbiosis, wall structure and habitat in foraminifera. *Contributions from the Cushman Foundation for Foraminiferal Research* **16**: 40-43

Haynes, J.R., 1981. *Foraminifera*. MacMillan, London: 350 pp.

Haynes, J.R., 1988. Massively cordate nummulitids (Foraminifera) at the Palaeocene/Eocene boundary in Tethys. *Indian Journal of Geology* **60** (4): 215-247.

Haynes, J.R., Racey, A. & Whittaker, J.E. In press. A revision of the Early Palaeogene nummulitids from northern Oman, with implications for their classification. *Bulletin of the British Museum (Natural History)* Geology.

Henrici, H., 1934. Foraminiferen aus dem Eocän und Altmiocän von Timor. *Palaeontographica* **4**: 56 pp.

Hodell, D.A. & Vayavananda, A., 1993. Middle Miocene paleoceanography of the western equatorial Pacific (DSDP site 289) and the evolution of *Globorotalia (Fohsella). Marine Micropaleontology* **22** (4): 279-310.

Hoeksema, B.W., 1990. *Systematics and Ecology of Mushroom Corals (Scleractinia, Fungiidae).* Ph.D. Thesis, University of Leiden: 470 pp.

Hofker, J., 1930. Foraminifera of the Siboga expedition, Part 2, Families Astrorhizidae, Rhizamidae, Rheophacidae, Anomalinidae, Peneroplidae. *In: Siboga expeditie.* Monographie IVa. Brill, Leiden: 79-170.

Hohenegger, J., 1994. Distribution of living larger Foraminifera NW of Sesoko-Jima, Okinawa, Japan. *PSNI Marine Ecology* **15**: 291-334.

Hohenegger, J., 1995. Depth estimation by proportions of living larger foraminifera. *Marine Micropaleontology* **26**: 31-47.

Hohenegger, J., 1996. Remarks on the distribution of larger Foraminifera (Protozoa) from Belau (western Carolines). *Kagoshima University Research Center for the South Pacific Occasional Papers* **30**: 85-90.

Hohenegger, J., 2000. Coenoclines of larger foraminifera. *Micropaleontology* **46** (supplement 1)*:* 127-152.

Hohenegger, J. *&* Yordanova, E., 2001. Displacement of larger foraminifera at the western slope of Motobu peninsula (Okinawa, Japan). *Palaios* **16** (1)*:* 53-72.

Hohenegger, J., Yordanova, E. & Hatta, A., 2000. Remarks on West Pacififc Nummulitidae (Foraminifera). *Journal of Foraminiferal Research* **30** (1): 3-28.

Hohenegger, J., Yordanova, E., Nakano, Y. & Tatzreiter, F., 1999. Habitats of larger Foraminifera on the upper reef slope of Sesoko Island, Okinawa, Japan. *Marine Micropaleontology* **36** **(**2-3): 109-168.

Hollaus, S.-S. & Hottinger, L., 1997. Temperature dependance of endosymbiotic relationships? Evidence from the depth range of mediterranean *Amphistegina lessonii* (foraminiferida) truncated by the thermocline. *Ecologae Geologicae Helvetiae* **90**: 591-597.

Hottinger, L., 1960. Recherches sur les Alvéolines du Paléocène et de l'Eocène. *Schweizerische Palaeontologische Abhandlungen* **75-76**: 1-243.

Hottinger, L., 1977a, Distribution of larger Peneroplidae, *Borelis* and Nummulitidae in the Gulf of Elat, Red Sea. *Utrecht Micropaleontological Bulletins* **15**: 35-109.

Hottinger, L., 1977b. Foraminifères operculiniformes. *Mémoires du Muséum National d'Histoire Naturelle, Paris, série C* **40**: 159 pp.

Hottinger, L., 1983, Processes determining the distribution of larger Foraminifera in space and time. *Utrecht Micropaleontological Bulletins* **30**: 239-253.

Hottinger, L., 1990. Significance of diversity in shallow benthic foraminifera. *Atti del Quattro Simposio di Ecologia e Paleoecologia delle Comunita Bentoniche*: 35-51.

Hottinger, L., 1997. Shallow benthic foraminiferal assemblages as signals for depth of their deposition and their limitations. *Bulletin de la Société Géologique de France* **168** (4): 491-505.

Hottinger, L., 1998. Shallow benthic foraminifera at the Paleocene-Eocene boundary. *Strata* **9**: 61-64.

Hottinger, L., 2000. Functional morphology of benthic foraminiferal shells, envelopes of shells beyond measure. *Micropaleontology* **46** (supplement 1): 57-86.

Hottinger, L., 2001. Archiasinids and related porcelaneous larger foraminifera from the late Miocene of the Dominican Republic. *Journal of Paleontology* **75** (3): 475-512.

Hottinger, L., Halicz, E. *&* Reiss, Z., 1991. The foraminiferal genera *Pararotalia*, *Neorotalia* and *Calcarina*: taxonomic revision. *Journal of Paleontology* **65** (1): 18-33.

Hottinger, L. & Leutenegger, S., 1980. The structure of calcarinid Foraminifera*. Schweizerische Palaeontologische Abhandlungen* **101**: 115-151.

Hubbard, D.K., 1997. Reefs as dynamic systems. *In:* C. Birkeland (ed.), *Life and Death of Coral Reefs*. Chapman & Hall, New York: 43-67.

Jones, R. W., 1999. Marine invertebrate (chiefly foraminiferal) evidence for the palaeogeography of the Oligocene-Miocene of western Eurasia, and consequences for terrestrial vertebrate migration. *In*: Agustí, J., Rook, L. & Andrews, P. (eds), *The Evolution of Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, Cambridge: 274-309.

Jones, T.R., 1887. Notes on *Nummulites elegans* and other English *Nummulites. Quarterly Journal of the Geological Society, London* **43**: 132-150.

Keller, G., MacLeod, N.& Barrera, E., 1992. Eocene-Oligocne faunal turnover in planktic foraminifera, and Antarctic Galciation. *In:* Prothero, D.P. & Berggren, W.A. (eds)*, Eocene-Oligocene Climatic and Biotic Evolution.* Princeton University Press, Princeton: 218-244.

Khan, M.A. & C.W. Drooger, 1970. On variation in *Nummulites* assemblages*. Verhandelingen van de Koninklijke Nederlandse Academie voor Wetenschappen* **B 74**: 97-121.

Kidwell, S.M., 1991. The stratigraphy of shell concentrations. *In:* P.A. Allison *&* D.E.G. Briggs (eds), *Taphonomy: Releasing the Data Locked in the Fossil Record*. *Topics in geobiology*. Plenum press: 211-290.

Kidwell, S.M. *&* Flessa, K.W., 1996. The quality of the fossil record: populations, species and communities. *Annual review Earth Planetary Sciences* **24**: 433-464.

Kiessling, W., Flügel, E. & Golonka, J., 1999. Paleoreef Maps: evaluation of a comprehensive database on Phanerozoic reefs. *American Association of Petroleum Geologists Bulletin* **83**: 1552-1587.

Klerk, L.G. de, 1983. Zeespiegels, riffen en kustvlakten in Zuidwest Sulawesi. *Utrechtse Geografische Studies* **27**: 172 pp.

Koolhoven, W.C.B., 1933. Geologische kaart van Java 1:100,000. Toelichting bij bl. 14. Badjah.

Kotler, E., Martin, R.E. & Liddell, W.D., 1989. Experimental analysis of abrasion-resistance of modern reef-dwelling foraminifera from Discovery Bay, Jamaica. *In:* R.F. Dymek & K.L. Shelton (eds), *Geological Society of America, 1989 annual meeting. Abstracts with Programs*. Geological Society of America, Boulder: A46.

Krüger, R., Röttger, R., Lietz, R. & Hohenegger, J., 1996. Biology and reproductive processes of the Larger benthic foraminiferan *Cycloclypeus carpenteri* (Protozoa, Nummulitidae). *Archiv für Protistenkunde* **147**: 307-321.

Kuile, B. ter, 1991. Mechanisms for calcification and carbon cycling in algal symbiont-bearing foraminifera. *In:* J.J. Lee & O.R. Anderson, O.R. (eds), *Biology of Foraminifera*. Academic Press, London: 73-89.

Kuile, B. ter & Erez, J., 1987. Uptake of inorganic carbon and internal carbon cycling in benthonic symbiont-bearing foraminifera. *Marine Biology* **94:** 499-510.

Kuile, B. ter, Erez, J. & Lee, J., 1987. The role of feeding in the metabolism of larger symbiont-bearing foraminifera. *Symbiosis* **4**: 499-510.

Lamarck, J.B. de, 1801. *Système des animaux sans vertebrés*. Paris: published by the author, 432 pp.

Lamarck, J.B. de, 1804. Suite des mémoires sur les fossiles des environs de Paris. *Annales du Muséum National de la Histoire Naturelle* **V**: 1-241.

Langer, M.R. & Hottinger, L., 2000. Biogeography of selected "larger" foraminifera. *Micropaleontology* **46** (supplement 1*)*: 105-127.

Larssen, A.R. 1976. Studies of Recent *Amphistegina*, taxonomy and some ecological aspects. *Israel Journal of Earth-Sciences* **25**: 1-26.

Lawver, L.A., Gahagen, L.M. & Coffin, M.F., 1992. The development of palaeo seaways around Antarctica. *American Geophysical Union, Antarctic Research Series* **56**: 7-30.

Lee, J.J. & Anderson, O.R., 1991. Symbiosis in Foraminifera. *In:* J.J. Lee & O.R. Anderson (eds), *Biology of Foraminifera*. Academic Press, London: 157-220.

Lee, J.J. & Lanners, E., 1988. The retention of chloroplasts by the foraminifer *Elphidium crispum*. *Symbiosis* **5** (1-2): 45-59.

Less, G., 1987. Paleontology and stratigraphy of the European Orthophragminae. *Geologica Hungarica Series Palaeontologica* **51**: 373 pp.

Less, G., 1998. The zonation of the mediterranean upper Paleocene and Eocene by Orthophragminae. *Opera Dela Sazu* **34**: 21-43.

Leupold, W. & van der Vlerk, I.M., 1931.The Tertiary. *Leidsche Geologische Meededelingen* **5**: 54-78.

Leutenegger, 1977. Ultrastructure de Foraminfères perforés et imperforés ainsi que leur symbiotes. *Cahiers de Micropaleontologie* **3**: 1-52.

Leutenegger, S., 1984, Symbiosis in benthic Foraminifera: specificity and host adaptations. *Journal of Foraminiferal Research* **14**: 16-35.

Leymerie, A., 1846. Mémoire sur le terrain a *Nummulites* (épicrètacé) des Corbières et de la Montagne Noire. *Mémoire de la Société géologique de France* **1** (2): 5-41.

Lipps, J.H. & Severin, K.P., 1986. *Alveolinella quoyi*, a living fusiform foraminifera at Motupore Island, Papua New Guinea. *Science in New Guinea* **11**: 126-137.

Loeblich, A.R., Jr. & Tappan, H., 1987. *Foraminiferal genera and their classification*. Van Nostrand Reinhold Company, New York: 970 pp.

Lopez, E., 1979. Algal chloroplasts in the protoplasm of three species of benthic foraminifera: taxonomic affinity, viability and persistence. *Marine Biology* **53**: 201-211.

Lunt, P., 2000a. Review of the Eocene and Oligocene outcrops in the Nanggulan area, south Central Java. Bali 2000 AAPG/IPA fieldtrip- appendix on the Nanngulan outcrops: 1-19.

Lunt, P., 2000b. Biogeography of some Eocene larger foraminifera, and their potential in distinguishing geological plates. available at: http//www.nummulites.net/pal/lunt_2000.pdf: 1-11.

Maiklem, W.R., 1968. Some hydraulic properties of bioclastic carbonate grains. *Sedimentology* **10**: 101-109.

Martin, K., 1881. Tertiaer Versteinerungen von östlichen Java. *Sammlungen des Geologischen Reichsmuseums in Leiden* **1**: 105-130.

Martin, K., 1915. Die Fauna des Obereocäns von Nanggulan, auf Java. *Sammlungen des Geologischen Rieichsmuseums in Leiden. N.F.* **II** (5): 194-200.

Martin, R.E., 1999. *Taphonomy: a Process Approach*. Cambridge Paleobiology Series, 4. Cambridge Univeristy Press, Cambridge: 508 pp.

Matsumaru, K., 1984. Larger foraminiferal associations useful for the correlation of the Eocene and Oligocene sediments in the Ogasawara Islands, Japan, and an examiniation *of Nummulites bonninensis* Hanzawa. *Benthos '83; 2nd Internstional Symposium Benthic Foraminifera (Pau, April 1983)*: 415-422.

Matsumaru, K., 1994. A megalospheric schizont of *Nummulites perforatus* (Montfort) from upper Lutetian of the Yusan Formation, Haha-Jima (Hillsborough Island), Ogasawara Islands, Japan. *Revue de Micropaléontologie* **37**: 161-165.

Matsumaru, K., 1996. Tertiary larger foraminifera (foraminiferida) from the Ogasawara Islands, Japan. *Paleontological society of Japan, Special papers* **36**: 239 pp.

McConaughley, T.A., 1989. Biominieralization mechanisms. *In:* Crick, R.E. (ed.) *Origin, evolution, and Modern aspects of biomineralisation in Plants and Animals.* Plenum Press, New York: 57-73.

McConaughley, T.A. & Wehlan, J.F., 1997. Calcification generates protons for nutrients and bicarbonate uptake. *Earth-Science Reviews* **42**: 95-117.

McCune, B. *&* Mefford, M.J., 1999. PC-ORD. *Multivariate Analysis of ecological data*. MjM software design, Oregon, USA.

McGowran, B. & Li, Q., 2000. Evolutionary palaeoecology of Cainozoic Foraminfera: Tethys, Indo-Pacific, Southern Australia. *Historical Biology* **15**: 3-27.

Michelotti, G., 1841. Saggio storico del rizpodi carracteristici dei terreni supracretacei. *Memorie della Societa Italiana dell' Scienze Modena* **22**: 1-296.

Molengraaff, G.A.F. & Weber, M., 1919. Het verband tussen den Plistocenen ijstijd en het ontstaan der Soenda-Zee en de invloed daarvan op de verspreiding der koraalriffen en op de land- en zoetwater-fauna. *Verslag van de Gewone vergadering der Wis- en Natuurkundige Afdeeling van de Koninklijke Akademie van Wetenschappen te Amsterdam* **28**: 497-544.

Moll, H., 1983. *Zonation and Diversityof Scleractinia on Reefs off Southwest Sulawesi, Indonesia*. Ph.D. Thesis, University of Leiden.

Morley, R.J., 2000. *Origin and Evolution of Tropical Rain Forests*. Wiley, London: 362 pp.

Moss, S.J.& Wilson, M.E.J., 1998. Biogeographic implactions of the Tertiary palaeogeographic evolution of Sulawesi and Borneo. *In:* Hall, R. & Holloway, J.D. (eds*), Biogeography and Geological Evolution of Southeast Asia.* Backhuys, Leiden: 133-163.

Muller-Parker, G. *&* Elia, C.F. d', 1997. Interactions between corals and their symbiotic algae. *In:* Birkeland, C. (ed.), *Life and Death of Coral Reefs*. Chapman & Hall, New York: 96-113.

Murray, J.W., 1991. *Ecology and Palaeoecology of Benthic Foraminifera*. Longman Science & Technology, Essex: 397 pp.

Nagappa, Y., 1959. Foraminiferal biostratigraphy of the Cretaceous-Eocene succession in the India-Pakistan- Burma region. *Micropaleontology* **5**: 145-192.

Netherwood, R., 2000. *The Petroleum Geology of Indonesia*. Schlumberger: 174-227.

Newton, R.B. & Holland, R., 1899. On some Tertiary foraminifera from Borneo and their comparison with similar forms from Sumatra. *Annals and Magazine of Natural History* **3** (7): 245-264.

Nuttall, W.L.F., 1926a. The zonal distribution and description of the larger foraminifera of the Middle and Lower Kirthar series (Middle Eocene) or parts of western India. *Records of the Geological Survey of India* **59**: 115-164.

Nuttall, W.L.F., 1926b. The zonal distribution of the larger foraminifera of the Eocene of western India. *Geological Magazine* **63**: 495-504.

Okada, H., 1981. Calcareous nannofossils of Cenozoic formations in Central Java. *In:* Saito, H. (ed.) *Micropaleontology, Petrography and Lithostratigraphy of Cenozoic Rocks of the Yogyakarta Region, Central Java*. Department of Earth Sciences, Yamagata University, Jogjakarta: 65-78.

Orbigny, A. d', 1826. Tableau méthodologique de la classe des Céphalopodes. *Annales des Sciences Naturrelles* **7**: 245-314.

Orbigny, A. d', 1839. *Voyage dans l'Amérique meridionale- Foraminifères*. Vol5, pt 5 P. Bertrand, Paris. 86 pp.

Orbigny, A.d'., 1850. *Prodrome de Paléontologie stratigraphie universielle des animaux mollusques et rayonnés*. Renard, Paris. Vol 1 and 2.

Orue-Extebarria, X., Pujalte, V., Bernaola, G., Apellaniz, E., Baceta, J.I., Payros, A., Nuñez-Betelu, K., Serra-Kiel, J. & Tosquella, J., 2001. Did the Late Paleocene thermal maximum affect the evolution of larger foraminifers? Evidence from calcareous plankton of the Campo Section (Pyrenees, Spain). *Marine Micropaleontology* **41** (1-2): 45-71.

Osimo, G., 1908. Di alcuni foraminiferi dell 'Eocene superiore di Celebes. *Rivista Italiana di Paleontologia* **14**: 28-54.

Paltrinieri, F., Sri Sajekti & Suminta, 1976. Biostratigraphy in the Jatibungkus section (Lokulo area) in Central Java. *Proceedings Fifth Indonesian Petroleum Association Convention*: 195-203.

Parker, W.K. & Jones, T.R.,1860. On the nomenclature of the foraminifera. *Annals and Magazine of the Natural History Museum London series* 3, **6**: 29-40;337-347.

Parrish, J.T. & Curtis, R.L., 1982. Atmospheric circulation, upwelling, and organic rich rocks in the Mesozoic and Cenozoic eras. *Palaegeography, Palaeoclimatology, Palaeoecology* **40**: 31-66.

Paulay, G., 1997. Diversity and distribution of reef organisms. *In:* Birkeland, C. (ed.), *Live and Death of Coral Reefs.* Chapman & Hall, New York: 298-352.

Pearson, P.N., Ditchfield, P.W., Singano, J., Harcourt-Brown, K.G., Nicholas, C.J., Olsson, R., Shackleton, N.J. & Hall, M.,2001. Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs. *Nature* **413**: 481-487.

Pecheux, M.J.F., 1995. Ecomorphology of a Recent large foraminifer, *Operculina ammonoides*. *Geobios* **28** (5): 529-566.

Prentice, M.L. & Matthews, R.K., 1988. Cenozoic ice-volume history; development of a composite oxygen isotope record; with Suppl. Data 88-26. *Geology (Boulder)* **16** (11): 963-966.

Prever, P.L., 1905. *Le Nummuliti della Forca di Presta nell' Apennino centrale e dei dintorni di potenza nell'Apeninno meridionale*. Schweizerische Palaeontologische Gesellschaft. Frankfurt. 121 pp.

Pringgoprawiro, H., Kadar, K. & Skwarko, S.K., 1998. *Foraminifera in Indonesian Stratigraphy.* GRDC, Bandung volume 2: Cenozoic Benthonic Foraminifera: 824 pp.

Provale, I., 1908. Di alcune Nummulitine e Orbitoidine dell'Isola di Borneo. *Rivista Italiana di Paleontologia* **14**: 55-88.

Provale, I., 1909. Di alcuni Nummulitine ed Orbitoidine del Isola di Borneo. *Rivista Italiana di Paleontologia* **15**: 65-113.

Purton, L.M.A. & Brasier, M.D., 1999. Giant protist *Nummulites* and its Eocene environment; life span and habitat insights from δ^{18}O and δ^{13}C data from *Nummulites* and *Venericardia*, Hampshire Basin, UK. *Geology* **27**: 711-714.

Racey, A., 1992, The relative taxonomic value of morphological characters in the genus *Nummulites* (Foraminiferida). *Journal of Micropalaeontology* **11**: 197-209.

Racey, A., 1995. Lithostratigraphy and larger foraminiferal (nummulitid) biostratigraphy of the Tertiary of northern Oman. *Micropaleontology* **41**: 1-123.

Reiss, Z. & Hottinger, L., 1984. The Gulf of Aqaba. Ecological micropaleontology. Ecological Studies *Analysis and Synthesis* **50**: 1-354.

Renema, W., Hoeksema, B.W. & van Hinte, J.E., 2001. Larger benthic foraminifera and their distribution patterns on the Spermonde shelf, South Sulawesi. *Zoologische Verhandelingen* **334**: 115-149.

Renema, W. & Troelstra, S. R., 2001. Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia). *Palaeogeografie, Paleoclimatologie, Paleoecologie.* **175** (1-4): 125-147

Renema, W., Racey, A. & Lunt, P., in press. Paleogene nummulitids (Foraminiferida) from the Indonesian Archipelago: a review. *Cainozoic Research* **2** (2) (2002)

Rögl, F., 1998. Paleogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Annales des Naturhistorisches Museums Wien* **99A**: 279-310.

Roissy, F. de, 1805. Histoire naturelle génèrale et particuliere des mollusques, volume 5. Paris, Dufart: 450 pp. [not seen.]

Romero, J., Hottinger, L. & Caus, E., 1999. Early appearance of larger foraminifera supposedly characteristic for Late Eocene in the Igualada Basin NE Spain. *Revista Española de Paleontología* **14** (1): 79-92.

Rosen, B.R., 1988. From fossils to earth history; applied historical biogeography. *In:* Myers, A.A. & Giller, P. S. (eds), *Analytical Biogeography; an Integrated Approach to the Study of Animal and Plant Distributions.* Chapman & Hall, London: 437-481.

Rosen, B.R., 1999. Paleoclimatic implications of the energy hypothesis from Neogene corals of the Mediterranean region. *In:* Agustí, J., Rook, L. & Andrews, P. (eds), *The Evolution of Neogene Terrestrial Ecosystems in Europe. Homonoid Evolution and Climatic Change in Europe vol 1*. Cambridge University Press, Cambridge: 309-327.

Ross, C.A., 1972. Biology and ecology of *Marginopora vertebralis* (Foraminiferida), Great Barrier Reef. *Journal of Protozoology* **19**: 181-192.

Röttger, R., 1974. Larger foraminifera: reproduction and early stages of development in *Heterostegina depressa*. *Marine Biology* **26**: 5-12.

Röttger, R. & Krüger, R., 1990. Observations on the biology of Calcarinidae (Foraminiferida). *Marine Biology* **106** (3): 419-425.

Röttger, R., Krüger & Rijk, S. de, R., 1990. Larger Foraminifera: variation in outer morphology and prolocular size in *Calcarina gaudichaudii. Journal of Foraminiferal Research* **20**(2): 170-174.

Said, R., 1949. Foraminifera of the Northern Red Sea. *Special Publicatons of the Cushman Laboratory for foraminiferal Research* **26**: 1-44.

Salamy, K. A. & Zachos, J., 1999. Latest Eocene-Early Oligocene climate change and Southern Ocean fertility: inferences from sediment accumulation and stable isotope data. *Palaeogeography, Palaeoclimatology, Palaeoecology* **145**: 61-77.

Samanta, B.K., 1968. *Nummulites* (foraminifera) from the upper Eocene Kopili Formation of Assam, India. *Palaeontology* **11(5)**: 669-682.

Samanta, B.K., 1981a. Morphology and stratigraphic distribution of *Nummulites maculatus* Nuttall with observations on the extinction of large *Nummulites* near the middle upper Eocene boundary. *Quarterly Journal of the Geological, Mineralogical and Metalurgical Society of India* **53**: 14-35.

Samanta, B.K., 1981b. Two stratigraphically important *Nummulites* species from the Middle Eocene of India and Europe. *Palaeontology* **24**: 803-826.

Samanta, B.K., 1982. A restudy of two middle Eocene species of *Nummulites* (Foraminiferida) from Cutch, Gujarat. *Bulletin Indian Geological Association* **15**(1): 21-50.

Sander, N.J., 1962. Apercu micropaléontologie et stratigraphie du Paléogène en Arabie Sauoudate orientale. *Revue de Micropaléontologi*e **5**: 3-40.

Saraswati, P.K., 1997. Eustatic changes and the evolution of Palaeogene larger foraminifera- a numeric analysis. *Journal of the Geological Society of India* **50**: 61-67.

Saraswati, P.K., Patra, P.K. & R.K. Banerji, 2000. Biometric study of some Eocene Nummulites and Assilina from Kutch and Jaiasalmer, India. *Journal of the Palaeontological Society of India* **45**: 91-122.

Schaub, H., 1981. Nummulites et Assilines de la Tethys paleogène. Taxonomie, phylogenèse et biostratigraphie. *Schweizerische Palaeontologische Abhandlungen* **104**: 1-238.

Schaub, H., 1995. *Nummulites* of Israel. *Schweizerische Palaeontologische Abhandlungen* **117**: 19-32.

Scoffin, T.P. & Tudhope, A.W., 1985, Sedimentary environments of the central region of the Great Barrier Reef of Australia. *Coral Reefs* **4**: 81-93.

Sen Gupta, S., 2000. Problems of classifying Early Oligocene Reticulate *Nummulites* (Foraminiferida) from Southwestern Kutch, Gujarat. *Journal Geological Society of India* **56**: 673-677.

Serra-Kiel, J., Hottinger, L., Caus, E., Drobne, K., Fernandez, C., Jauhri, A.K., Less, G., Pavlovec, R., Pignatti, J., Samso, J.M., Schaub, H., Sirel, E., Strougo, A., Tambareau, Y., Tosquella, Y. & Zakrevskaya, E., 1998. Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bulletin de la Société Géologique de France* **169**: 281-299.

Sirotti, A., 1982. A tentative phylogenetic interpretation of Lepidocyclinidae. *In*: Gallitelli, E.M. (ed.), *Proceedings of the First International Meeting on "Paleontology, Essential of Historical Geology"* STEM. Mucchi, Modena: 467-480.

Smet, M.E.M. de, Fortuin, A.R., Tjokrosapoetro, S. & Hinte, J.E. van, 1989. Late Cenozoic vertical movements of of non-volcanic islands in the Banda arc area. *Netherlands Journal of Sea Research* **24** (2/3): 263-275.

Sowerby, J. de, 1829. *Mineral Conchology* VI. B. Meredith, London: 73-76.

Sowerby, J. de, 1840. *In*: Stykes, W.H. A notice respecting some fossils collected in Cutch by capt. Walter Smee, of the Bombay army. *Transactions of the Geological Society, London* **5**: 317-329.

Storm, C., 1989. *Influence of River Systems and Coastal Hydrodynamics on the Waterquality During one*

Monsoonal Period. Msc. Thesis, University of Utrecht (unpublished).

Tan, S.H., 1932. In the genus *Cycloclypeus* Carpenter. *Wetenschappelijke Mededeelingen Dienst van den Mijnbouw in Nederlands-Indië* **19**: 3-194.

Thomas, E., 1992. Middle Eocene- Late Oligocene bathyal benthic foraminifera (Weddell Sea): Faunal changes and implications for ocean circulation. *In:* Prothero, D.P. & Berggren, W.A. (eds), *Eocene-Oligocene Climatic and Biotic Evolution.* Princeton University Press, Princeton (NJ): 245-271.

Tobler, A., 1923. Unsere palaeontologischen Kentnisse von Sumatra. *Eclogae Geologiae Helvetiae* **18** (2): 313-342.

Toler, S.K. *&* Hallock, P., 1998. Shell malformation in stressed *Amphistegina* populations; relation to biomineralization and paleoenvironmental potential. *Marine Micropaleontology* **34** (1-2): 107-115.

Troelstra, S.R., Jonkers, H.M. *&* Rijk, S. de, 1996. Larger foraminifera from the Spermonde Archipelago (Sulawesi, Indonesia). *Scripta Geologica* **113**: 93-120.

Tudhope, A.W. *&* Scoffin, T.P., 1988. The relative importance of benthic foraminiferans in the production of sediments on the central Queensland shelf. *Proceedings of the Sixth International Coral Reef Symposium Australia* **2**: 583-588.

Umbgrove, J.H.F., 1929. The influence of the monsoons on the geomorphology of coral islands. *In*: *Proceedings 4th Pacific Scientific Congress, Batavia-Bandoeng* (Java): 49-54.

Umbgrove, J.H.F., 1930. De koraalriffen van de Spermonde Archipel, S. Selebes. *Leidsche Geologische Mededeelingen* **3**: 227-247.

Umbgrove, J.H.F., 1931. Tertiary foraminifera. *Leidsche Geologische Mededeelingen* **5:** 35-92.

Vénec-Peyré, M., 1991. Distribution of living benthic Foraminifera on the back-reef and outer slopes of a high island (Moorea, French Polynesia). *Coral Reefs* **9**: 193-203.

Verbeek, R.D.M., 1871. Die Nummuliten des Borneo-kalksteines. *Neues Jahrbuch für Mineralogie und Geologie* **B9**: 1-14.

Verbeek, R.D.M., 1874. De nummuliten uit den Eocenen kalksteen van Borneo. *Jaarboek van het Mijnwezen in Nederlansch Oost-Indië* **3** (2): 133-161.

Verbeek, R.D.M., 1891. Voorlopig bericht over den Nummulieten, Orbitoiden en Alveolinen van Java, en over den ouderdom der gesteenten waarin zij optreden. *Natuurkundig Tijdschrift voor Nederlansch Oost-Indië* **51** (12): 101-139.

Verbeek, R.D.M., Boettger, O. & Fritsch, K. von, 1881. Die Tertiärformation von Sumatra und ihre Thierreste. *Jaarboek van het Mijnwezen in Nederlansch Oost-Indië* **2** (2): 3-210.

Verbeek, R.D.M. & Fennema, R., 1896. *Geologische Beschrijving van Java en Madoera.* Amsterdam, J.G. Stemler Cz.: 1155 pp.

Verheij, E., 1993. *Marine plants on the reefs of the Spermonde Archipelago, SW Sulawesi. Indonesia: aspects of taxonomy, ecology and floristics*. Ph.D. Thesis, University of Leiden.

Veron, J.E.N., 1995. *Corals in Space and Time. The Biogeography and Evolution of the Scleractinia*. University of New South Wales Press, Sydney: 700 pp.

Vlerk, I.M. van der, 1929. Groote foraminiferen van NO Borneo. *Wetenschappelijke Mededeelingen, Dienst Mijnbouw Bandoeng* **9**: 1-44.

Vlerk, I.M. van der, 1951. Tabulation of determinations of larger foraminifera. *In:* Reinhard, M. & Wenk, E. (eds), *Geology of the Colony of North Borneo. Bulletin of the Geological Survey Department of the British territories in Borneo* **1**: 137-145.

Vlerk, I.M. van der, 1955. Correlation of the Tertiary of the Far East and Europe. *Micropaleontology* **1**: 72-75.

Vlerk, I.M. van der & Dozy, J.J., 1934. The Tertiary rocks of the Celebes expedition 1929. *Verhandelingen van het Koninklijk Nederlandsch Geologisch en Mijnbouwkundig Genootschap voor Nederland en Koloniën* **10**: 183-217.

Vlerk, I.M. van der & Umbgrove, J.H.L., 1927. Tertiaire gidsforaminiferen uit Nederlandsch Oost-Indie. *Wetenschappelijke Mededeelingen, Dienst Mijnbouw Bandoeng* **6**: 1-31.

Voris, H.K., 2000. Maps of Pleistocene sealevels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* **27**: 1153-1167.

Vredenburg, E.W., 1906. *Nummulites douvillei*, an undescribed species from Kachh with remarks on the zonal distribution of Indian *Nummulites*. *Records of the Geological Survey of India* **34**: 79-95

Vredenburg, E.W., 1908. *Nummulites vredenburgi* Prever, nom. mut. *Records of the Geological Survey of India* **36**: 239.

Vuuren, L. van, 1920. Barrière-riffen en atollen in den Nederlandsch Indischen Archipel. *Handboek 1ste Nederlandsch Indischen Natuurwetenschappelijken Congres, Batavia, 1919*: 186-198.

Wang, L., 1994. Sea surface temperature history of the low latitude western Pacific during the last 5.3 million years. *Palaegeography, Palaeoclimatology, Palaeoecology* **108**: 379-436.

Wanner, J., 1907. Zur Geologie von West-Buru. *Neues Jarhbuch für Mineralogie, Geologie und Palaeontologie* **BB 24**: 133-160.

Wanner, J., 1910. Beiträge zur geologischen Kenntnis der Insel Misol. *Tijdschrift Koninklijk Nederlandsch Aardrijkskundig Genootschap* **2,** 27: 469-500.

Wanner, J., 1912. Beiträge zur Geologie des Ostarmes der Insel Celebes *Neues Jarhbuch für Mineralogie, Geologie und Palaeontologie* **BB 29**: 739-778.

Wanner, J., 1922. Geologische Ergebnisse der Reisen K.Deningers in den Molukken. I. Beiträge zur Geologie der Insel Buru. *Palaeontographica, suplement* **IV-3(3)-I**: 59-112.

Waterschoot van der Gracht, W.A.J.M. van, 1915. Bijdrage tot de geologie van Centraal-Celebes. *Jaarboek van het Mijnwezen in Nederlandsch Oost-Indië* **43**: 16-73.

Wetmore, K.L., & Plotnick, R.E., 1992. Correlations between test morphology, crushing strength, and habitat in *Amphistegina gibbosa*, *Archaias angulatus*, and *Laevipeneroplis proteus* from Bermuda. *Journal of Foraminiferal Research* **22** (1): 1-12

White, M.R., 1994. Foramniniferal biozonation of the northern Oman Tertiary carbonate succession. *In:* Simmons, M.D. (ed.), *Micropalaeontology and Hydrocarbon Exploration in the Middle East*. Chapman & Hall, London: 309-341.

Whittaker, J.E. & Hodgkinson, R.L., 1979. Foraminifera of the Togopi Formation, eastern Sabah, Malaysia. *Bulletin of the British Museum.* (*Natural History)* Geology **31** (1): 1-120.

Wielandt, U., 1999. Early progressive evolutionary features in *Nummulites luterbacheri* from the western desert of Egypt. *Journal of Foraminiferal Research* **29**: 130-142.

Wilson, M.E.J., 1995. *The Tonasa Limestone Formation, Sulawesi, Indonesia: development of a Tertiary carbonate platform*. Ph.D. Thesis London, Royal Holloway University.

Wilson, M.E.J., 1996. Evolution and hydrocarbon potential of the Tertiary Tonasa Limestone Formation, Sulawesi, Indonesia. *Proceedings Indonesian Petroleum Association, 25th Anniversary convention*: 227-240.

Wilson, M.E.J., 2002. Cenozoic carbonates in Southeast Asia: implications for equatorial carbonate development. *Sedimentary Geology* **147**: 295-428.

Wilson, M.E.J. & Bosence, D.W.J., 1996. The Tertiary evolution of South Sulawesi: a record in redeposited carbonates of the Tonasa Limestone Formation. *In:* Hall, R. & Blundell, D. (eds), *Tectonic Evolution of Southeast Asia. Geological Society Special Publication* **106**: 365-389.

Wilson, M.E.J. & Rosen, B.R., 1998. Implications of paucity of corals in the Paleogene of SE Asia: plate tectonics or Centre of Origin. *In*: Hall, R. & Holloway, J.D. (eds), *Biogeography and Geological Evolution of Southeast Asia*. Leiden, Backhuys: 165-195.

Yabe, H., 1921. Notes on some Eocene foraminifera. *Science Reports of the Tohoku Imperial University second series* **V**: 97-108.

Yabe, H. & Hanzawa, S., 1930. Tertiary foraminiferous rocks of Taiwan (Formosa). *Science Reports of the Tohoku University, Sendai* serie 2 Geology **14**: 1-46.

Yamano, H., Miyajima, T. & I. Koike, 2000. Importance of foraminifera for the formation and maintenance of a coral sand cay: Green Island, Australia. *Coral Reefs* **19**: 51-58.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K., 2001. Trends, rhytms, and aberrations in global climate 65 Ma to present. *Science* **292**: 686-693.

Zachos, J., Stott, L.D. & Lohmann, K.D., 1994. Evolution of early Cenozoic marine temperature. *Paleoceanography* **9**: 353-387.

Zohary, T., Reiss, Z. & Hottinger, L., 1980. Population dynamics *of Amphisorus hemprichii* (Foraminifera) in the Gulf of Elat (Aqaba), Red Sea. *Eclogae Geologiae Helvetiae* **73** (3): 1071-1094.

10. Groot foraminiferen als milieu-indicatoren

Groot foraminiferen zijn, zoals hun naam al doet vermoeden, grote, eencellige organismen. Ze komen voor in vergelijkbare omstandigheden als rifbouwende koralen, te weten in ondiepe, warme zeeën. Aangezien ze afhankelijk zijn van de energie die algjes waarmee ze samenleven (symbionten) uit fotosynthese produceren zijn ze beperkt in hun voorkomen tot de fotische zone. Net als andere rif geassocieerde groepen, zijn groot foraminiferen het meest divers in het grensgebied tussen de Indische Oceaan en het westelijke deel van de Stille Oceaan (IWP).

Alle Recente groot foraminiferen produceren een kalkskeletje dat, als ze doodgaan, bewaard kan blijven als fossiel. Op zowel Recente als fossiele riffen en carbonaat platformen in Zuidoost-Azië spelen groot foraminiferen een belangrijke rol in de kalkproductie, waarvan zij soms wel 80% voor hun rekening nemen. Omdat andere groepen die veel gebruikt worden voor ouderdomsbepalingen (biostratigrafie) op carbonaatplatformen niet zo veel voorkomen, of niet bewaard blijven, worden in deze setting vaak groot foraminiferen voor de ouderdomsbepaling gebruikt.

Het onderzoek waarvan in dit proefschrift verslag wordt gedaan heeft als doelen:

- Het beschrijven van de verspreiding van levende groot foraminiferen in verschillende rifsystemen.
- Het herkennen van de belangrijkste parameters die de verspreiding van groot foraminiferen beïnvloeden.
- Het vergelijken van de verspreiding van lege skeletjes van groot foraminiferen met die van de levende eencelligen, zodat kan worden nagegaan of het voorkomen van bepaalde soorten foraminiferen kan worden gebruikt voor het reconstrueren van omgevingsomstandigheden in het verleden.
- De resultaten hiervan gebruiken voor het interpreteren van vondsten in de fossiele overlevering.

Om beter te begrijpen wat groot foraminiferen nu eigenlijk precies zijn, geef ik hier eerst een korte inleiding over groot foraminiferen in het algemeen.

Groot foraminiferen zijn een informele groep. Meestal wordt als maat een cel volume van meer dan 0.5 mm^3 gebruikt. Daarnaast moet een foraminifeer afhankelijk zijn van symbionten om tot de groot foraminiferen gerekend te worden. Tijdens de ontwikkeling van de groep (het houden van symbionten) is dit kenmerk meermalen opgetreden. Dientengevolge komen groot foraminiferen Recent voor in twee orders van de foraminiferen, de perforate en imperforate foraminiferen. De samenstelling van het kalkskelet van deze groepen verschilt op een aantal punten, o.a. in de doorlaatbaarheid van licht.

Milieuparameters die van belang zijn voor groot foraminiferen

De verspreiding van groot foraminiferen wordt bepaald door een groot aantal parameters die vaak met elkaar gecorreleerd zijn. Figuur 10.1 vat deze parameters en de interactie met de foraminiferen samen.

Het deel van de oceanen waarin groot foraminiferen voorkomen wordt begrensd door watertemperatuur in de koudste maand en de beschikbaarheid van nutriënten. Ook

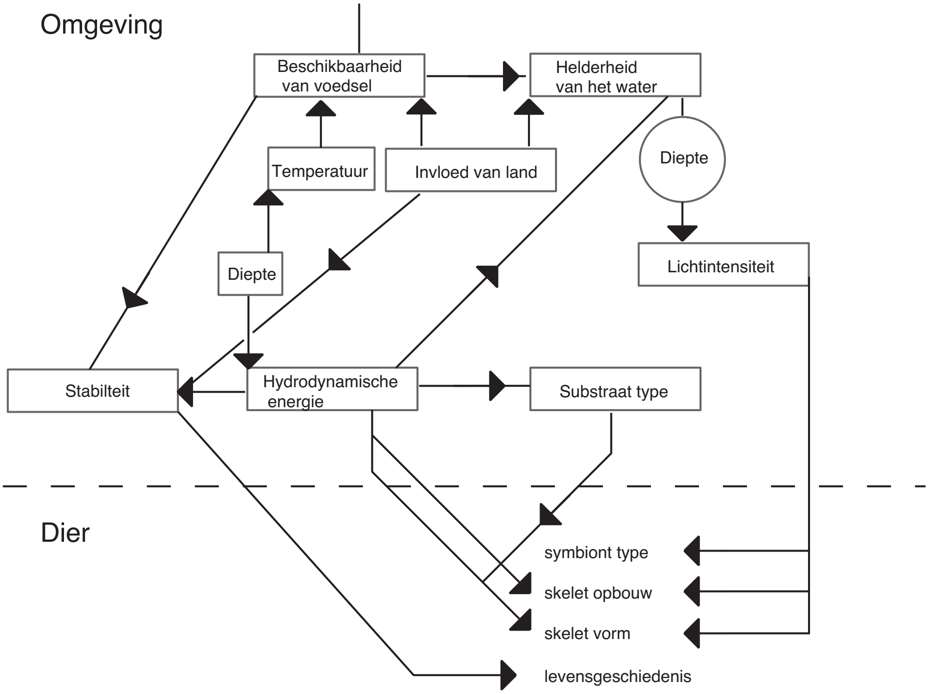


Fig. 10.1. Schema dat de omgevingsparameters die de verspreiding van groot foraminiferen bepalen en aanpassingen daaraan weergeeft.

deze twee parameters zijn gecorreleerd, aangezien de metabolische activiteit toeneemt als het water warmer wordt en ze dus meer energie nodig hebben om in leven te blijven.

Symbiose is alleen maar voordelig voor zowel de symbiont als de gastheer als deeltjes organische stof (POC) zeldzaam zijn. In deze omstandigheden voedt de gastheer zich met dit POC, terwijl de symbiont de afvalproducten van de gastheer gebruikt, tezamen met energie uit fotosynthese. De overtollige energie wordt dan weer gebruikt door de gastheer (Hallock, 1981c). Laboratorium experimenten hebben uitgewezen dat sommige groot foraminiferen wel 90% van hun energie van hun symbionten betrekken (ter Kuile, 1991). Het houden van symbionten beperkt het voorkomen van groot foraminiferen dus tot het voorkomen in de fotische zone.

De metabolische activiteit verdubbelt met iedere temperatuur stijging van 10 graden. De kans om voldoende voedselarme omstandigheden aan te treffen neemt dus toe met een hogere watertemperatuur. Groot foraminiferen zijn dan ook beperkt tot het gebied met een oppervlakte temperatuur in de koudste maand van hoger dan 16°C (Langer & Hottinger, 2000).

Hoewel vaak als belangrijkste parameter aangeduid, bepaalt diepte slechts indirect de verspreiding van groot foraminiferen. Erg belangrijk is dat met diepte de hoeveelheid licht, en de frequentie van het licht afneemt. Hoe snel dit gebeurt (de helderheid van het water) wordt beïnvloed door de beschikbare hoeveelheid voedsel en landinvloed. Beide parameters verhogen de hoeveelheid deeltjes (organisch dan wel sediment) in het water en verminderen dus de helderheid.

Daarnaast neemt de hydrodynamische energie en de temperatuur af met diepte. Hydrodynamische energie vertaalt zich zowel direct als indirect in het voorkomen van groot foraminiferen. Als er continu hoge golven breken op een deel van het rif, moeten de foraminiferen zich goed kunnen verankeren en niet snel breken om te kunnen overleven. Ook op niet verkitte sedimenten verstoren golven foraminiferen omdat ze steeds bedolven worden onder het sediment en er dan geen licht meer bij hun symbionten komt. Overigens zijn er ook soorten die zich juist gedeeltelijk bedekken met zand om zich zo tegen te hoge lichtintensiteit beschermen en dus ondieper leven dan anders mogelijk zou zijn.

Soorten reageren verschillend op golfenergie. *Palaeonummulites venosus* komt bijvoorbeeld alleen maar voor dieper dan de mooi weer golfbasis, terwijl *Cycloclypeus carpenteri* alleen maar onder de storm golfbasis voorkomt.

Aanpassingen van groot foraminiferen aan de omgeving

In Figuur 10.1 worden in de onderste helft een aantal tactieken genoemd die groot foraminiferen gebruiken om zich aan te passen aan de omgeving waarin ze leven. Alle soorten hebben een geheel eigen combinatie van grenzen waarbinnen de milieu parameters moeten blijven om voor te kunnen komen. Deze combinatie wordt bepaald door een aantal eigenschappen van de foraminifeer.

1. Samenstelling en opbouw van het kalkskeletje. De structuur van de kalk in het skeletje van imperforate foraminiferen is minder transparant dan die van perforate foraminiferen. Daarnaast zitten er kleine poriën die de licht doorval ook verbeteren in de kalkwanden van perforate foraminiferen. Dientengevolge kunnen perforate foraminiferen dieper voorkomen dan imperforate foraminiferen.

2. Het type symbiont. Er komen vier groepen algen voor als symbiont in foraminiferen: groene en rode algen, diatomeeën en dinoflagellaten. Iedere groep gebruikt zijn eigen golflengte bereik en de gastheer wordt daardoor beperkt in het voorkomen. Groenalgen gebruiken oranje licht, en dat wordt als eerste door het water geabsorbeerd. Hierom komen *Parasorites* en *Laevipeneroplis* die groenalgen als symbiont hebben alleen ondiep voor. Bij Nummulitidae en Amphisteginidae is een andere aanpassing vastgesteld: ze veranderen het soort symbiont. Hoewel ze wel gebonden zijn aan een bepaald type (in beide gevallen diatomeeën) kunnen ze hun diepte bereik uitbreiden door als ze dieper voorkomen een andere soort diatomee op te pikken dan ondiep.

3. Vorm van het skeletje. Zowel binnen als tussen soorten is de vorm afhankelijk van de omgeving. Dieplevende soorten zijn platter dan ondiep levende. Enerzijds kunnen ze zich dit veroorloven omdat er minder hydrodynamische energie is en de kans op breken dus geringer is, anderzijds hebben ze op die manier een grotere oppervlakte en kunnen beter profiteren van de geringere hoeveelheid licht die op die grotere diepte aanwezig is. In ondiep water is de lichtintensiteit te hoog en wordt het skeletje dikker, waardoor de kans op breken door golven ook kleiner wordt. Ook worden er pilaartjes gevormd die dienen ter versteviging, maar ook als lensjes fungeren en dan het licht bij de symbionten concentreren.

4. Er zijn allerlei mechanismen ontstaan om te voorkomen dat golven of stroming het huisje wegspoelen. *Amphisorus hemprichii*, die op de onstuimigste plekken voor-

komt, cementeert zich vast aan het substraat. *Calcarina's* houden zich vast door middel van een prop protoplasma aan hun stekels. *Amphistegina* ontwikkeld het deel van het skelet rond de mondopening zo dat ze zich beter kunnen verankeren aan het substraat.

De Spermonde Archipel

Een groot deel van het onderzoek is uitgevoerd op de Spermonde Archipel (hoofdstukken 2 t/m 4). Dit is een ondiepe kustzee (maximaal 70 m diep) die door een bar-

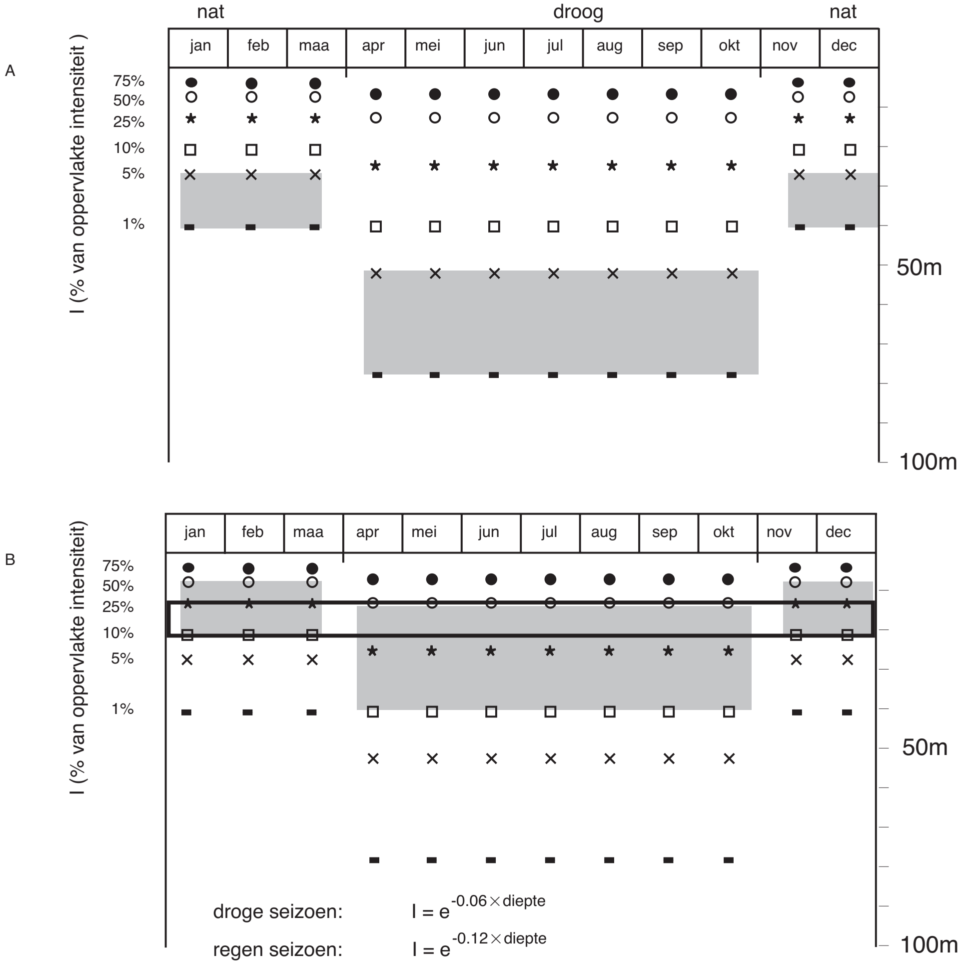


Fig. 10.2. Model dat laat zien dat diep levende soorten gevoeliger zijn voor veranderingen in milieuparameters (en dan vooral helderheid van het water) dan ondiep levende soorten. Het grijze blok geeft de lichtintensiteit aan waarin de soort kan leven. Omdat aangenomen wordt dat een groot foraminifeer als hij zich eenmaal gevestigd heeft niet meer kan verplaatsen, moeten de goede omstandigheden een jaar lang aanwezig zijn om te kunnen overleven.
A: diep levende soort I = 1-5% lichtintensiteit aan de oppervlakte
B: ondiep levende soort I = 10-50% lichtintensiteit aan de oppervlakte

rière van de Straat van Makassar wordt afgeschermd (Fig. 2.1). In het Zuidwesten mondt een grote rivier, de Jene Berang, uit en wordt er veel sediment en voedingsstoffen over de Spermonde gespoeld (vooral in het natte seizoen). Riffen komen voor ten noorden van de Jene Berang op variabele afstand van de kust. Deze riffen zijn bemonsterd door middel van SCUBA duiken, terwijl er ook drie transecten met een bodemhapper bemonsterd zijn.

In totaal zijn er 20 soorten levende obligate symbionthoudende soorten en een facultatieve chloroplast onderhoudende soort (*Elphidium craticulatum*) aangetroffen. Deze 21 soorten kwamen in zes assemblages voor. Eén hiervan was beperkt tot het deel het dichtst bij de kust, terwijl de andere vijf in de overige gebieden voorkwamen. Hoe verder je van de kust kwam, hoe dieper deze assemblages voorkwamen.

Dit patroon is te verklaren als je naast voedselrijkheid en lichtintensiteit ook stabiliteit van het ecosysteem (voorspelbaarheid) meeneemt bij het verklaren van deze patronen. Stabiliteit is belangrijk omdat groot foraminiferen een lange generatietijd hebben voor ze zich voortplanten (dit doen ze door zich op te delen, en daarna is de ouder dus dood). Diep levende soorten worden groter en hebben een langere generatietijd (*Cycloclypeus carpenteri* die wel 12 cm groot kan worden, heeft een generatietijd van 1-4 jaar). Gedurende deze hele tijd moeten de omstandigheden goed genoeg zijn om te overleven. Dit betekent dat de hoeveelheid licht gedurende die hele tijd binnen de tolerantiegrenzen moet blijven. Omdat lichtintensiteit logaritmisch afneemt met waterdiepte, heeft een afname in de helderheid vooral op grote diepte grote gevolgen, en hebben vooral de diep levende soorten last van seizoensveranderingen in bijvoorbeeld run off (Fig. 10.2).

Het gevolg hiervan is dat in zeer voedselarme condities er een grotere differentiatie met de diepte optreed. De soorten zijn meer gespecialiseerd op een bepaald bereik in

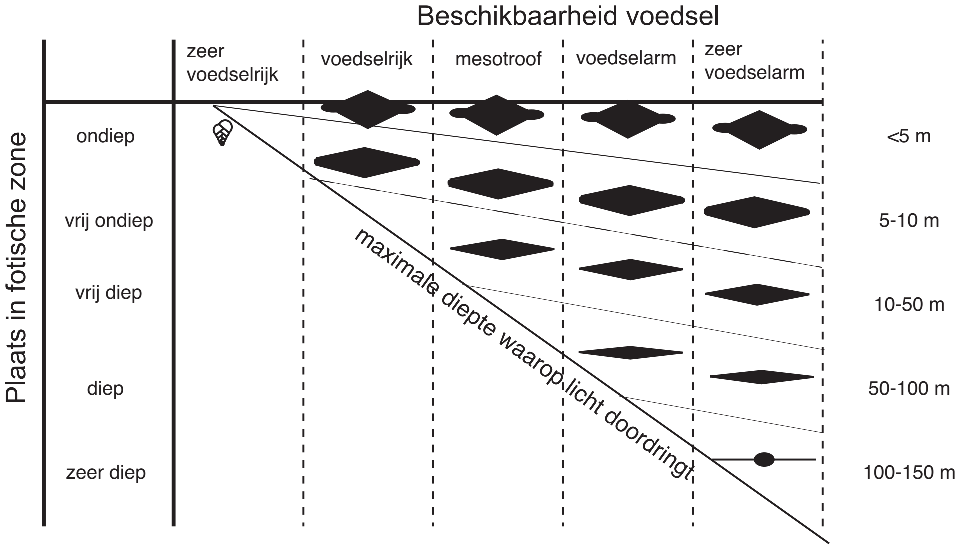


Fig. 10.3. Weergave van het habitat gebruik van groot foraminiferen (naar Hallock, 1987). In voedselarme omstandigheden komen groot foraminiferen dieper voor, en zijn ze soorten en vormen rijker.

lichtintensiteit. Een van de aanpassingen hieraan is hun vorm. Dieplevende soorten (en dieper levende individuen van dezelfde soort) zijn platter dan ondiep levende soorten. Juist deze platte, dieplevende soorten ontbreken in voedselrijkere situaties, waardoor daar zowel de soortenrijkdom als de vormenrijkdom minder is (Fig. 10.3).

In hoofdstuk 4 wordt de verspreiding van lege skeletjes vergeleken met die van de levende foraminiferen. Over het algemeen komt deze verspreiding erg mooi overeen, maar er zijn toch een aantal verschillen. Soorten die op niet-verkit sediment leven onder de riffen gedragen zich het meest zoals het model voorspelt, tot deze groep horen onder andere de Nummulitidae. Soorten die op de riffen zelf voorkomen daarentegen hebben een veel geringere kans op preservatie. Ze worden alleen maar gevonden in monsters die op of erg dichtbij een rif genomen zijn. Daarnaast is het onderscheid tussen monsters die aan de lijzijde en de loefzijde van de riffen genomen zijn vervaagd, hetgeen duidt op transport van de lege skeletjes door golf energie van de west naar de oostzijde van het rif.

In het vijfde hoofdstuk worden de groot foraminiferen op een rif in de Filippijnen bekeken (rond Cabilao), en de resultaten vergeleken met de Spermonde situatie en gepubliceerde waarnemingen. Veel soorten komen op vergelijkbare plekken voor, maar er zijn ook weer een aantal opmerkelijke verschillen.

In de Spermonde komen de hoogste dichtheden voor op de rifbasis, en wordt het rifvlak nauwelijks door (groot) foraminiferen bewoond omdat hier te veel los zand ligt in combinatie met altijd aanwezige golven. Het eerste deel (gezien vanaf zee) van het rifvlak in de Spermonde is vergelijkbaar, maar op het tweede deel groeien grote algen die beschutting bieden aan de foraminiferen. Op Cabilao is de dichtheid hier het hoogst. Hier komen een aantal soorten voor die in de Spermonde veel dieper voorkomen, terwijl op Cabilao ze dieper juist afwezig zijn. De algemeenste soort (zeker in aantal) op de Spermonde, *Operculina ammonoides*, is zeldzaam rond Cabilao, en hij komt hier ook tussen ‘coral rubble’ voor, terwijl hij in dat habitat op de Spermonde juist niet voorkomt.

Fossielen

In het tweede deel, de hoofdstukken 6 en 7, komen fossiele voorkomens juist meer aan bod. Uitgaande van de constatering dat vormenrijkdom en diversiteit aan elkaar gerelateerd zijn, is de diversiteitsontwikkeling in het Cenozoicum van Zuidoost-Azië vergeleken met die in Europa.

Om dit te kunnen doen moest in eerste instantie de ouderdomsbepaling in het oudste deel van het Cenozoicum verbeterd worden. Tot nu toe werd het Eoceen in Zuidoost-Azië onderverdeeld in vier eenheden, Ta_{1-3} en Tb. Hiervan was eigenlijk alleen Tb goed te onderscheiden en te correleren met andere delen van de toenmalige Tethys Oceaan (die zich uitstrekte langs de zuidgrenzen van Azië, Europa en Noord-Amerika). Om dit doel te bereiken was een revisie van een belangrijke groep gidsfossielen, nummulieten, in Zuidoost-Azië noodzakelijk.

Deze revisie vormt hoofdstuk 6 van dit proefschrift, en zal ook verschijnen in Cainozoic Research, waarin de nieuwe soorten een formele naam zullen krijgen. Het resultaat van de revisie is dat van de meer dan 70 namen die in deze groep gebruikt zijn in de afgelopen 150 jaar, er slechts 16 geldig zijn, waarbij dan ook twee soorten zitten die nog nooit eerder herkend en benoemd waren. Van deze 16 soorten is de stratigrafische verspreiding afgegrensd, zodat ze voor ouderdomsbepalingen gebruikt kunnen worden (Fig. 10.4).

Een bijkomend resultaat was dat het geslacht *Assilina*, zeer talrijk aanwezig in het Midden Eoceen van Europa, niet in Indonesië voorkwam. Ook komen er maar drie soorten (ook nog zeer zeldzaam) voor van het zeer nauw verwante geslacht *Planocamerinoides*. Een ander geslacht (*Ranikothalia)* dat ook vermeld was uit het Midden Eoceen in Indonesië, bleek ook een misidentificatie te betreffen. Elders in het verspreidingsgebied is *Ranikothalia* beperkt tot het Vroeg Eoceen, en het voorkomen in het Midden Eoceen zou dan ook een grote verrassing zijn.

Bovengenoemde resultaten zijn in hoofdstuk 7 gebruikt om diversiteitspatronen in

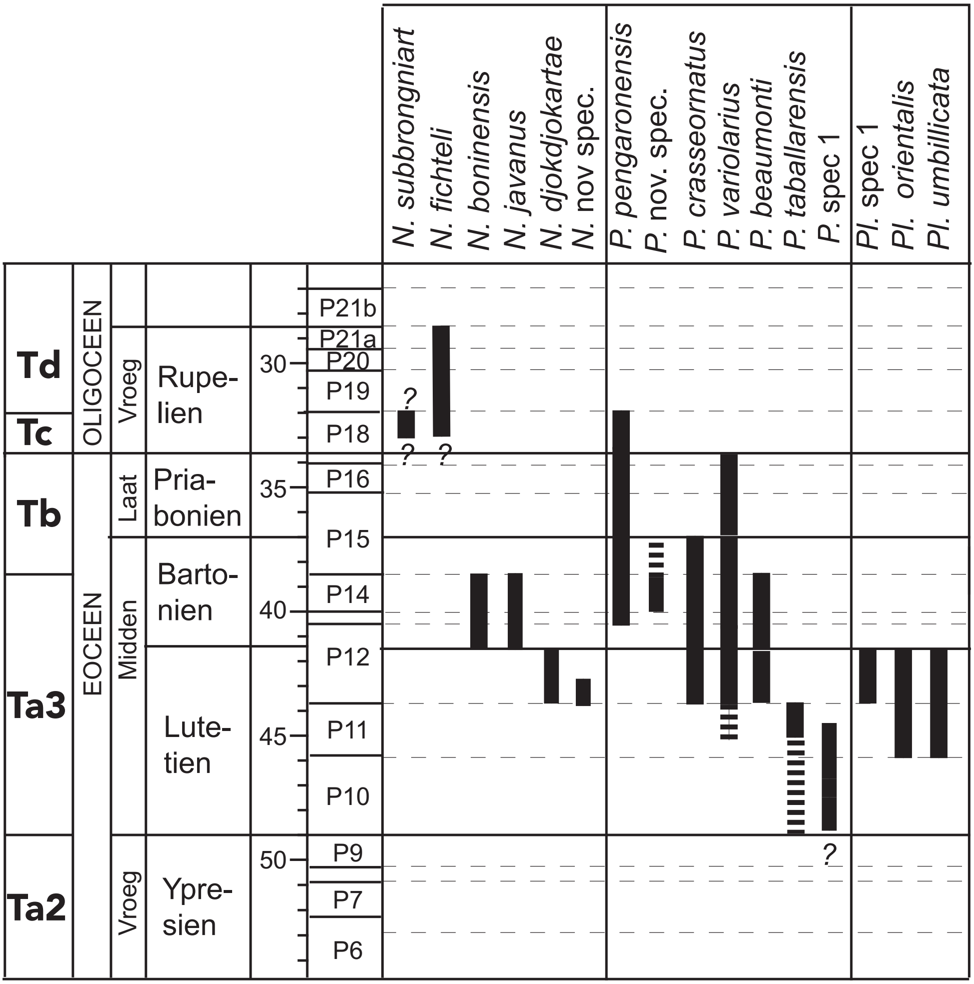


Fig. 10.4. Stratigrafische verspreiding van de soorten in de genera *Nummulites, Palaeonummulites* en *Planocamerinoides* in Indonesie.

het Eoceen (soortsniveau) en Cenozoicum (genusniveau) te bekijken. Uitgangspunt hierbij waren de vragen:

- Was gedurende het Eoceen Zuidoost-Azië inderdaad soortenarmer dan Europa of andere delen van de Tethys?
- Als dit zo is, wanneer ontstaat dan het huidige diversiteitspatroon, waarin de IWP wel het meest diverse gebied is?

Als we kijken naar het aantal soorten in het genus *Nummulites,* dan is Zuidoost-Azië inderdaad veel armer dan Europa. Europa is echter veel groter, beter bestudeerd en dus zou er wel eens een waarnemers effect op hebben kunnen treden. Er zijn echter ook vergelijkbare data bekend uit Oman (Racey, 1995) en Noord-Afrika (Schaub, 1981). Deze twee gebieden komen qua oppervlakte (Noord-Afrika), en Oman qua hoeveelheid ontsloten Laat-Midden Eocene afzettingen beter overeen met Indonesië. Oman is wel veel kleiner dan Indonesië, dus de kans op endemische soorten is daar wel kleiner.

De soortaantallen van de nummulieten zijn in alle tijdvakken (vroeg, midden, laat Lutetien en Bartonien) van het Midden Eoceen veel lager dan in de drie overige gebieden (Fig. 10.5). In hoofdstuk 4 was gebleken dat morfologische variabiliteit ook gerelateerd is aan taxonomische diversiteit. Daarom is, als verdere controle, ook de vormenrijkdom vergeleken en die bleek eveneens veel lager te zijn in Zuidoost-Azië. Terwijl in Europa de grootse diameter van *Nummulites* meer dan 10 cm bedraagt is de

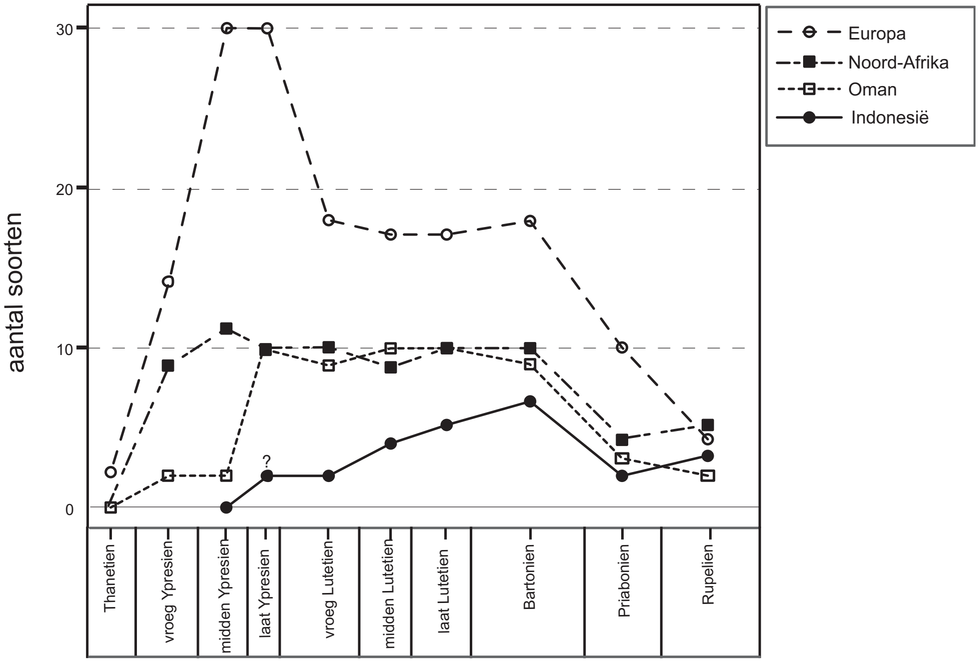


Fig. 10.5. Aantal soorten in de genera *Nummulites* en *Palaeonummulites* in vier delen van de Tethys Oceaan. De hoge aantallen soorten in het Ypresien van Europa is een overschatting van de werkelijkheid, omdat hier veel soorten met een erg korte stratigrafische verspreiding voorkomen, die bij elkaar opgeteld worden in de langere periodes die hier gebruikt worden.

grootste Indonesische soort slecht 4,5 cm. De maximum diameter wordt wel op hetzelfde tijdstip bereikt, namelijk in de eerste helft van het Bartonien (Fig. 10.6).

Opvallend is dat veel van de soorten die in Europa een belangrijk deel van de assemblages vormen en een langere stratigrafische range hebben ook in Indonesië voorkomen (soms zonder te veranderen, soms net genoeg veranderd om tot een andere soort gerekend te kunnen worden). Opvallend is daarbij dat *N. fabiani* niet in Zuidoost-Azië is aangetroffen, terwijl zijn opvolger, *N. fichteli*, wel talrijk vertegenwoordigd is in Zuidoost-Azië. Dit is een duidelijk voorbeeld van een immigratie gebeurtenis na de Eoceen-Oligoceen grens.

Ook in de generieke diversiteit is Zuidoost-Azië veel armer dan Europa in het Eoceen (Fig. 10.7). De faunaverandering op de Eoceen-Oligoceen overgang (die geleidelijk plaatsvindt over ongeveer 8 Mj) heeft een minder groot effect in Zuidoost-Azië dan in Europa. In Europa neemt de diversiteit af, terwijl in Zuidoost-Azië een veel sneller herstel optreedt en de diversiteit ondanks enkele extincties toeneemt. In hoofd-

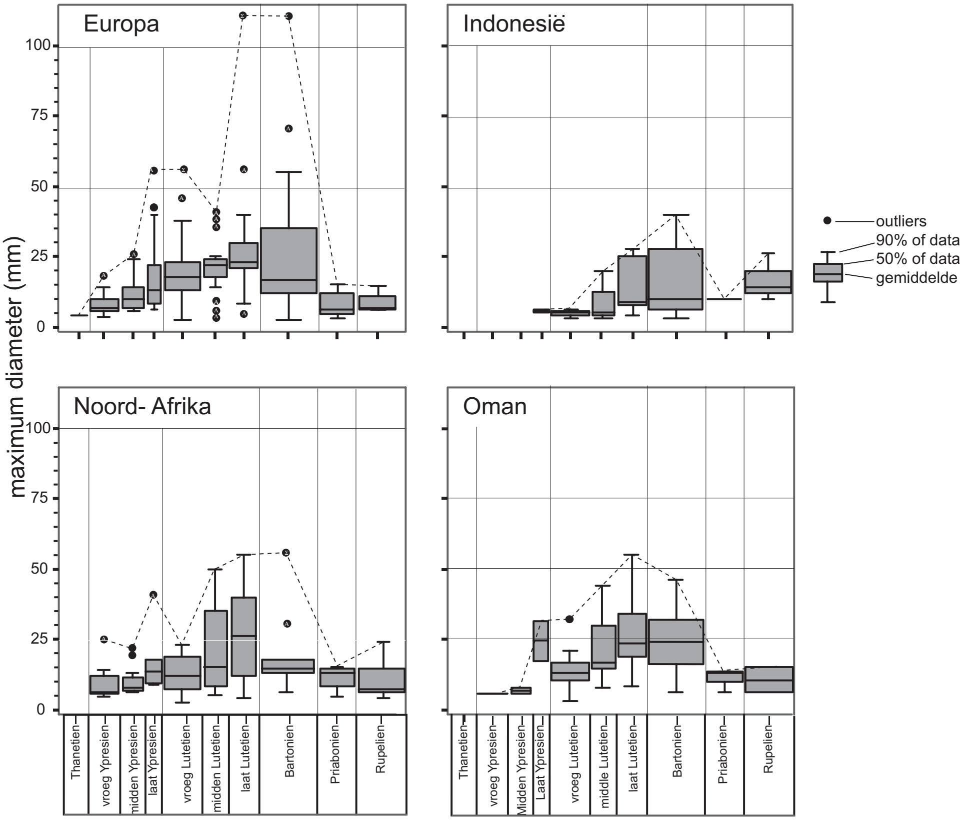


Fig. 10.6. Mediane (middenwaarde van de opgegeven minimale en maximale diameter) diameter van de microsfere vorm van soorten uit het genus Nummulites en Palaeonummilites in vier deelgebieden van de Tethys-oceaan (met gebruik van gegevens van Schaub, 1981 en Racey, 1995).

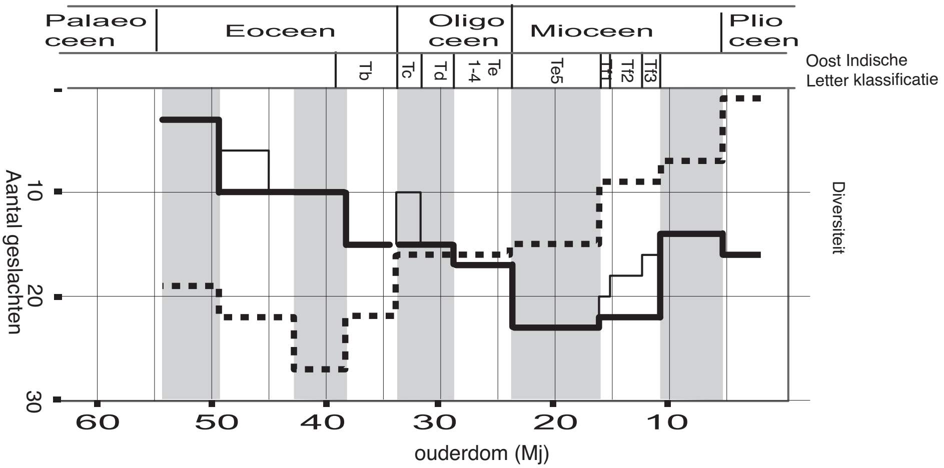


Fig. 10.7. Aantal genera in het Cenozoicum van Europa en Zuidoost-Azië

stuk 8 wordt beargumenteerd dat dit mogelijk komt door de afkoeling die op dit tijdstip plaatsvond. Mogelijk was de Eocene fauna gelimiteerd door de erg hoge zeewater temperaturen, terwijl deze temperaturen in het koelere Priabonien (Laat Eoceen) en Rupelien wel weer in het optimale bereik vielen.

Vanaf het Chatien (Laat Oligoceen) is Zuidoost-Azië het rijkste gebied op aarde, hoewel de fauna samenstelling nog sterk afwijkt van de Recente fauna. Door het botsen van Afrika met Eurazië wordt Europa afgesloten van de IWP, en vond daar geen immigratie van nieuwe genera meer plaats, ondanks het (voor groot foraminiferen) verbeterende klimaat.

In het Midden Mioceen vindt nog een belangrijke uitstervingsgolf plaats, waarna vanaf het einde van Plioceen de Recente fauna zich ontwikkelt in Zuidoost-Azië Tegen die tijd zijn de groot foraminiferen in Europa al bijna uitgestorven. In de Middellandse Zee komt nu nog een soort voor (aangevuld met een nieuwe soort na het openen van het Suez kanaal).

11. Dankwoord

Zonder de hulp van velen in mijn omgeving was dit proefschrift niet tot stand gekomen. Dit gegeven gecombineerd met het feit dat een dankwoord schrijven zeker niet mijn sterkste kant is, maakt dat ik vrijwel zeker mensen zal vergeten te noemen. Ik verontschuldig mij daar dan ook al bij voorbaat voor aan diegenen die hier wel een plaats verdiend hebben. Zij zullen wel weten dat ik hen niet vergeten ben.

Ten eerste dank ik een aantal mensen zonder wie dit proefschrift zeker niet tot stand gekomen zouden zijn: mijn promotor prof. Jan van Hinte en mijn co-promotores drs Simon Troelstra en Cor Winkler Prins, voor de stimulerende discussies, raad en bijstand tijdens de verschillende fases van het onderzoek.

The members of the dissertation committee, Profs Martin Langer, G.J. van der Zwaan and Johann Hohenegger, Drs Brian Rosen and Bert Hoeksema are thanked for

their critical comments and time they put into the manuscript.

Next I thank the co-authors of severall of the chapters Bert Hoeksema, Simon Troelstra, Jan van Hinte, Andrew Racey en Peter Lunt for their contributions to these papers, and discussions on some of the other chapters.

I also thank other colleagues with whom I had stimulating discussions and whose comments improved earlier versions of the manuscripts: Stephen Donovan, Brian Rosen, Johann Hohenegger, Martin Langer and Ulrike Wielandt.

De editors van Scripta Geologica, Cor Winkler Prins en Stephen Donovan, en het NNM Naturalis worden bedankt voor hun bereidheid dit proefschrift in de serie op te nemen, en de energie die ze erin hebben gestoken om de typefouten eruit te halen, referenties te controleren etc. Het manuscript is er zeer zeker van opgeknapt.

Vervolgens worden de collegae op Naturalis bedankt, er zijn er teveel om bij naam te noemen. Wel genoemd dienen te worden Charles Barnard, voor het verwerken van een groot deel van de monsters, en Jeroen Goud die mij wegwijs heeft gemaakt op de SEM en Peter Wittekoek en Wouter Wildenberg, die slijpplaatjes hebben gemaakt. Georg Oleschinski fotografeerde de nummulieten uit de collectie in Bonn.

Hein, René, John, Frank, Lars, Jeroen, Hanneke, Stephen en Steven hebben menig kopje koffie dan wel thee met me genipt en zorgden voor de broodnodige ontspanning op het werk.

Paul van Dijk (verspreiding dode foraminiferen over de Spermonde) en Minke van Det (voorkomen van Recente gastropoden over de Spermonde) werkten aan dezelfde monsterset.

Bert, Sylvie en Rindu Hoeksema bedank ik van harte voor hun gastvrijheid gedurende mijn verblijf in Ujung Pandang tijdens het veldonderzoek voor de hoofdstukken 2-4.

De leden van het zeeteam (Bert, Charles, Leen, Koos, Koos, Jeroen, Chiel, Nicole, Arjan) bedank ik van harte voor hun gezelschap bij en samenwerking op expedities naar Cebu en Bali.

Ook wil ik Frank, Maaike en Michiel bedanken voor de vele avonden en dagen gezelschap, deze zijn zeer goed bevallen en hebben voor de broodnodige afleiding gezorgd.

Tenslotte gaat mijn dank natuurlijk ook nog uit naar mijn paranimfen, Lútsen Renema en Frank Wesselingh voor hun bijstand in de laatste stadia van de afronding.

12. Curriculum vitae

Willem Renema is geboren op 6 januari 1972 in Apeldoorn. Hij behaalde in 1991 aan B.C. Shöndeln te Roermond het VWO diploma. In datzelfde jaar begon hij met de studie Geologie aan de faculteit Aardwetenschappen van de Universiteit Utrecht. In 1992 behaalde hij zij propedeuse examen en in 1996 zijn doctoraal examen in de Geologie. De afstudeeronderzoeken betroffen een vergelijking van het voorkomen van levende en dode benthische foraminiferen in een transect in de West Atlantische Oceaan (aan het NIOZ, Texel) en een onderzoek aan fossiele lacustriene gastropoden in Pliocene meer-afzettingen in Griekenland.

In 1997 werd hij als AIO/Conservator aangesteld aan het Nationaal Natuurhistorisch Museum Naturalis, en begon hij met zijn promotie-onderzoek, waarbij de begeleiders verbonden waren aan de Vrije Universiteit Amsterdam. In 2001 is dit dienstverband omgezet in een vaste aanstelling als conservator Micropaleontologie.

Voor het onderzoek werd veldwerk in Zuidwest-Sulawesi (Ujung Pandang, tegenwoordig Makassar), Java en Cabilao uitgevoerd. Daarnaast heeft hij ook nog deelgenomen aan veldwerk op Luzon (Filippijnen, tweemaal) en Bali.

In zijn vrije tijd houdt hij zich bezig met Europese, in het bijzonder Nederlandse, zweefvliegen (Syrphidae).

Publicaties

Wesselingh, F.P., Cadée, G.C. & **Renema, W.** , 1999. Flying high: on the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera Tryonia and Planorbarius. *Geologie & Mijnbouw* **78**: 165-174.

Reemer, M., B. van Aartsen, **W. Renema**, J. Smit & W. van Steenis. 2000. Bijzondere vondsten van zweefvliegen in Nederland (Diptera: Syrphidae). *Nederlandse Faunistische Mededelingen* **12**: 155-164.

Renema, W. & Wakkie, B. 2001. Het zweefvliegengenus *Callicera* in Nederland en België (Diptera: Syrphidae). *Nederlandse Faunistische Mededelingen* **14**: 1-12

Renema, W., Hoeksema, B.W. & Van Hinte, J.E., 2001. Larger benthic foraminifera and their distribution patterns on the Spermonde Shelf, South Sulawesi. *Zoologische Verhandelingen* **334**: 115-150

Renema, W. & Troelstra, S. R., 2001. Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia). *Palaeogeografie, Paleoclimatologie, Paleoecologie.* **175** (1-4): 125-147

Wesselingh, F.P., T. Meijer, R.H. de Bruyne, P. de Wolf, G.C. Cadee & **W. Renema** (2001). Fossiele schelpen van het Texelse strand. *Spirula* **321**: 69-71.

Smit, J., **Renema, W**. and Aartsen, B. van. De zweefvliegen *Chrysotoxum intermedium* en *Chrysotoxum fasciolatum* nieuw voor de Nederlandse fauna (Diptera: Syrphidae). *Nederlandse Faunistische Mededelingen* **15**: 117-122.

Renema, W., 2001. Drie maal is scheepsrecht, de zweefvlieg *Chalcosyrphus eunotus* terug op de Nederlandse lijst (Diptera: Syrphidae). *Nederlandse Faunistische Mededelingen* **15**: 111-116.

Smit, J., Reemer, M. & **Renema, W.,** 2000. Vijf soorten van het zweefvliegengenus *Cheilosia* nieuw voor Nederland (Diptera: Syrphidae). *Nederlandse Faunistische Mededelingen* **15**: 123-139.

Plate 1

a-b. *Peneroplis planatus* (Fichtel & Moll, 1798) KKW-6 (RGM 214609 and RGM 214610).

c-d. *Dendritina ambigua* (Forskål, 1775) KKW 27 (RGM 214611 and RGM 214612).

e-f. *Laevipeneroplis proteus* (d'Orbigny, 1839) LW 2 (RGM 214613 and RGM 214614).

g-h. *Parasoritoides orbitolitoides* (Hofker, 1930) SE 21 (RGM 214615 and RGM 214616).

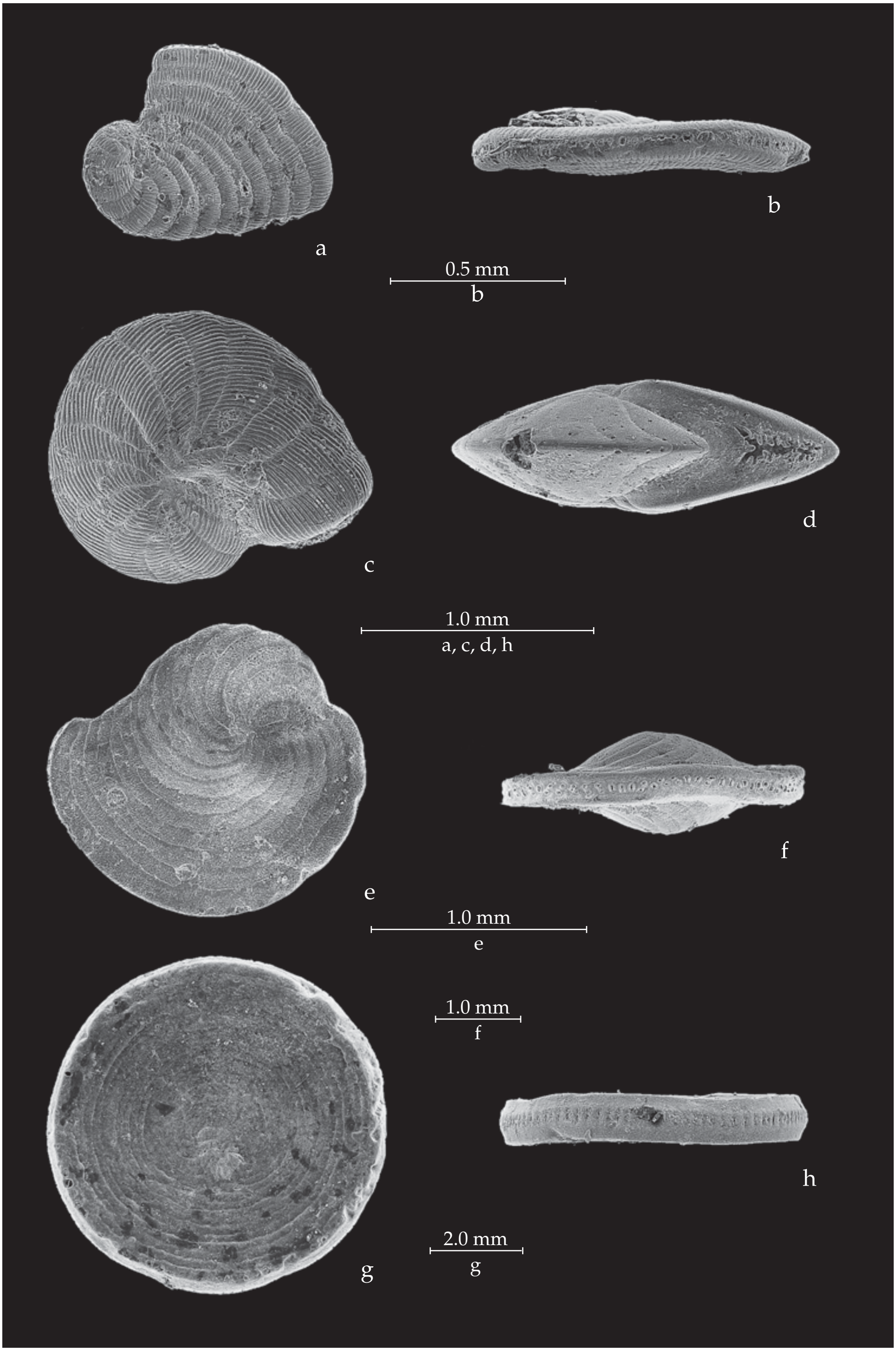

a
b
0.5 mm
b
c
d
1.0 mm
a, c, d, h
e
f
1.0 mm
e
1.0 mm
f
h
g
2.0 mm
g

Plate 2

a-b. *Sorites orbiculus* (Forskål, 1775) KKW 9 (RGM 214617 and RGM 214618).

c-d. *Amphisorus hemprichii* Ehrenberg, 1839 LKW 18 (RGM 214619 and RGM 214620): c showing a malformation of the test.

e. *Alveolinella quoyii* (d'Orbigny, 1826) SW 24 (RGM 214621).

f. *Amphistegina lessonii* d'Orbigny, 1826 KKW 12 (RGM 214622).

g. *Amphistegina radiata* (Fichtel & Moll, 1798) KKW 18 (RGM 214623).

h. *Amphistegina lobifera* Larsen, 1976 KKW 6 (RGM 214624)

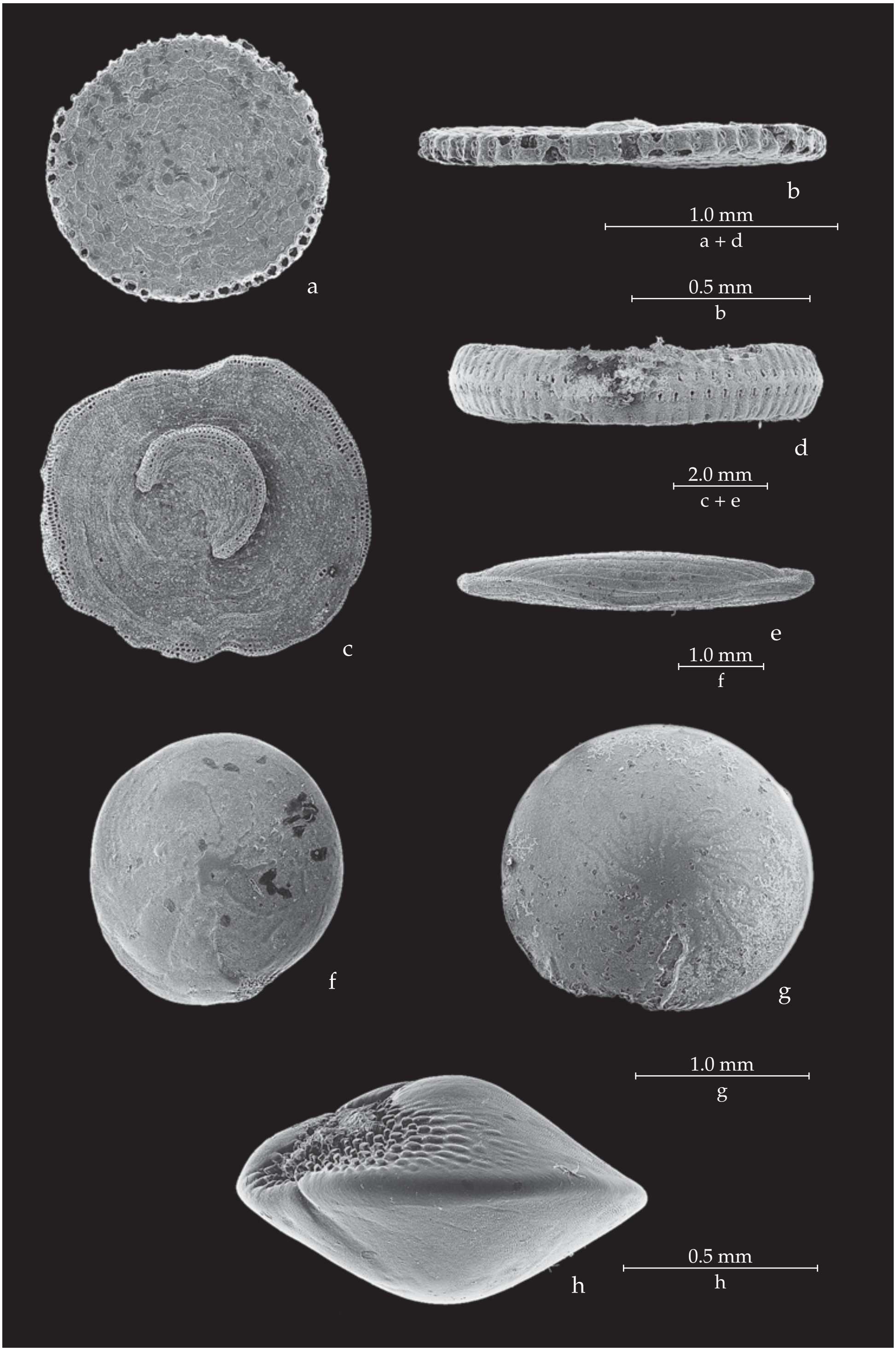

a
b
1.0 mm
a + d
0.5 mm
b
c
d
2.0 mm
c + e
e
1.0 mm
f
f
g
1.0 mm
g
h
0.5 mm
h

Plate 3

a-b. *Calcarina hispida* Brady, 1876 C05-0.5 (RGM 214607 and RGM 214608).

c. *Baculogypsinoides spinosus* Yabe & Hanzawa, 1930 KKW 24 (RGM 214625).

d. *Calcarina spengleri* (Gmelin, 1791) KKW 18 (RGM 214626).

e-f. *Neorotalia calcar* (d'Orbigny, 1839) SE 6 (RGM 214627 and RGM 214628).

g-h. *Elphidium craticulatumm* (Fichtel & Moll, 1798) LLW 6 (RGM 214629 and RGM 214630).

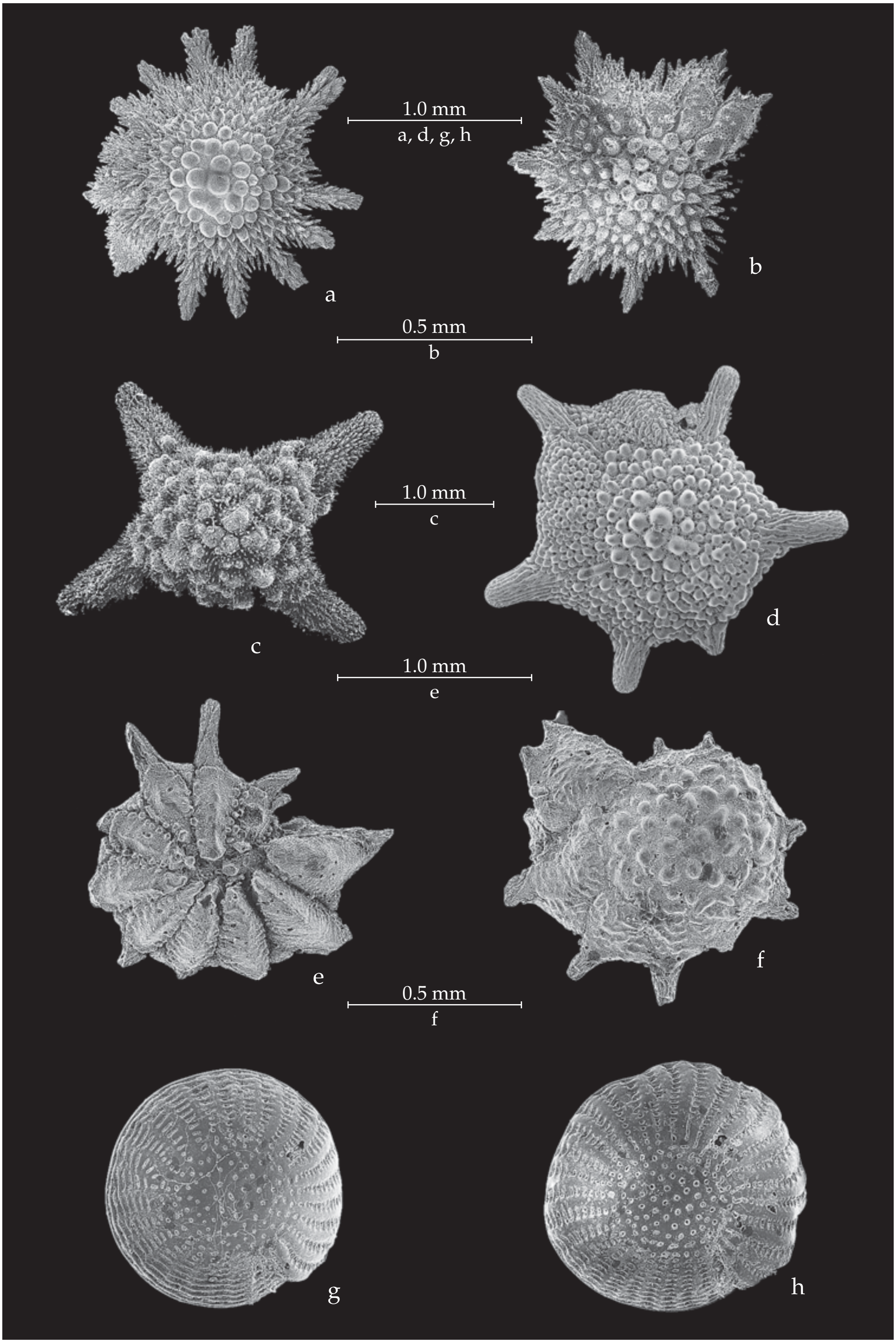

1.0 mm
a, d, g, h
a
b
0.5 mm
b
1.0 mm
c
c
d
1.0 mm
e
e
f
0.5 mm
f
g
h

Plate 4

a. *Heterostegina depressa* d'Orbigny, 1826 KKW 18 (RGM 214631).

b-c. *Operculina ammonoides* (Gronovius, 1781) SW 27 (RGM 214632 and RGM 214633) b: macrosphere showing normal growth, c: microsphere showing irregular growth.

d-e. *Palaeonummulites venosus* (Fichtel & Moll, 1798) KKW 33 (RGM 214634 and RGM 214635).

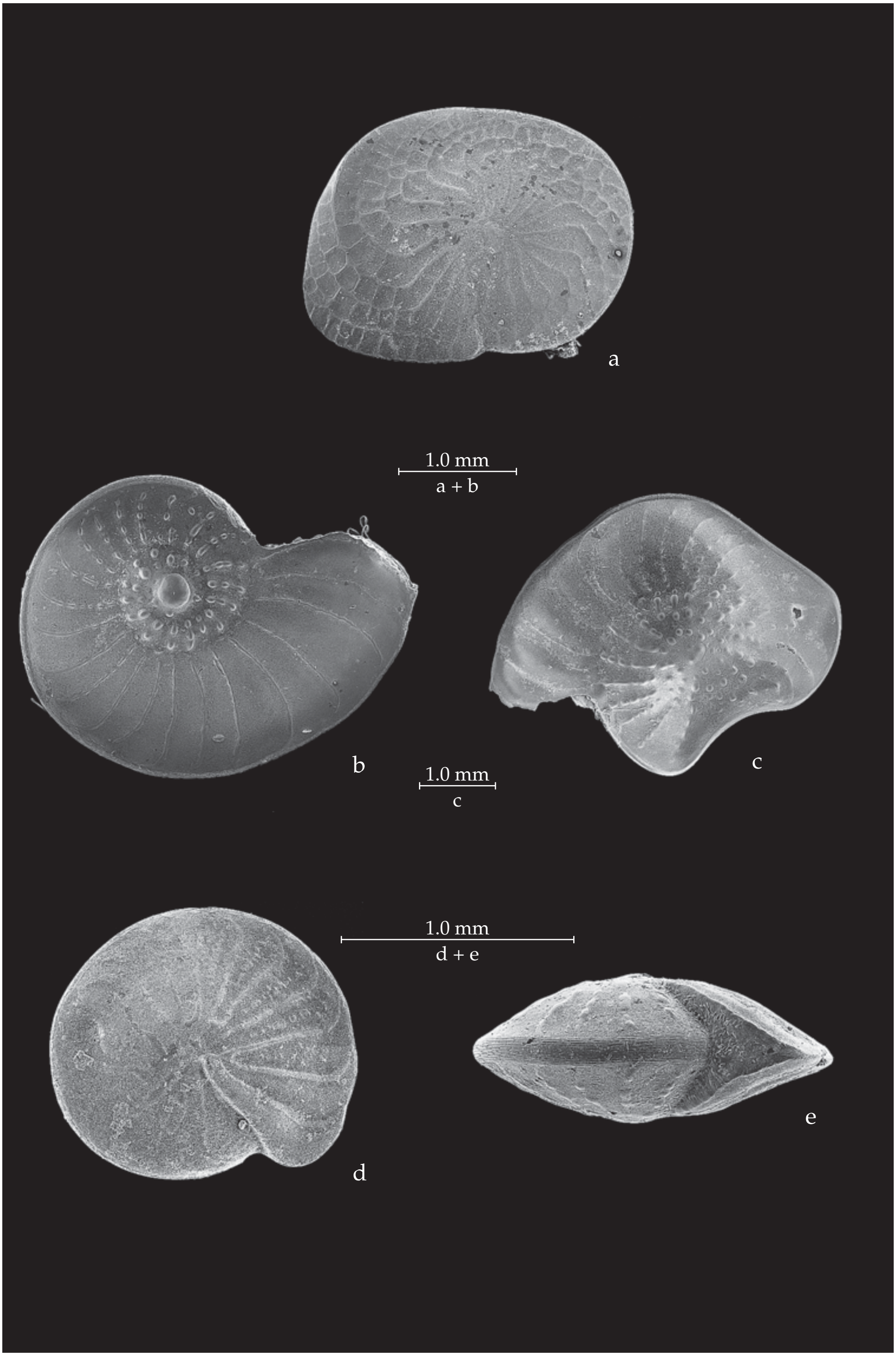

a
1.0 mm
a + b
b
c
1.0 mm
c
1.0 mm
d + e
d
e

Plate 5

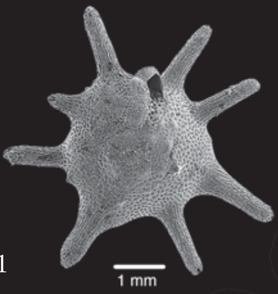
1-2. *Calcarina spengleri* (Gmelin, 1791) s.s. C05-0.5 (RGM 214601 and RGM 214602).

3-4. *Calcarina spengleri* (Gmelin, 1791) type A, C06-06 (RGM 214603 and RGM 214604).

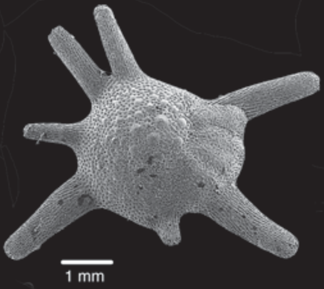
5-6. *Calcarina mayori* Cushman, 1924 C12-12 (RGM 214605 and RGM 214606).

7-8. *Calcarina hispida* Brady, 1876 C05-0.5 (RGM 214607 and RGM 214608).

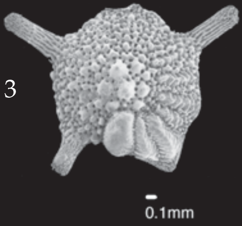
1



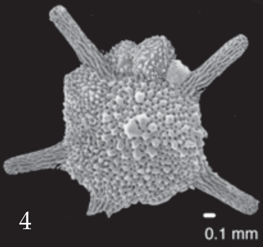
2



3



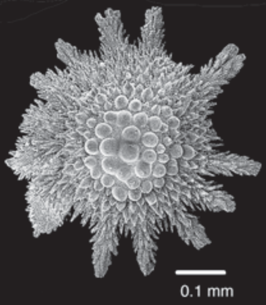
4



5

6

7



8

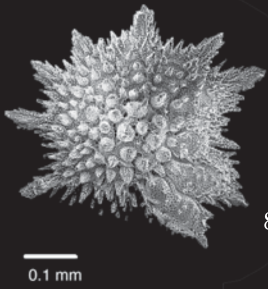


Plate 6

A-B, G-J. *Nummulites djokdjokartae (*Martin, 1881)
A-B: Axial section of B-form; Kali Puru (Nanggulan) (RGM 47196A) (A × 2.5, B × 5). Note the abundant splitting of the spiral laminae very near to the equatorial plane.
G: External view of juvenile B-form; Kali Puru (Nanggulan) (RGM 3334B) (× 2.5). Note straight peripheral part of the septal philaments. This specimen was labeled *N. vredenburgi* by Douvillé.
H: Equatorial section of juvenile B-form; Kali Puru (Nanggulan) (RGM 3334A) (× 2.5). This specimen was labeled *N. vredenburgi* by Douvillé.
I: Equatorial section of B-form; Kali Puru (Nanggulan) (RGM 3320C).
J: External view of B-form; Kali Puru (Nanggulan) (RGM 47196B).

C-E. *Nummulites* nov. spec.
C-D: Axial section of B-form; Kali Puru (Nanggulan) (RGM 3322A) (C × 2.5, D × 5). Note the rare splitting of the spiral laminae. If they split, it is more in the polar region than in *N. djokdjokartae* Martin.
E: Equatorial section of B-form; Kali Puru (Nanggulan) (RGM 3322B) (× 2.5).

Plate 7

A-C. *Nummulites* nov. spec.
A: External view of B-form (× 5); Kali Bawang (Nanggulan) (RGM 3339).
B: Equatorial section (split specimen) of A-form; Kali Puru (Nanggulan) (RGM 3325A) (× 10).
C: External view of A-form; Kali Puru (Nanggulan) (RGM 3325B) (× 10).

D-E: *Nummulites djokdjokartae (*Martin, 1881)
D: Equatorial section (split specimen) of A-form; Kali Puru (Nanggulan) (RGM 3321A) (× 10).
E: External view of A-form; Kali Puru (Nanggulan) (RGM 3332) (× 10).

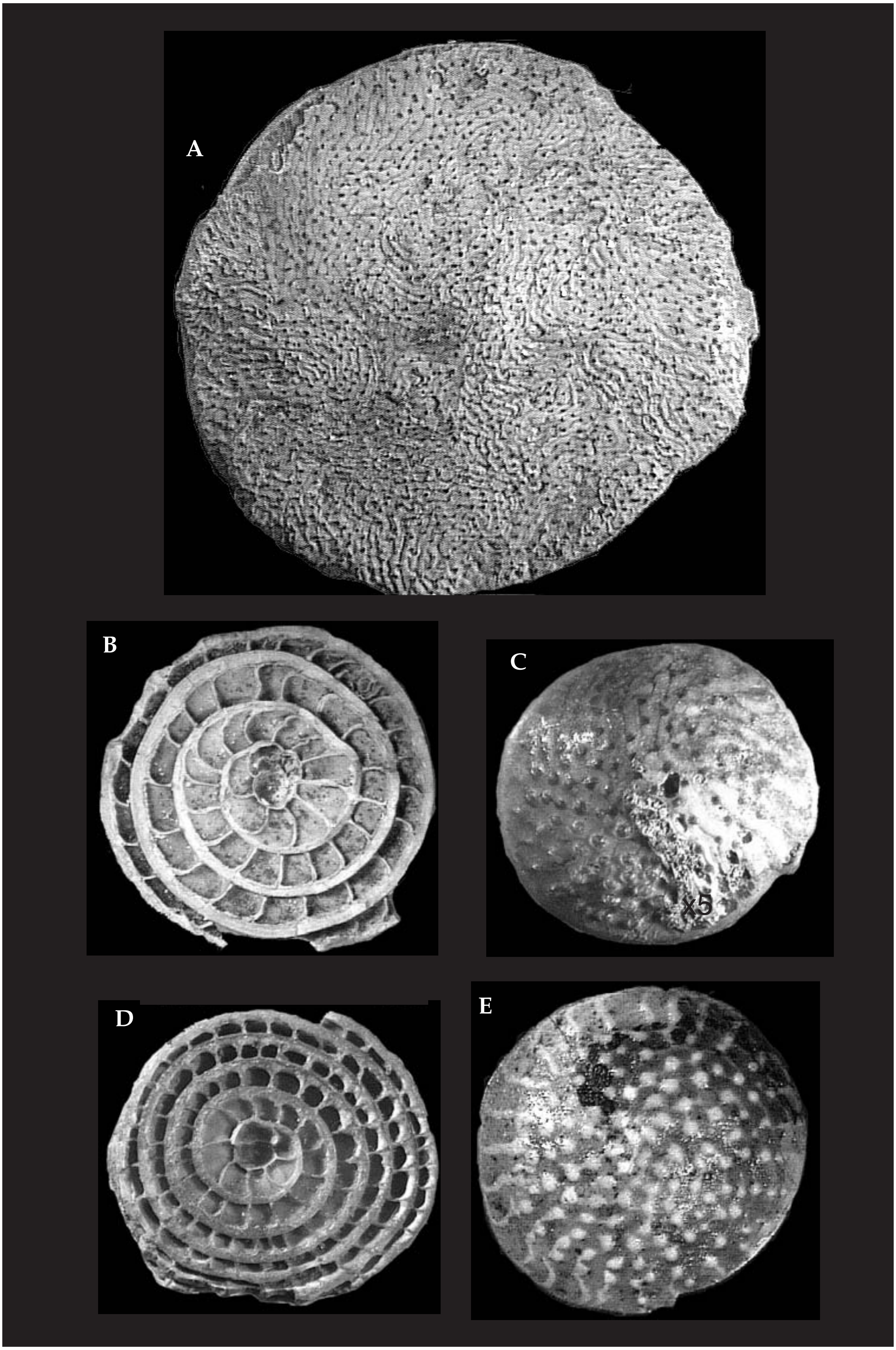

A
B
C
x5
D
E

Plate 8

A-F. *Nummulites javanus* Verbeek, 1891 (Palaeontological Museum, University of Bonn)
A-B: Equatorial section of B-form; Timor (× 2.5).
C: Equatorial section (split section) of B-form; Karangsambung (Java) (RGM20119) (× 2.5). Specimen from a type locality. Shows typical preservation with well preserved marginal cord and very thin septa.
D: Axial section of B-form. Jetis (Java) (RGM 20118) (× 2.5).
E: Equatorial section of A-form; Timor (Palaeontological Institute, University of Bonn) (× 5).
F: Axial section of A-form; Timor (Palaeontological Institute, University of Bonn) (× 5).

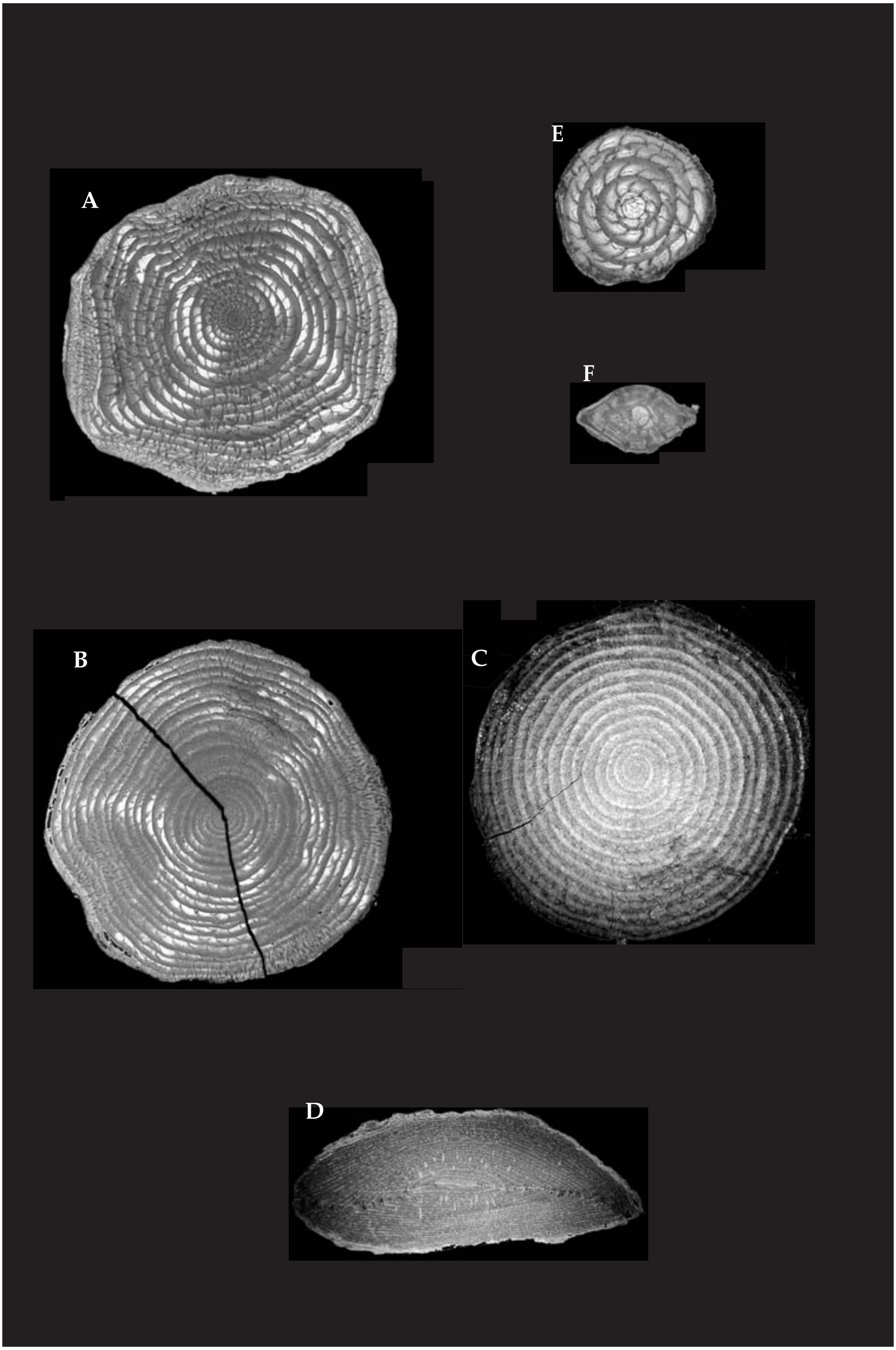
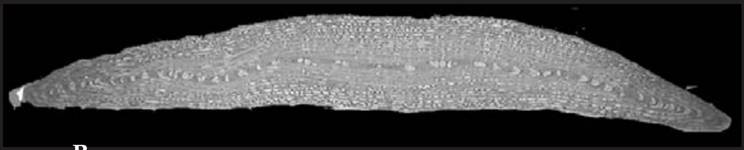

A
B
C
D
E
F

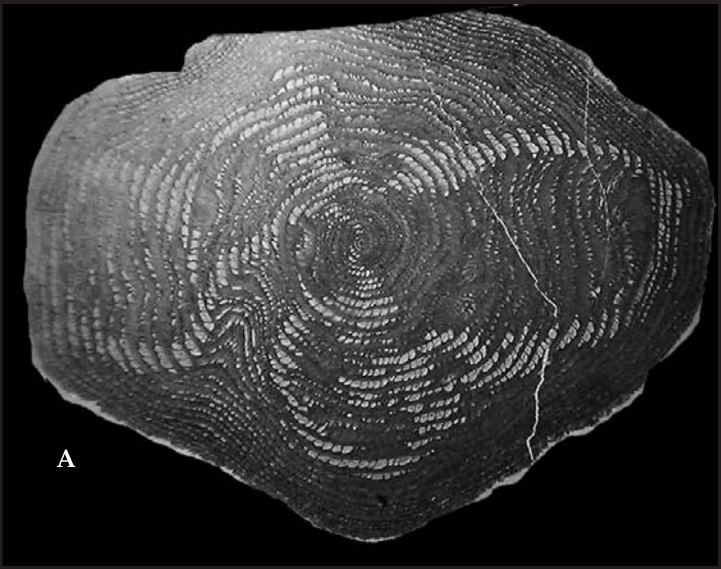
Plate 9

A-C. *Nummulites boninensis* Hanzawa, 1947
A: Equatorial section of B-from; Sungai Ular, SW Sulawesi (RGM 20117) (× 3.75).
B: Axial section of A-form; Timor (Geological Museum, University Delft, KA903), 1947 (× 7.5).
C: Axial section of B-form; Sungai Ular, SW Sulawesi (RGM 20116) (× 3.75).

C



B



A

Plate 10

A-E. *Palaeonummulites pengaronensis* (Verbeek, 1871)
A: Axial section of A-form; Timor (Palaeontological Institute, University of Bonn) (× 5).
B: Equatorial section of A-form; Sungai Temoe (Kalimantan) (RGM 19108) (× 5).
C: Equatorial section of A-form; Sungai Temoe (Kalimantan) (RGM 109) (× 5).
D-E: Equatorial section of B-forms; Timor (Palaeontological Institute, University of Bonn) (× 2.5).

F-G. *Palaeonummulites* sp. 1
F: Equatorial section of B-form; Timor (Palaeontological Institute, University of Bonn) (× 5).
G: Axial section of B-form; Timor (Palaeontological Institute, University of Bonn) (× 5).

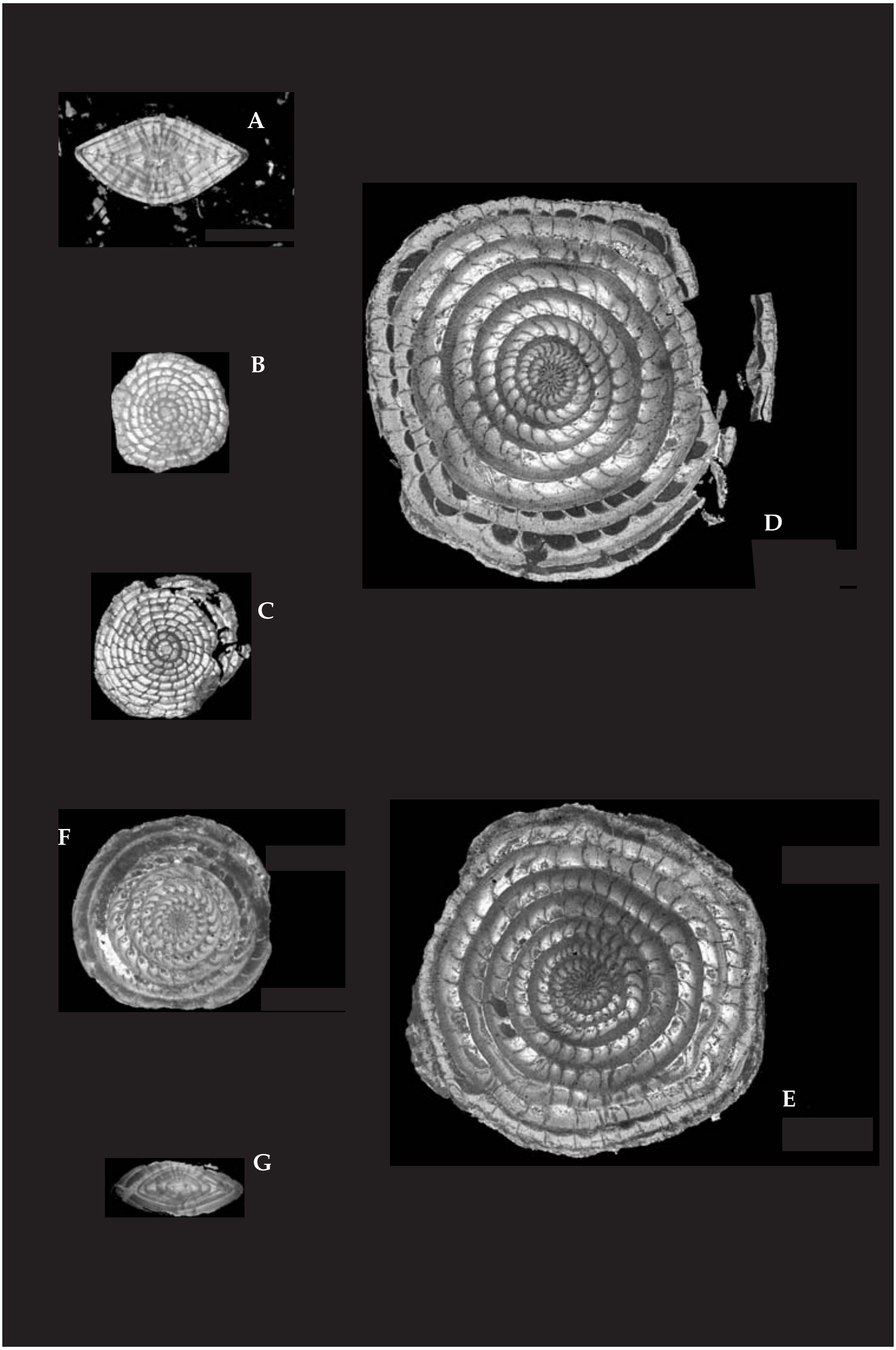

A
B
C
D
F
E
G

Plate 11

A-D *Palaeonummulites beaumonti* (d'Archiac & Haime, 1853)
A: Equatorial section of B-form; Timor (Palaeontological Institute, University of Bonn) (× 5).
B: Split specimen of B-form; Sungai Mangkalihat (Kalimantan) (RGM 19114) (× 5).
C: Exterior view of B-form; same specimen as B (× 5).
D: Axial section of B-form; Sungai Mangkalihat (Kalimantan). (RGM 19009) (× 10). Note the pillars that stop half way from the equatorial plane to the outside of the test.

E-H *Palaeonummulites variolarius* (Lamarck, 1804)
E: Axial section of A-form; Sungai Mangkalihat (Kalimantan) (RGM 19124) (× 10).
F: Equatorial section of A-form; Sungai Mangkalihat (Kalimantan) (RGM 19122) (× 10).
G: Split specimen of A-form; Sungai Ular (SW Sulawesi) (RGM 202015) (× 10).

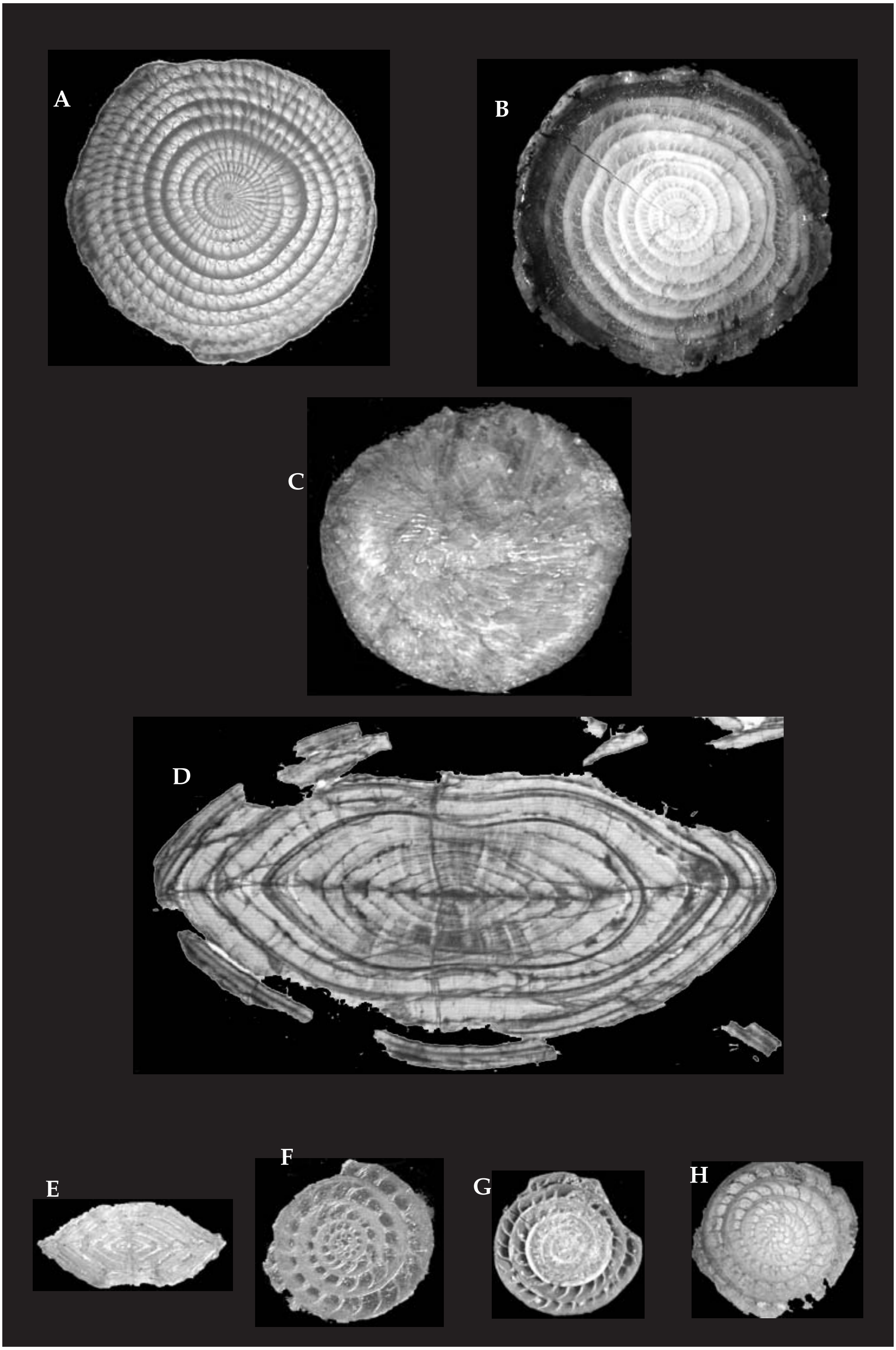

A
B
C
D
E
F
G
H

Plate 12

A-C. *Nummulites subbrongniarti* Verbeek, 1871
A: Equatorial section of A-form; Sungai Seilor (Kalimantan) (RGM 19056) (× 10).
B: Axial section of A-form; Sungai Seilor (Kalimantan) (RGM 19057) (× 10).
C: Axial section of B-form; Sungai Temoe (Kalimantan) (RGM 10949) (× 2.5).

D-E. *Nummulites fichteli* Michelotti, 1841
D: Equatorial section of B-form; Sungai Seilor (Kalimantan) (RGM 19118A) (× 5).
E: Axial section of B-form; Sungai Seilor (Kalimantan) (RGM 19118B) (× 2.5).

F: *Planocamerinoides orientalis* (Douvillé, 1912)
Axial section of A-form, type specimen; Nias (RGM 11879) (× 2.5).

G-K. *Planocamerinoides* sp. 1
G: External view of B-form; Pengging (Java) RGM 20214 (× 2.5).
H: Drawing of axial section, Fig. 89 in Verbeek & Fennema (1896) (× 2.5) (as *Nummulites (Assilina) spira* de Roissy).
I: Drawing of equatorial section, Fig. 87 in Verbeek & Fennema (1896) (× 2.5) (as *Nummulites (Assilina) spira* de Roissy).
J: Drawing of axial section of A form, Fig. 93 in Verbeek & Fennema (1896) (× 5) (as *Nummulites (Assilina) leymeriei* d'Archiac & Haime).
K: Drawing of equatorial section of A form, Fig. 92 in Verbeek & Fennema (1896) (× 2.5) (as *Nummulites (Assilina) leymeriei* d'Archiac & Haime).

L-P: *Planocamerinoides umbilicata* (Verbeek *in* van Waterschoot van der Gracht, 1915)
L: Equatorial section of B-form; Sumba; same specimen as pl. I Fig. 2 in Caudri (1934) (× 2.5).
M-P: Drawings reproduced from type description; M: axial section B-form (× 2.5); N: external view B-form (× 2.5); O: equatorial section B-form (× 2.5); P: axial section A-form (× 10).

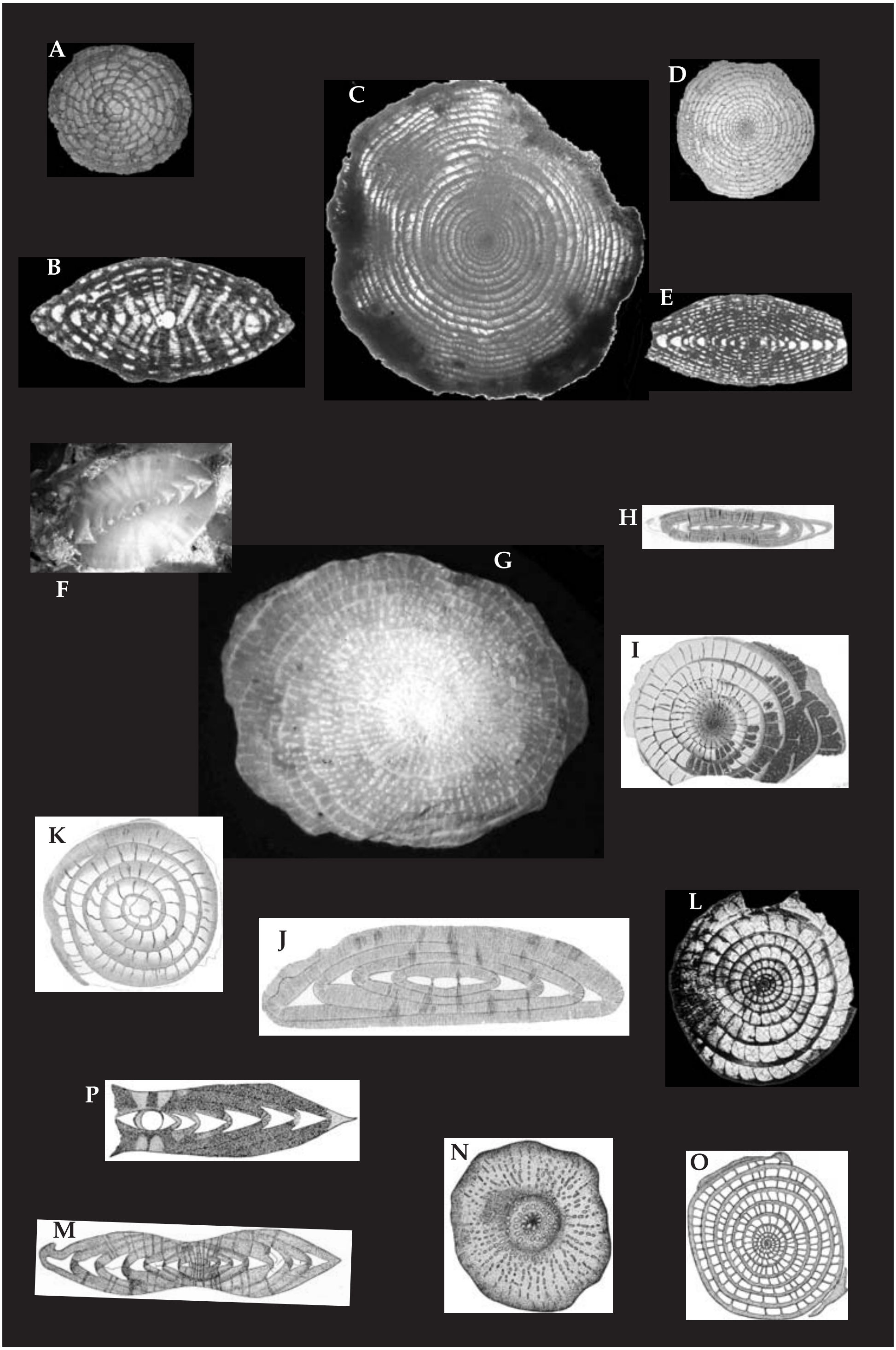
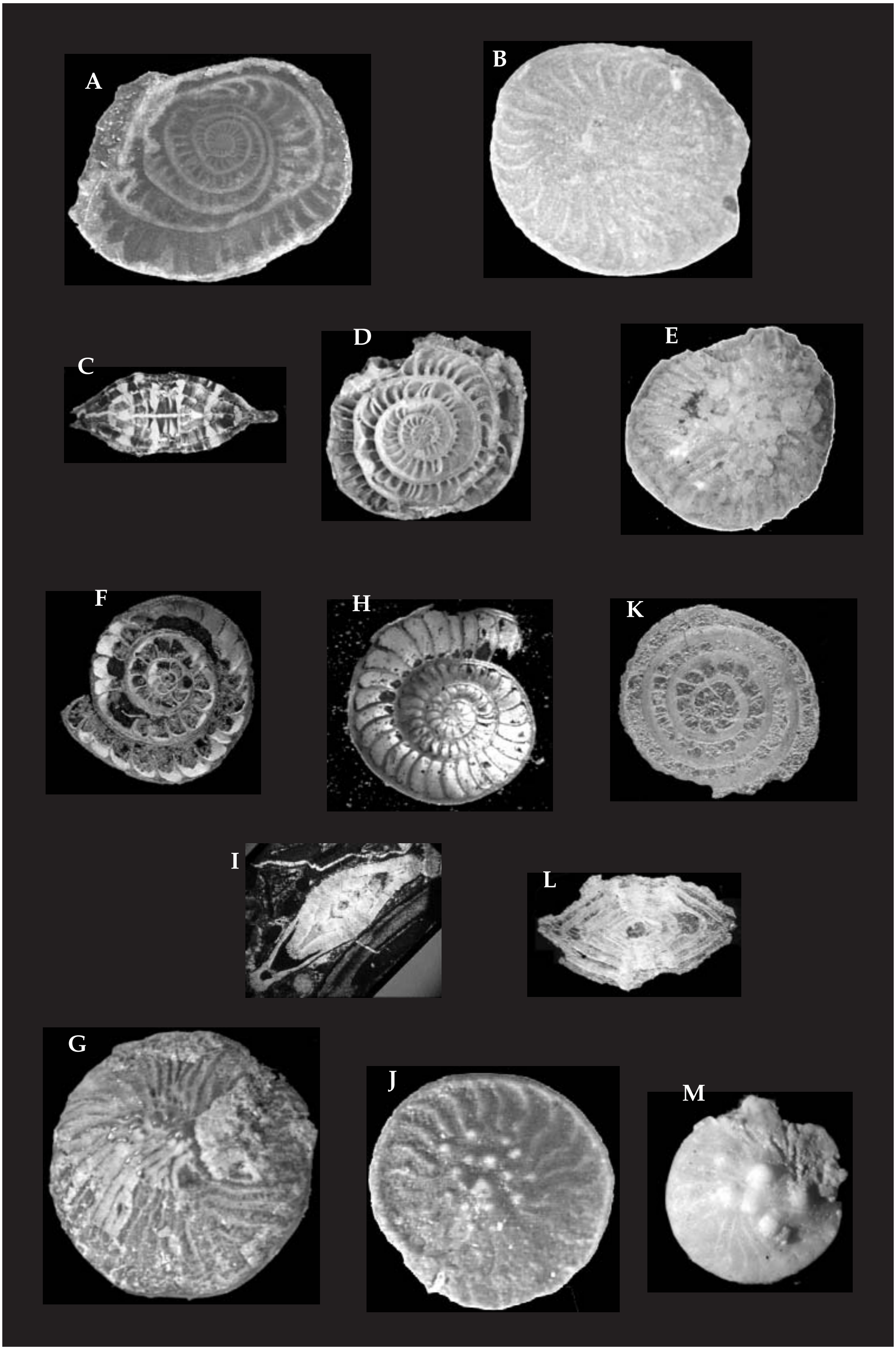

A
C
D
B
E
F
H
G
I
K
J
L
P
N
O
M

Plate 13

A-B, H-J. *Palaeonummulites crasseornatus* (Henrici, 1934)
A: Equatorial section of B-form. Miomaffo (Timor) (RGM 202012) (× 2.5).
B: External view of B-form. Miomaffo (Timor) (RGM 202013) (× 2.5).
H: Equatorial section of A-form. Miomaffo (Timor)(RGM 202014) (× 5).
I: Axial thinsection of A-form (× 5). Jati Bungkus, Karangsambung (Java). specimen in collection PL.
J: External view of A-form (× 5). Miomaffo (Timor) (RGM 202011).

C-E, F, G: *Paleonummulites* nov. spec.
C: Axial section of B-form; O5743-2 (Geological Museum, University of Amsterdam) (× 2.5).
D: Equatorial section (split specimen) of B-form; Kali Songo (Nanggulan) (RGM202000) (× 2.5).
E: External view of B-form; Kali Songo (Nanggulan) (RGM202005) (× 2.5).
F: Equatorial section of A-form; Kali Semah (Nanggulan); O5743-1 (Geological Museum, University of Amsterdam) (× 5).
G: External view of A-form; Kali Songo (Nanggulan) (RGM 202006) (× 5).

K-M: *Palaeonummulites taballarensis* (Caudri, 1934)
K: Equatorial section of A-form; Sungai Taballar, Kalimantan (RGM 19132) (× 5).
L: Axial section of A-form; Sungai Taballar, Kalimantan (RGM 19139) (× 5).
M: Equatorial view of A-form; Sungai Taballar, Kalimantan (RGM 19141) (× 5).


A
B
C
D
E
F
H
K
I
L
G
J
M