Implications of paucity of corals in the Paleogene of SE Asia: plate tectonics or Centre of Origin?

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Abstract

The modern Indo-West Pacific centre of marine diversity, embracing SE Asia, has the highest zooxanthellate coral diversity in the world, and is characterised by abundant coral reefs. In contrast, field and literature studies show that in Paleogene carbonates of SE Asia, corals are rare, and extensive coral reefs have not been reported. Corals and reefs of this age may have been better developed in the mid-Pacific, especially in the late Eocene, but the most diverse regions at this time were in Europe, and to a lesser degree, the Caribbean. The apparent scarcity of Paleogene corals in SE Asia is surprising in view of the long-standing theory that the Indo-West Pacific is a Centre of Origin. The question therefore arises whether this ‘Paleogene gap’ is a sampling problem, and if not what are its causes and implications?

A review of SE Asian Tertiary carbonates in their tectonic context shows that many shallow-water Eocene-Oligocene carbonates were dominated by larger benthic foraminifera and coralline algae. A new Eocene coral fauna (12 spp.) from Sulawesi accords with earlier views that there was little endemism in SE Asia during the Paleogene. The general paucity of corals in carbonate platform deposits confirms that the ‘Paleogene gap’ is real, and not an artefact. Since SE Asia, particularly the western part, has remained in, or close to, tropical latitudes throughout the Tertiary, climatic reasons cannot account for this. Although local ecological factors would have been important, the tectonics point to a degree of geographical isolation from other coral rich regions as a key factor. These patterns changed dramatically, however, in the earliest Neogene, as Australian fragments collided with SE Asia. Collision led to decreased isolation of the region and generation of numerous shallow-water areas, with diverse and abundant zooxanthellate corals occurring in the Miocene of SE Asia, similarly to the present day. The geographical complexity of SE Asia appears to have favoured localized isolation and origination of new taxa, though the fauna also consists of older relicts and taxa which migrated into the region from elsewhere. All these processes contributed to making the Indo-West Pacific the richest region for corals from the Neogene onwards.

We compare these patterns with the three main models of high diversity in the Indo-West Pacific Centre (Centres of Origin, Accumulation and Survival). During the Paleogene the region was not a centre of any kind. From the Neogene onwards, no single model is applicable, but a combination of all three models is preferred. Comparison with Mesozoic coral data and the history of the region suggests that the patterns discussed here also apply to the Late Triassic and Late Jurassic. As with the Neogene, these were times when blocks rifted from Gondwana moved across the tropics to dock against Asia. We therefore emphasize the role of plate tectonics in controlling regional high diversity patterns of zooxanthellate corals. Since corals and coral reefs provide habitats for a myriad of marine organisms, the biogeographic history of Cenozoic reef corals has implications for the evolution of tropical reef ecosystems.

Introduction

The waters of SE Asia contain the highest marine faunal diversity in the world (Stehli, 1968; Briggs, 1974; Paulay, 1997), explanation of which has long attracted the attention of biogeographers. Reef-dwelling scleractinian corals typify this pattern, and the highest species diversity (c.400-500, Veron, 1995) and 55% of the world’s coral reefs (Veron, 1995) occur in these waters (Figs 1 and 2).

The most enduring explanation of these kinds of high diversity foci is that they represent Centres of Origin (evolutionary source or ‘cradle’): Ekman, 1953; Stehli and Wells, 1971; Briggs, 1974, 1992; Zinsmeister and Emerson, 1981; Veron, 1995). Although detailed definitions and interpretations of Centres of Origin vary (Rosen, 1984, 1985), they all assume that taxonomic rich-
Fig. 1. Diversity (numbers of genera) of Recent zooxanthellate corals. Localities and data are mostly based on unpublished compilation by Professor John W. Wells. Map after Rosen (1984) and see this work for locality data.

ness has resulted from a concentration of evolutionary appearances over tens of millions of years (Table 1). Alternatively, the Indo-West Pacific high diversity foci may represent a Centre of Accumulation (evolutionary sinks or ‘museums’), whereby species originate in other regions, but over time, their geographical ranges changed to coincide in the present high diversity focus (Table 1; Ladd, 1960; Newell, 1971; McCoy and Heck, 1976; Kay, 1984; Wallace, 1998; Rosen, 1984, 1988; Jokiel and Martinelli, 1992; Pandolfi, 1992). A third Centre of Survival

<table>
<thead>
<tr>
<th>WITHIN THE FOCAL REGION</th>
<th>‘CRADLE’ Source</th>
<th>‘MUSEUM’ Sink</th>
<th>‘REFUGE’</th>
</tr>
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<tbody>
<tr>
<td>Speciation rates</td>
<td>high</td>
<td>low</td>
<td>low</td>
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<tr>
<td>Extinction rates</td>
<td>low</td>
<td>high</td>
<td>low</td>
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<tr>
<td>Immigration rates</td>
<td>low</td>
<td>low</td>
<td>low</td>
</tr>
</tbody>
</table>

OUTSIDE THE FOCAL REGION

| Speciation rates | high |
| Extinction rates | high |
| Immigration rates | high |

PREDICTED DIVERSITY PATTERNS THROUGH GEOLOGICAL TIME IN FOSSIL RECORD

Diversity conspicuously higher in the centre than in outside regions, and of greater duration than species turnover timescale (< 30 Ma)

Increasing high diversity through time in the centre, relative to outside regions.

No particular pattern of change in high diversity in the centre; through time, but diversity elsewhere diminishing through time.

OLDEST RECORDS

Mostly within centre

No particular pattern or mostly outside centre

No particular pattern

Table 1. The three main models for the origin of the Indo-West Pacific high diversity centre. See text for references. The table shows the main evolutionary characteristics within and beyond the centre, together with predicted patterns for fossil record. ‘High’ and ‘Low’ convey relative not absolute rates. The classic arguments about patterns of oldest/youngest and/or most primitive/derived taxa are reduced here to what can be reasonably easily investigated in the fossil record, especially in the context of this paper. Related ideas about competitive displacement are omitted. The dichotomy, “cradle or museum?” was posed by Stebbins (1974) for the tropics as a whole, but is here applied regionally to a feature within the tropics.
or refuge model postulates that the fauna of SE Asia is a vestige of a formerly rich, cosmopolitan distribution of broadly Cretaceous origin (Table 1; McCoy and Heck, 1976). Other ideas mostly incorporate aspects of the three main hypotheses and vary in having an ecological to a historical emphasis (Rosen 1988; Cramer, 1992; Veron, 1995; Palumbi, 1996; Paulay, 1997).

This paper concentrates on the three main alternatives (Table 1). The models are essentially historical, yet paradoxically, little regional palaeontological or historical evidence has been assimilated into theories of coral evolution in SE Asia. The main way in which palaeontology has been applied to the history of the Indo-West Pacific corals is through age-and-area studies, i.e., region by region analysis of global stratigraphic ages of extant taxa (Stehli and Wells, 1971; Rosen, 1984; Veron, 1995), although, as shown below, this approach is flawed. Cladistic biogeographical studies on extant corals have now also commenced (Pandolfi, 1992; Hoeksema, 1989, 1993; Wallace et al., 1991) but so far, only Hoeksema (1989) has incorporated fossil evidence. He was however unable to resolve his particular fungiid patterns sufficiently to develop robust biogeographical hypotheses. Veron’s (1995) theory of ‘surface circulation vicariance’, though drawing on fossil evidence from age-and-area patterns and evolutionary rates, is not critically dependent on the fossil record. A regional palaeontological approach is limited to pioneering endemicty work by Gerth (especially 1925, 1930), and brief observations by Umbgrove (1946) and Rosen (1988). Rosen and Smith (1988) subsequently analysed endemicty patterns of reef corals, worldwide, for the early Miocene. This modest body of work contrasts sharply with the extensive investigations of the much smaller and less diverse Caribbean fauna (e.g., Budd et al., 1992, 1994, 1996).

If the Indo-West Pacific focus was indeed a Centre of Origin, it should be recognizable in the fossil record as a region of persistent high diversity (Table 1) lasting significantly longer than the <30 Ma timescale of species turnover. Although the fossil record must be incomplete, it can provide constraints, particularly when compared with evidence from living species, and it provides historical clues from large scale
spatio-temporal patterns (Table 1). This paper therefore examines the Cenozoic fossil coral record of this local region, and interprets this in the light of new knowledge of the tectonics and stratigraphical distribution of carbonates and coral facies.

Background

Regional terminology

As a physical region, SE Asia broadly corresponds to Ekman’s (1953) ‘Indo-Malayan’ biogeographical region, within which a triangular area formed by the Philippines, the Malay peninsula and New Guinea shows the richest species diversity for numerous shallow marine groups of organisms (Stehli, 1968; Briggs, 1974, 1992). Richness of corals progressively declines in all directions with increasing distance from this central triangular area (Fig.1; Rosen, 1984 – frequency plot of coral genera; Veron 1995 – interpolated ‘contour’ plots of coral species). In this paper, we use ‘SE Asia’ for the marine region of the SE Asian mainland, the Australian margins and the areas between these, and use the same term for the Cenozoic equivalents of this region (Figs.2-8). This is preferred to ‘Indo-Malayan’ which presumes a rigorous biogeographical definition, criteria for which may not have applied in the past.

The marine fauna of SE Asia falls within a much larger biogeographical region, the ‘Indo-West Pacific’ (Ekman, 1953; Paulay, 1997), which stretches from the Red Sea and western Indian Ocean to the eastern fringe of the main archipelagos of the mid-Pacific. Across the eastern Pacific is the East Pacific Barrier, with the East Pacific region beyond. The combined Indo-West Pacific and East Pacific constitute the ‘Indo-Pacific’. The SE Asian area of high diversity is also referred to loosely as the ‘Indo-West Pacific centre’ or ‘focus’, though the boundaries are not rigidly defined, and to the east and southeast, the westernmost Pacific and northeast Australia are often included (Fig.1). Tectonically therefore, this centre lies across several plate boundaries, covering parts of the Indo-Australian, Eurasian, Philippine Sea and Pacific plates.

Zooxanthellate corals

Some knowledge of scleractinian coral ecology is essential to understand the significance of patterns discussed later in this paper. Scleractinians secrete hard calcareous skeletons, and those under discussion mostly belong to a broad ecological group that is confined to warm shallow waters often on, or close to, coral reefs. Today most of these scleractinian corals host symbiotic unicellular algae (zooxanthellae) within their soft parts and hence are ‘zooxanthellate corals’ or ‘z-corals’. The algae require sunlight to photosynthesise and this restricts the corals to the euphotic zone (about 100 m depth). Scleractinians mainly occur within a low latitude circum-global band between 35-40°N and about 35°S (Fig.2). The lowest mean annual surface sea-water temperatures are about 16°C, although species tolerance may be lower (Rosen, 1984; Veron, 1995), and the richest faunas are generally found in the warmest waters (Wells, 1954a; Rosen, 1984; Veron, 1995; Fraser and Currie, 1996).

Superimposed on this latitudinal pattern are regional ecological and historical biogeographical factors, the most important of which is availability of habitable areas, itself a combination of numerous factors including temperature, nutrient flux, substrate, water depth and quality. Z-coral distributions are therefore patchy in space and time, with modern examples found especially in clear, shallow conditions along land-mass margins, and particularly in archipelagos. Although z-corals are common reefal inhabitants, the temperature limit of reefs (minimum of 18°C; Veron, 1995) is slightly warmer than that of z-corals, and the distribution of reefs and z-corals do not correspond precisely. Contrary to widespread belief, fossil z-coral faunas are often found in both reefal formations and bedded deposits, the latter being often silty, marly or even pyroclastic.

Corals mostly disperse by planktonic gametes and larvae, and the potential migration distances and biogeographic patterns of corals depend on numerous factors including duration of larval phase, life history patterns, water conditions, substrate factors, coastal and sea-floor configuration, hydrodynamics and ocean currents (Jackson, 1986; Harrison and Wallace, 1990; Done et al., 1996).

Populations of living corals tend to consist largely of either z-corals, or azooxanthellate corals (az-coral), with z-corals dominating in warm shallow conditions (Stanley and Cairns, 1988; Coates and Jackson, 1987). Mixed assemblages also occur, so simple ‘either/or’ assumptions cannot be made about the composition of past faunas. Hence, for present purposes, the z-coral
component of a fossil fauna has to be identified and the az-corall component removed, in order to filter out the potentially conflicting ecological and biogeographical signals of az-corals.

The ‘Paleogene gap’ in Indo-West Pacific coral records

Preliminary evidence in the existing literature suggests that the high diversity centre of the Indo-West Pacific is relatively young, since coral diversity in the region was lower than elsewhere until the Neogene. Gerth (1925; see also Gerth, 1930) for a similar discussion in English but without his previous data compilations and map) indicated four localities with Paleogene ‘reef corals’ in Borneo, Java, Sulawesi, Papua New Guinea and a dubious reefal locality in New Zealand. In contrast, for the Neogene, he identified nine coral areas within the Indonean archipelago alone, and noted a three-fold increase in generic diversity of ‘reef-building corals’ from 29 in the Paleogene to 76 in the Neogene-Quaternary. Unbgrove (1930), conveyed a similar picture, and in his review of the Tertiary fossil record of extant Indo-Pacific corals, made no note of any from Paleogene strata (Ta-Td; East India Letter Classification, cf., Adams, 1970). In comparison, for Ta-Tf strata (regarded then as entirely Miocene), he mentions formations that were known to contain rich and well-described coral faunas. Unbgrove (1946) subsequently suggested that increased speciation of corals in SE Asia occurred during the late Miocene (Tg).

An Oligocene to Recent generic level comparison of the various major reef coral regions of the world (Rosen, 1988; his Table 2) showed that reef coral richness in the Oligocene was highest in the Caribbean and Mediterranean, but from the Miocene onwards the Indo-West Pacific centre became the richest region, increasing more than four-fold, from 14 genera in the Oligocene to 58 in the early Miocene (below and Fig.9). Despite the prevalent theory that the Indo-West Pacific focus represents an evolutionary centre, it is surprising that the Paleogene of this region is apparently so poor in z-corals, thus implying that this centre is only a post-Paleogene phenomenon. Although evidence for this ‘Paleogene coral gap’ goes back 70 years, the numerous ideas that have been developed concerning Indo-Pacific marine biogeography (e.g., Rosen, 1988; Veron, 1995; Flessa and Jablonski, 1996; Paulay, 1997), have mostly made little reference to this palaeontological pattern, preferring indirect evidence from age-and-area studies. One reason for this may be an uncertainty over how ‘real’ the gap is, and one of the main aims of this paper is to assess this.

Approach and Methods

Coral records

To investigate the main relevant biogeographical hypotheses (Table 1), we have compiled previously published z-corall data for SE Asia and neighbouring regions, and also included an important new fossil coral fauna found mostly in the upper Eocene part of the Tonasa Formation of Sulawesi (Wilson, 1995; Fig.10). Knowledge of fossil corals in SE Asia is derived largely from investigations made during the days of the former Dutch colonial era. More recently, the French have studied the Mesozoic of the region (see below), but no recent taxonomic accounts exist for the Tertiary. Taxonomic revision of the entire Tertiary scleractinian fauna is undoubtedly necessary. Unfortunately, the published coral collections often consist of single small samples of each species, and it is difficult to obtain any picture of species variability from them. Revisionary taxonomy is outside the present scope, and estimates of species numbers here are based on existing nomenclature, with taxonomic adjustments made only in obvious cases. Moreover, the stratigraphic, palaeoenvironmental and tectonic context of these corals in the old literature was poorly documented by modern standards. Today, since exploration for natural resources often focuses on carbonate rocks, which commonly include the remains of corals and other marine organisms, new, well-documented collections are being made. The nature, extent and history of carbonate development in SE Asia is therefore becoming clearer.

Inference of algal symbiosis in fossil corals

Zooxanthellae are not preserved in fossil coral skeletons, but algal symbiosis often needs to be inferred for palaeobiogeographical studies. A range of evidence can be used to infer symbiosis, but methods based on intrinsic features of the corals, including colonial characters, skeletal stable isotope geochemistry, palaeoecology and phylogenetic relationships, are preferable.
Table 2. Simplified scheme for designating levels of confidence in methods for inferring algal symbiosis in a fossil coral species. Note criterion 3(a) is particularly unreliable because although most living forms in such habitats are zooxanthellate, such habitats today also contain az-corals. With respect to 4, note that 'nkz' status is a neutral category, and does not signify inference of azo-xanthellate status. The latter can be inferred under criteria parallel to 1-3. Inference of symbiosis in genera (e.g., Fig. 9) can be derived from integration of respective member species, or approximately, by applying the parallel criteria at generic level. Examples of corals in different z-categories are shown in Figs. 10 and 12. In this paper, we use criteria 1-2 to obtain a minimum estimate of frequency of z-corals in a given fauna, and criteria 1-4 to obtain a maximum estimate (Table 3).

<table>
<thead>
<tr>
<th>CONFIDENCE LEVELS</th>
<th>CRITERIA</th>
<th>TERMS (abbreviated)</th>
</tr>
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<tbody>
<tr>
<td>1.</td>
<td>Species is still living today and known to be zooxanthellate</td>
<td>z-coral</td>
</tr>
<tr>
<td>2.</td>
<td>Species is extinct, but (a) belongs to a genus whose living species are all z-corals and/or (b) has skeletal characteristics found only in living z-corals (mainly stable isotopes, morphology)</td>
<td>z-like coral</td>
</tr>
<tr>
<td>3.</td>
<td>Species is extinct but (a) occurs in warm shallow-water carbonate facies and/or (b) lacks skeletal characteristics consistently found in living z-corals and/or (c) there is doubt about applicability of other stronger lines of evidence (i.e., 1 and 2)</td>
<td>z-like?</td>
</tr>
<tr>
<td>4.</td>
<td>Species is extinct and there is currently no evidence for inferring algal symbiosis, but symbiosis cannot be ruled out (i.e., status of algal symbiosis not known)</td>
<td>nkz-like</td>
</tr>
</tbody>
</table>

(Table 2; Rosen, 1998). Different methods have different merits so corals can be grouped according to a broad, albeit subjective, level of confidence according to method, strengthened where applicable by corroboration from different independent methods. Since algal symbiosis in fossil corals is an inference, it is more precise to regard fossil examples as 'z-like' or 'az-like' rather than 'z-corals' and 'az-corals' respectively (Rosen and Turnsek, 1989), although the latter pair of terms may be used for simplicity.

A simplified summary of methods, criteria and approach is shown in Table 2. Each group of criteria and its respective confidence level is denoted in the third column. If inference from first order criteria is not applicable, then second order criteria are used, and so on, working through criteria with decreasing levels of confidence. A given faunal list can then be partitioned into those for which symbiosis has been inferred (or not) according to these levels of confidence (see captions to Tables 2 and 3).

The sampling problem and reconstruction of habitable areas

The regional geographical and stratigraphic locations of all the Paleogene coral faunas have been compared with facies distributions and regional tectonics. The aim is to assess whether there are significant areas in SE Asia which are potentially rich in z-corals, but which lack coral information. Inhabitable areas for z-corals can then be assessed against other factors such as taphonomic effects, climate, and biogeographical barriers.

Tertiary carbonate rocks of SE Asia are formed mostly in shallow marine environments away from clastic input and are composed of the calcareous skeletons of marine organisms. Modern z-corals are mostly restricted to carbonate environments and through a study of these lithified sediments and their constituent components it is possible to track the availability of potential habitats for reef corals in the past. Data on the carbonate rocks of SE Asia have been extracted from the literature and are also based on current field research by the authors and other members of the London University SE Asia Research Group.

In SE Asia, local carbonate studies usually concentrate on the sedimentological rather than palaeontological aspects of the rocks, and taxonomic studies rarely include information on the sediments. However, sedimentologists usually note the presence of corals and, although taxa are not always identified, information on growth forms, together with an indication of coral abundance and diversity are commonly
given. This is clearly not ideal for detailed bio-
 geographical work, but when combined with
taxonomic data, provides information on Ceno-
zoic z-coral distributions for the region.

Reconstructions

To track the location and nature of potentially
available habitats for corals during the Ceno-
zoi, three main carbonate rock types have been
plotted onto time slices of Hall’s (1996) recon-
structions between the late Eocene (about 37
Ma) and Recent (Figs.3-8). Paleocene and lower
Eocene carbonates are rare in SE Asia and there
have been no published reports of z-corals of
this age, although a Paleocene locality has been
reported in Java (A. Russo, J. Pignatti, pers.
commns., 1997). This suggests that conditions
suitable for z-coral growth were sparse, and re-
constructions for these intervals are not shown.
The ages of the Cenozoic carbonate formations
are based on a range of nannofossil, planktonic
and larger benthic foraminifera, and, in a few
cases, strontium isotope dates. Although full
documentation is not possible here, these have
been gleaned from a large literature database
and the authors’ own work, and in a few cases it
has been necessary to revise ages (see Table 3).

The main environments illustrated on the
reconstructions of relevance to marine bio-
geographers are: shallow marine carbonate
depositional environments, major land areas
which would usually have been surrounded by
clastic shelves, and deep marine areas (below
100-200 m water depth).

A wide variety of skeletal remains of shallow
marine organisms are present in Cenozoic car-
bonate deposits, including corals, larger benthic
foraminifera, coraline algae, Halimeda, echinoids
and molluscs. However, in most SE Asian car-
bonates the dominant constituent grains are
coral fragments and larger benthic foraminifera,
although coralline algae may be locally abun-
dant. Carbonate deposits have been divided
here into three categories on the basis of these
components, and the different types are illus-
trated on the maps (Figs.3-8). These are carbon-
ates where z-like corals are abundant, carbon-
ates dominated by larger benthic foraminifera
and carbonates where both z-like corals and
larger benthic foraminifera are abundant.

Modern larger benthic foraminifera, similar to
many living corals, contain symbiotic algae, and
their growth is thought to be restricted to the
euphotic zone (Haynes, 1965; Hallock, 1985;
Brasier, 1995). They occur in similar tropical en-
vvironments to corals and have broadly equiv-
alent global distribution patterns (Adams, 1983;
Hallock and Glenn, 1986; Adams et al., 1990). A
number of depth zonation schemes for larger
benthic foraminifera (Ghose, 1977; Hottinger,
1983; Hallock and Glenn, 1986; Gorsel, 1988;
Racey, 1994) and other shallow marine
bioclasts, such as coraline algae (review in
Perrin et al., 1995) have been deduced for differ-
ent stages during the Cenozoic. The taxa, to-
gether with their forms and the nature of the en-
closing sediment, can be used to infer depositionsal depths for carbonate sediments
(Fig.11). Therefore an ancient carbonate forma-
tion in which specific larger benthic foraminif-
era dominate, such as robust Nummulites,
would have been deposited in a shallow marine
area during the Eocene or early Oligocene,
where one might also expect to find z-corals. For
each carbonate formation illustrated on the
maps (Figs.3-8), the setting (S) and the nature of
corals (C) present are briefly described.

The limits of the maps correspond to 30°N and
20°S (Figs.3-8) – close to the latitudinal limits of
the modern reef coral belt to the north, and
somewhat within the belt to the south. The
‘reefal belt’ has variously widened and nar-
rowed through geological time in response to
phases of global warming and cooling. For ex-
ample, the early to middle Miocene corresponds
to a period of global warming, and the reef belt,
together with distributions of z-like corals and
larger benthic foraminifera, was as much as 10°
of latitude wider (Fulthorpe and Schlanger,
1989; Adams et al., 1990; James et al., 1996).
Davies et al. (1987) constructed an oceanic sur-
face water temperature curve for NE Australia
and suggested that the earliest part of the
Paleocene was also a period of global warming,
sufficient to sustain reefal coral growth.

Summary of Mesozoic scleractinian records
in SE Asia

The earliest global records of scleractinian cor-
als are Middle Triassic (Wells, 1956; Stanley,
1988), since when scleractinians have occurred
discontinuously in SE Asia, concentrated over
particular time spans. Triassic corals (largely
Upper Triassic) are represented on the Asian
mainland (Yunnan and around the Burma-Thail-
and border) and in the Indonesian archipelago,
mostly east of Borneo in Sulawesi, Buru,
Misool, Seram, Timor and Roti (Stanley, 1988;
Martini et al., 1997). The Timor fauna appears to be the richest with over 30 nominal species. The Jurassic is represented by some Middle Jurassic, but more extensively by Upper Jurassic faunas (Beauvais, 1986), some, like those of Sarawak, being quite rich (about 20 species or more). They may continue in some places into the lowermost Cretaceous (Beauvais and Fontaine, 1990). Upper Jurassic corals are also known from Sumatra, Burma, Thailand and the Philippines (e.g., Beauvais, 1983), whilst substantial Middle to Upper Jurassic faunas occur in Japan (Eguchi, 1951). In contrast, although Cretaceous carbonate platforms do occur in SE Asia (Cebu, Misool, Timor and Papua New Guinea), Cretaceous corals are rare throughout the region, except, again in Japan. A few Cretaceous corals are known from the Upper Cretaceous of western Borneo and northern Sumatra, but rudists appear to be the dominant shallow water element (P. Skelton, pers. comm., 1997). Overall, corals were most common in the Upper Triassic and Upper Jurassic, partly reflecting times when corals flourished globally.

**Cenozoic plate tectonics of SE Asia and implications for coral history**

SE Asia is an extremely active tectonic area, and considerable lateral and vertical movements of the Earth’s crust throughout the Mesozoic and Cenozoic have affected the spatio-temporal variations in carbonate depositional environments and hence the potential habitats for corals. During this time the Indo-Australian and Philippine-Pacific plates, and a large number of smaller microcontinental and oceanic fragments, interacted and collided with Sundaland, the stable eastern margin of the SE Asian craton (Figs. 3-8 and in Hall, 1998 this volume). The reconstructions of Hall (1996), were used for Figs. 3-8, but other recent reconstructions (Rangin et al., 1990, Daly et al., 1991; Lee and Lawver, 1995) yield a similar picture for the purposes of plotting shallow marine carbonate depositional environments, although variations in timing may give slightly differing patterns (cf. Pandolfi, 1992).

At the beginning of the Tertiary, the separation of Australia from mainland SE Asia across this ‘Indo-Pacific gateway’ was about 3000 km. This distance, particularly if the current directions were unfavourable, is sufficient to have been a potential biogeographical barrier to the dispersal of z-coral larvae, comparable in scale with the East Pacific Barrier today (Ekman, 1953; Paulay, 1997). Until the latest Paleogene, the whole Australian craton and its coastal waters lay too far south to fall within the boundaries of the z-coral belt. It was not until between 25 to 16 Ma (late Oligocene to early Miocene) that the transition from temperate to tropical carbonates, with abundant z-coral and reef development, occurred in the northern part of what is now the Great Barrier Reef (Davies et al., 1987). The central part of the Great Barrier Reef did not experience a tropical climate until 15 to 10 Ma, and the southern part only became tropical in the last few million years (Davies et al., 1987).

The Indo-Pacific gateway progressively narrowed during the Cenozoic as Australia moved northwards (Figs.3-8), and closer to SE Asia. This, combined with the northward drift of various microcontinental blocks, and emergence of new islands, or development of new shallow carbonate producing areas, would have increased the potential for exchange of coral larvae with other regions and the development of z-coral communities and coral reefs (Rosen, 1988; Pandolfi, 1992). Davies et al. (1989) noted that the closure of this seaway would also have restricted equatorial current flow and caused the diversion of warm tropical waters to the south along NE Australia (see also Grigg, 1988).

The Indian continent drifted northwards across the zone of reef coral growth during the Late Cretaceous and early Paleogene, and is inferred to have collided with the SE Asian mainland during the Eocene (Hall, 1998 this volume). During this time suitable habitats for z-coral development may have occurred on narrow shelves with limited clastic input around the landmasses of India and mainland SE Asia. Examples include the z-like coral communities known from upper Paleocene to Miocene strata along the NW side of the Indian continent in Kaachchh and western Pakistan (Duncan, 1880; Gregory, 1930; Ghose, 1982; Rosen, 1988; revised dates in Adams 1970), belonging tectonically to India (C. Izatt, pers. comm., 1997).

Following the Eocene collision of India with Asia, and the subsequent uplift of the Himalayas and other related mountain chains, large quantities of clastic material were shed into the adjacent seas via large delta systems. These deltas, including those of the Irrawaddy and Ganges, currently inhibit reef coral growth, and form local coastal barriers to biogeographical exchange of many shallow marine organisms. Substantial clastic input along the southern margin of the Asian continent during the Paleogene may similarly have inhibited z-coral growth. The closure
of the intervening seaway may also have hindered the migration of shallow marine organisms between areas such as the Middle East and SE Asia.

There are very few islands in the modern Indian Ocean between the Maldives-Chagos line and Indonesia, although volcanic islands along the Ninetyeast Ridge were emergent during the Paleogene (Kemp and Harris, 1975). Prior to the Paleogene, islands may have existed in the seaway between India and mainland Asia. However, following the juxtaposition of India with Asia the islands of the Ninetyeast Ridge would have been among the few habitable areas for corals in the eastern Indian Ocean and the Indo-Pacific gateway, and this otherwise open seaway may have formed a barrier to the survival of most coral larvae. In contrast, in the western and southern Pacific, numerous atolls, reefs and islands existed from the Cretaceous onwards (Menard, 1964; Schlanger and Premoli Silva, 1981; Grigg, 1988; Winterer, 1991), and zonal communities existed there throughout the Cenozoic. The mid-plate foundations of most of these shallow areas of the western Pacific originated in a geographically restricted phase of volcanism during the Mesozoic (Darwin Rise/Superswell). Since then, they have all been moving in unison, towards Asia, so narrowing deeper water areas to their west and widening those to the east (East Pacific Barrier). This must have contributed to the development of zonal coral habitats and larval exchange around SE Asia, while further diminishing potential for larval exchange across the East Pacific Barrier.

**Cenozoic geological evolution and coral faunas**

**Overview of Paleogene corals**

At the start of the Paleocene, the global scleractinian record mainly comprises azonal corals, with an apparent hiatus of up to 2-3 Ma before the first Tertiary records of azonal corals (Rosen, 1998). In the Indo-West Pacific centre the oldest recorded Tertiary corals are Eocene (Table 3), and superficially seem quite rich, although an unpublished Paleocene fauna has been found in Java (A. Russo, pers. comm., 1997). On checking the Eocene records and their associated larger benthic foraminifera (Table 3), two of the richest faunas (SE Borneo and Papua New Guinea) are probably Oligocene or younger, and a third (Tonga), although confirmed as upper Eocene, consists entirely of azonal corals. This leaves a small number of published azonal faunas of Eocene age, but even the dating of some of these is uncertain. In fact, our new coral fauna of late Eocene (Tb) age from Sulawesi (Wilson, 1995), though modest, is currently the richest known zonal fauna of definite Eocene age in SE Asia (Fig.10). A zonal fauna from the Enewetak boreholes of the Marshall Islands on the Pacific plate, has an even smaller number of species (Table 3).

Chevalier et al. (1971) compiled other Eocene 'reefal and parareefal' coral records including their own from New Caledonia. Most are included in Table 3 and some are probably younger than Eocene (see above). Localities mentioned by these authors, not in Table 3, are: Sumatra (no references given), Sulawesi (after Bemmelen, 1970), Saipan in the Marianas (after Yabe and Sugiyama, 1935), and Makatea in the Tuamotus (after Obellanne, 1962). We have failed to find the Sulawesi records in Bemmelen (1970). Of Makatea, the authors say that Eocene corals ‘should exist’, as well as in “several other raised islands of the Pacific” but they cited no further work. For Saipan, Yabe and Sugiyama (1935) describe only Saiapania, which in our opinion is a chettedt sponge, not a coral. However, Eocene carbonates of Saipan (Matansa Limestone and Densinyama Formation), and Eocene volcanioclastic rocks on Guam (Marianas) are all reported to contain zonal corals (G. Siegrist and D. Randall, pers. comm., 1997) and require further study.

Lower Oligocene records are even sparser than for the Eocene (Table 3), but from the middle Oligocene (Td) there are signs of increasing richness (SE Borneo). A silicifed Oligocene coral reef is reported from Guam by Siegrist and Randall (above). By the late Oligocene to early Miocene (Te), richer reefal coral faunas, similar to those today, seem to have become progressively more common throughout much of the region (Fig.9).

Fig.9 shows a Cenozoic compilation of generic richness of zonal corals for the four principal tropical marine regions (update of Table 2 in Rosen, 1988) incorporating new data from the Indo-West Pacific centre (Table 3) and other regions. This confirms the reality of the ‘Paleogene Gap’ in terms of available coral data, though not necessarily its biogeographical reality, and shows that substantially richer faunas occurred elsewhere, particularly in Europe. This pattern reversed itself in the early Miocene; as the Indo-West Pacific centre became noticeably richer,
<table>
<thead>
<tr>
<th>LOCALITY</th>
<th>FORMATION</th>
<th>ORIGINAL AGE</th>
<th>REVISED AGE</th>
<th>SOURCES</th>
<th>TOT-GEN SPECIES</th>
<th>Z-LIK SPECIES</th>
<th>REMARKS</th>
</tr>
</thead>
<tbody>
<tr>
<td>SULAWESI</td>
<td>Oligocene</td>
<td>Neoene</td>
<td></td>
<td>Dolfin, 1915; Gorth, 1931; Umbgrove, 1942b</td>
<td></td>
<td></td>
<td>Neogene according to Umbgrove (1942b)</td>
</tr>
<tr>
<td>BUTON</td>
<td>Asphalt deposits</td>
<td></td>
<td></td>
<td>Umbgrove, 1942a</td>
<td></td>
<td></td>
<td>Paleogene age ruled out by author</td>
</tr>
<tr>
<td>OOLIQUEENE</td>
<td>Miocene</td>
<td></td>
<td></td>
<td>(Rolled pebbles)</td>
<td></td>
<td></td>
<td>Z-like corals in brecciated reefal limestones (collected Rosen &amp; Darrell, NHM Collections; work in Papua by T.F.)</td>
</tr>
<tr>
<td>PAPUA NEW GUINEA (Boera Head, southern Papua)</td>
<td>Boera Formation</td>
<td></td>
<td></td>
<td>Gregory &amp; Trendschi, 1915, 1931</td>
<td>11 13</td>
<td>8 11 (11)</td>
<td>Outcrop, notwithstanding published age, the fauna looks mostly Neogene or of mixed age</td>
</tr>
<tr>
<td>MARSHALL ISLANDS (Bikini Atoll)</td>
<td>Boreholes: 845-355 m</td>
<td>Miocene</td>
<td></td>
<td>Wells, 1954b</td>
<td></td>
<td></td>
<td>Age revised by Adams (1970)</td>
</tr>
<tr>
<td>MARSHALL ISLANDS (Enewetak Atoll)</td>
<td>Boreholes: 931-901 m</td>
<td>Miocene</td>
<td></td>
<td>Wells, 1965</td>
<td>8 11 7 (13)</td>
<td>10 11 (11)</td>
<td></td>
</tr>
<tr>
<td>SERAM (custom part of the island near Mt. Tari)</td>
<td>Oligocene (Sannosea m = Early Oligocene)</td>
<td></td>
<td></td>
<td>Dolfin, 1908; Umbgrove, 1924, 1931</td>
<td>1 1</td>
<td>0 1 (1)</td>
<td>Umbgrove (1924) said coral was &quot;probably Oligocene&quot;</td>
</tr>
<tr>
<td>KALIMANTAN, SF (Riam-Kawa and Riam-Karan area, Metalus Complex)</td>
<td>Verbeck's Gamma Beds</td>
<td>Eocene</td>
<td></td>
<td>Fritsch, 1878, Gorth, 1931</td>
<td>23 25</td>
<td>9 10 (22)</td>
<td>Dolfin (1908) stated that Fritsch's fauna is Oligocene (Sannosea m = Lower Oligocene). Bemmelen (1975) cites foraminifers that suggest mid-Oligocene (Tid; Adams, 1970)</td>
</tr>
<tr>
<td>MARSHALL ISLANDS (Enewetak Atoll)</td>
<td>Boreholes: 931-901 m</td>
<td>Miocene</td>
<td></td>
<td>Wells, 1964</td>
<td>6 7 6 7</td>
<td>3 3 3</td>
<td></td>
</tr>
<tr>
<td>TONGA (Eua)</td>
<td>Late Eocene (Tb)</td>
<td></td>
<td></td>
<td>Wells, 1976</td>
<td>14 17 0 0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>MARSHALL ISLANDS (Enewetak Atoll)</td>
<td>Boreholes: 1220-1251 m</td>
<td>Late Eocene (Tb)</td>
<td></td>
<td>Wells, 1964</td>
<td>4 4 3 (4)</td>
<td>3 (4)</td>
<td></td>
</tr>
<tr>
<td>SUMBA (c.80 km from western end)</td>
<td>Eocene</td>
<td></td>
<td></td>
<td>Umbgrove, 1943</td>
<td>1 2</td>
<td>0 0 (2)</td>
<td></td>
</tr>
<tr>
<td>SULAWESI</td>
<td>Tortusa Formation (basal part)</td>
<td></td>
<td></td>
<td>this paper</td>
<td>11 12</td>
<td>6 7 (12)</td>
<td></td>
</tr>
<tr>
<td>JAVA (south central)</td>
<td>Nanagulan Beds</td>
<td>Late Eocene</td>
<td></td>
<td>Gerth, 1921; Gorth, 1931; Gorth, 1933</td>
<td>7 8</td>
<td>0 0 (5)</td>
<td></td>
</tr>
<tr>
<td>CALEDONIA, SW (Baie St Vincent (iles Dicou and Saint Phalle); Oua Lato)</td>
<td>Mid-Late Eocene (Eocene C)</td>
<td></td>
<td></td>
<td>Chevalier et al., 1971</td>
<td>2 2</td>
<td>1 1</td>
<td></td>
</tr>
</tbody>
</table>

| PALEOCENE                      |                               |              |             |                                             |                 |              |                                                        |
| JAVA Jati Bunkus, near Karamangumbang (Central Java) | reefal limestones | Late Paleocene (Thanetian) (Ta1) | Pigram (pers. comm., 1997) | 8 11 6 (8) | 8 (11) |                                                        |

Table 3. Summary of Paleogene coral faunas of the Indo-West Pacific centre including SE Asia. Ages based on foraminifera unless indicated. Revised ages show that the Eocene is even more poorly represented than previously realised. By the late Oligocene z-like corals were relatively common and the pattern is more Miocene-like. Tc1-i formations are therefore a selection only. For the period before the late Oligocene the data are as complete as possible apart from a few problematic or unstudied cases (see text). Top two rows show younger faunas which have been included because of their supposed Paleogene age. Minimum values of z-coral are in bold and maximum values are in parentheses (see caption to Table 2). Paleogene Indo-West Pacific data for Fig.9 are based on net totals of faunas in this table, except for the Oligocene (based on data from Kalimantan and the Marshall Islands).
37 Ma Late Eocene

Fig. 3. Late Eocene time slice from the reconstructions of Hall (1996) with carbonate deposits shown. The nature of the carbonate deposits (S) and any coral records (C) are shown. Abbreviations used in Figs.3-9 for coral records are: Br, branching, Pl, platy, M, massive, Ab, abundant, Div, diverse. Names shown are formations. Fig.8 shows present-day geography.

the Mediterranean declined. Since then, the Indo-West Pacific centre has remained the richest z-coral region. Throughout the Cenozoic, the Caribbean, by contrast, has remained relatively constant and moderately rich. The picture in SW Asia is unclear because of lack of adequate data, but Paleogene z-like faunas, such as those from western Pakistan, together with unpublished coral collections in the Natural History Museum, London, from Oman, Iran and Somalia suggest that this region was also richer than SE Asia during the Paleogene.

Late Eocene (Tb)

Carbonate deposition was common on microcontinental blocks in the eastern part of SE Asia (Fig.3) where emergent land areas were small and clastic input was low. Initiation of a number of basins occurred around Sundaland during the Paleogene (Hall, 1998 this volume), and those to the east quickly became marine and carbonates developed (Fig.3). In comparison, mainland SE Asia, Sumatra and much of Borneo (Fig.3) was a land area which was shedding considerable clastic material into the surrounding seas. Along the southern margin of this land area, the shelf would have been narrow, close to the adjacent subduction trench (Fig.3), and this, together with the amount of clastic input, would have hindered carbonate production. The distance between shallow marine areas across the Indo-Pacific gateway was greater than 2000 km in the late Eocene.

In eastern SE Asia carbonate development occurred mainly as extensive shallow-water platforms, such as in Sulawesi (Wilson, 1995), the Melinau Limestone of Sarawak (Adams, 1965) and New Guinea (Koesoemadinata, 1978). The
margins of these carbonate platforms varied from steep escarpments to gently dipping ramps, but reefal buildups have not been reported (Wilson, 1995). In western SE Asia, shelfal carbonates or localised areas of carbonate deposition occurred where clastic input was insufficient to hinder carbonate production.

The Eocene carbonates are dominated by larger benthic foraminifera (Fig.11) and in some cases coralline algae, while corals are extremely rare (Adams, 1965; Kohar, 1985; Siemers et al., 1992, Wilson, 1995). Within the carbonates, there occur a wide variety of larger benthic foraminifera showing various adaptations, which suggest they occupied the full range of habitats available on the platforms within the euphotic zone (Adams, 1965; Wilson, 1995).

The first well-dated, published appearance of z-like corals in the Indo-West Pacific centre occurred in the late Eocene. There is a possibility of older (middle Eocene) z-like corals occurring in New Caledonia and Java (Table 3), but the age range of these very limited faunas also includes the late Eocene. The Nanggulan Beds are mixed clastic-carbonate deposits and show no evidence of any reefal buildups or of in situ growth fabrics. An enigmatic Sumba locality whose place-name we have been unable to locate on modern maps, is of late Eocene age, but contains a single genus which may not be z-like.

Following revision of the ages of Paleogene corals in SE Asia (Table 3), the only known z-like corals of definite late Eocene age in SE Asia are from the basal part of one area of the Tonasa Formation in south Sulawesi (Fig.10 and Table 3). The fauna is small, consisting of 12 species, 7 z-like and 5 z-like?, mostly known also from the Paleogene of western Pakistan (Ranikot, Khithar and Nari series) and Europe, and therefore not strongly endemic. It includes small solitary discoidal (z-like?) forms such as Cyclloseris subcrenulata and Trochocyathus ? nummiformis from the lowermost beds of the formation at the Doi doi coal quarry. Well-preserved massive colonial forms found about 2 km away, slightly higher in the succession, include Favia pedunculata (z-like), Astrocoenia bistellata (z-like?), and a striking four-lobed flabellate z-like form, Trachyphyllia indica. Specimens of all of these show flattened bases in response to a soft substrate. There are also colonies of Stylocoenia sp. (z-like?) which, with their unique spheroidal corallith habit and stout stilt-like spines (but eroded), are also soft-substrate dwellers (Darga, 1991). The corals from the basal part of the Tonasa Formation occurred where there was some clastic input, and did not form reefal buildups (Wilson, 1995).

These SE Asian z-coral faunas are paltry compared with the rich European faunas of Eocene age, such as those known from former Yugoslavia with 85 z-like species, or the 42 z-like species known from Eocene of Panama (interpretation of data from Felix, 1925, and from Budd et al., 1992, respectively). Moreover, apparent paucity of corals in SE Asia should also be seen in the context of Ladd's statement (in Wells, 1976) that upper Eocene limestones have been reported from the Pacific at Palau, the Marianas, the Marshalls, Fiji and Tonga, across a distance of 6500 km (see also Schlanger and Premoli Silva, 1981; Winterer, 1991). While some of these, as in the Marshalls (Table 3), and Marianas (G. Steigrist and D. Randall, pers. comm., 1997) contain z-like corals, this cannot be assumed in all cases, since Eocene corals from Eua, Tonga, (Table 3) are entirely az-like. It may be that a largely concealed upper Eocene sequence with z-like corals is now submerged, or lies buried beneath younger volcanics or limestones throughout much of the Pacific. Thus whereas the 'Paleogene gap' is a sampling reality for the Eocene of SE Asia, it is possibly a sampling artefact for part of the Indo-West Pacific centre.

**Early (Tc) to middle (Td) Oligocene**

The early and middle Oligocene were similar to the late Eocene with carbonates common on microcontinental blocks in eastern Indonesia, but rare around the margins of mainland SE Asia (Fig.4). An open seaeway between the Pacific and Indian Oceans was still present and was about 1,400 km wide by the end of the middle Oligocene (Td). However, as Australia and the associated microcontinental blocks moved northwards, large carbonate platforms developed in New Guinea (Fig.4, Wilson et al., 1993), and the distance across this gateway decreased, altering the configuration of ocean currents (Grigg, 1988) and increasing the possibility of biogeographical exchange of marine biotas. Carbonates were also deposited around the margins of the developing South China Sea (Holloway, 1982). Their distribution was similar to the late Eocene, with platform and shelfal carbonates dominating to the east and west respectively. Larger benthic foraminifera again dominate in most of these deposits (Fig.11), and there is no evidence for any reefal buildups.
Corals are rare in the lower Oligocene (Tc) of SE Asia, and those that do occur are described as thin branching forms, such as Acropora from south Sulawesi (Fig. 10). Some massive and thick branching forms have been reported from shelf margin deposits in south Kalimantan (Saller et al., 1993). On the Pacific plate, a fauna possibly of this age is known from the Enewetak boreholes (Table 3). The richest Paleogene z-like fauna in SE Asia is that described by Fritsch (1878) from the Tanjung Formation of SE Borneo (Table 3). Fritsch and later workers (e.g., Gerth, 1925; 1930) regarded this fauna as Eocene, although the associated foraminifera, Nummulites fichteli and Lepidocyclina sp. (Bemmelen, 1970), point to an Oligocene (Td) age. The corals consist of only nine clearly z-like species, but if other corals of less certain z-status are included, the total increases to 22. This is small when compared with the rich contemporaneous faunas of Europe and the Caribbean (Fig. 9). No other published z-like fauna is known from Td strata in SE Asia, but its richness relative to older Paleogene localities hints at an increase in suitable areas for z-corals at this time in parts of SE Asia. A locality in Seram with just a single coral record is dated as Oligocene (Table 3) but its exact age is not known. On the Pacific plate, a modest z-fauna of possible mid-Oligocene age is known from the Enewetak boreholes (Table 3). Grigg (1988) discussed the Cenozoic coral record of the mid- and northern tropical Pacific and emphasized that z-corals started to become more widespread in the early Oligocene, the date of their first appearance in the Hawaii-Emperor chain.

**Late Oligocene (Te1-4)**

Carbonates were still common in eastern Indonesia (Fig. 5), and some of the basins, such as...
Java and Sumatra, started to become marine, with the development of carbonates. Carbonates also became more extensive along the eastern side of the Sundaland craton due to continued subsidence in the region. Shelfal and platform carbonates again dominated, particularly during the earlier part of the late Oligocene, although patch reefs and some reefal buildups may have developed later in the Oligocene. Larger benthic foraminifera, such as leptocyclinids, heterosteginids and various larger imperforate foraminifera, were still common (Fig.11). In formations which pass conformably upwards into the Miocene, such as those in Java, Sumatra or New Guinea, shelfal carbonates pass upwards into reefal buildups in the upper part of the succession (Gucci and Clark, 1993). However, it is often difficult to separate upper Oligocene from lower Miocene carbonates on the basis of information in the literature.

When corals are mentioned in the sedimentological literature, they tend to be thin delicate branching forms, or finger-like corals (such as Acropora), although massive framework corals occur in some localities forming patch reefs. The Boera Formation of Papua New Guinea, dated as uppermost Oligocene to lowest Miocene (Te: Rogerson et al., 1981), contains a moderate fauna of z-like corals (Fig.12c,d) which is unpublished but well-represented in the Natural History Museum, London. These are the oldest z-like corals known from outcrop on or around the Australian cratonic margin, and provide a minimum age for the arrival of the craton’s leading edge in tropical waters (cf., Davies et al., 1987). Initial identifications suggest affinities with European Oligocene faunas. Reefal corals are also common in the upper part of the upper Oligocene in the Batu Ash limestone in Java (A. Wonders, pers. comm., 1997). Quite a rich z-like fauna is emerging from the uppermost Oligocene or lowest Miocene Gomantong Lime-

Fig. 5. Late Oligocene time slice from the reconstructions of Hall (1996) with carbonate deposits shown; abbreviations on Fig.3.
stone in Sabah (J. Noad, pers. comm. 1997) with 17 z-like genera identified so far (work in progress, BRRR), many of them previously known from the lower Miocene elsewhere in Borneo.

**Neogene**

There was a striking increase in the distribution and extent of carbonates (Fig.6), and a marked change from larger foraminifera to coral dominated carbonates at the beginning of the Neogene. A distinct change also occurred in the coral faunas during the earliest Miocene, within Te time. Bemmelen’s (1970) Table 15 lists some of the key coral faunas of Neogene age, many of which consist of 30 or more z-like species. They are far richer and more widespread than Tertiary faunas of pre-Te age in the same region. These patterns are clearly reflected in the generic diversity patterns of Fig.9.

The ages and taxonomy of this rich and historically important SE Asian Neogene coral fauna are much in need of modern revision, as this is the key to more rigorous studies of the global endemicity patterns and biogeographical history of corals discussed by Gerth (1925, 1930) and Rosen (1988). Nevertheless, such work is unlikely to alter radically the existing picture of substantial increase in z-like coral faunas which seem to have developed relatively suddenly throughout the region, from the early Neogene onwards. Only a few key points concerning the Neogene are made here.

**Early and middle Miocene (Te5-Tf)**

The early Miocene was a major phase of carbonate deposition both in SE Asia (Fig.6), and throughout much of the tropics and subtropics, with reef corals occurring in much higher lati-
tudes than today, probably as a result of a global warm phase (Fulthorpe and Schlanger, 1989). Carbonates were common in marine basins around the margins of mainland SE Asia, although a combination of clastic input and a narrow shelf restricted carbonate development along the southeast coast (Fig.6). Carbonate production still occurred on microcontinental blocks in eastern SE Asia (Fig.6), although more islands were emerging due to collision-related uplift. During the mid-Miocene (Fig.7), the area of carbonate deposition, though still extensive and diverse, had been reduced, due to the emergence of more land areas, resulting partly from microcontinental collisions and related shedding of clastic material into adjacent marine areas.

Platform and reefal carbonates were common throughout the region and pinnacle reefs have been reported from many areas (Livingstone et al., 1992). Z-like corals were widespread, abundant and diverse throughout the region, in marked contrast to the earlier Cenozoic. Many modern genera, and even species (Umbrgrove, 1946; Rosen, 1984; Veron, 1995), as well as all the growth forms typical of modern reefs in the Indo-West Pacific, occur in these Miocene reefs (e.g., Fig.12a,b). The accompanying marine biota is also similar to modern reef biotas, with abundant benthic foraminifera, echinoderms, molluscs, coralline and calcareous green algae.

Comparison with present day

The modern situation (Fig.8; after Wells and Sheppard, 1988) is not unlike the Miocene (Figs.6 and 7), although the extent of coral-rich carbonate is reduced, especially when compared with the lower Miocene. This is due to the continued emergence of land areas and to a corresponding influx of clastic material into adjacent coastal waters hindering carbonate produc-
tion. However, despite this slight reduction in carbonate sedimentation, reefal development with z-corals is still common in SE Asian waters, particularly in the clearer waters of eastern Indonesia (Wells and Sheppard, 1988).

As already emphasized, modern z-corals have their highest species diversity in SE Asian waters, with the whole range of morphological growth forms present. At least 262 species and 78 genera have been recorded in Sulawesi (Moll, 1983), and Veron (1995) recorded 472 species in the northern Philippines. Coral reefs are abundant, and, of the estimated 600,000 km² of these complex ecosystems worldwide, 25-30% are located in SE Asia (Bernard, 1991).

**Summary of geology and coral faunas in SE Asia**

Eocene z-like coral faunas appear to be even less rich than previously thought, the only certain fauna of this age being our own new finds from the Tonasa Formation. Oligocene faunas are slightly richer than previously thought. Z-coral richness is much higher in other regions in the Paleogene, and higher in SE Asia from the Neogene onwards. In the Paleogene, facies and environments in which z-like corals could have thrived (mainly shallow water carbonates) were sparse, and SE Asia was really a wide oceanic seaway in which the dense arrangement of islands of the modern region did not yet exist. There was a fundamental change at or around the beginning of the Neogene (i.e., within Te time), coincident with the beginning of interaction between Australian fragments and SE Asia, leading to a notable increase in shallow water carbonates, widespread reefs, high z-coral abundance and fourfold increase in z-coral richness.

Tectonics controlled the emergence, disappearance, and movement in and out of the z-coral belt, of shallow marine areas, as well as...
their regional concentration. In the Paleogene however, even where shallow water carbonates did exist, they often lacked z-coral faunas, suggesting that other factors (biogeography, local ecology) were also important. In contrast to SE Asia, there are extensive Paleogene (especially upper Eocene) limestones in the tropical western Pacific, but they are mostly in the subsurface and have remained largely unsampled. The few limestones that have been sampled contain either z-like or az-like coral faunas. However, many of these limestones lay further east than now, representing perhaps a distinct region. The Cenozoic record of z-corals points to the modern Indo-West Pacific centre of diversity being a young feature, probably little older than around the beginning of the Neogene (c.24 Ma).

**Discussion**

*Global biogeographical context*

The most challenging biogeographical problem of the Indo-West Pacific centre is to understand the origins of its marked taxonomic richness, models for which are shown in Table 1. This can be partly attributed to a global pattern in which richness of numerous marine taxa increases as latitude decreases, related to available energy (Stehli, 1968; Jablonski, 1993; Fraser and Currie, 1996; Flessa and Jablonski, 1996; Paulay, 1997). This has long been known for z-corals (Yonge, 1940; Wells, 1954a), and more recently demonstrated quantitatively (Rosen, 1971, 1984; Fraser and Currie, 1996). There is also empirical evidence that more organisms originate in the tropics than elsewhere (Jablonski, 1993; Flessa and Jablonski, 1996). Temperature however cannot account for the entire global pattern. Z-corals, for example, are four times richer in the Indo-West Pacific centre than in the western Atlantic (Figs.1 and 9), but the prevailing temperatures in both are similar (Rosen, 1984), and this richness ratio has remained stable over decades of sampling and taxonomic study.

In order to consider regional anomalies, and the Indo-West Pacific centre in particular, it is useful to resolve diversity (and endemcity) patterns into two geographical components, ‘latitudinal’ (N-S) and ‘longitudinal’ (E-W) (Rosen, 1975). The strongest endemcity patterns are longitudinal. Four regions have dominated longitudinal discussion (Gerth, 1925, 1930; Paulay, 1997): the Indo-West Pacific, the eastern Pacific, western Atlantic and eastern Atlantic, and their Tertiary Tethyan counterparts (e.g., Mediterra-
nean), though the Indian Ocean (with Red Sea) is also sometimes considered separately (see Veron, 1995; Flessa and Jablonski, 1996; Budd *et al.*, 1996; Paulay, 1997; for reviews of these regions). We concentrate on the ideas shown in Table 1 for the Indo-West Pacific centre, particularly the extent to which patterns may have been affected by plate tectonics, though the influence of eustasy (not discussed here) was also impor-
tant, especially in the later Cenozoic (Schlanger, 1981; Rosen, 1984, 1988; Grigg, 1988; Veron, 1995). The emphasis here on physical factors differs from models which emphasise intrinsic evolutionary processes sustained in one region over great lengths of time (Centres of Origin).

Flessa and Jablonski (1996) have remarked that Rosen’s (1984,1988) physical contingency model “implies that intensive sampling of the Eocene, prior to global refrigeration and the northward migration of the Australian plate, would detect neither diversity gradient, nor age gradient, but perhaps only the legacy of the evo-
olutionary rebound from the end-Cretaceous ex-
tinction”. Their caveat that “few data are avail-
able to test (this) idea of ... young age” reflects in part the previous emphasis on age-and-area studies of extant taxa. We address Flessa and Jablonski’s prediction below.

In modelling the biogeography of a particular region, three sets of factors need to be consid-
ered (Rosen, 1988): (1) origins (patterns of evolutionary turnover); (2) distributional change (often also called ‘migrations’, ‘dispersal’ etc., and meaning changes through time of biogeographical ranges of taxa, combined with changes of biogeographical barriers); and (3) maintenance (the sum of local-to-regional eco-
logical factors). This framework is used to ad-
dress the Cenozoic history of z-like corals in the Indo-West Pacific and to discuss criteria for the alternative models for the high diversity foci (Table 1). In particular, since the main conclu-
sion of our stratigraphic review points to high diversity in the SE Asian part of the Indo-West Pacific centre being surprisingly young, we concen-
trate on possible reasons for this.

**Maintenance factors**

Although the paucity of Paleogene z-corals in SE Asia can be largely explained by sparseness of inhabitable areas (i.e., shallow water carbon-
nates) across a wide seaway, this does not ac-
count for the enigmatic absence of z-corals from
most of the few shallow water carbonates that did exist. Larger benthic foraminifera are usually the dominant constituents in these carbonates, and today they inhabit very similar shallow-marine tropical environments to corals.

Temperature and latitudinal effects cannot explain the lack of corals, especially since these Paleogene habitats clearly lay within the global limits of the z-coral belt, and climatic conditions were particularly warm in the middle and late Eocene (Miller et al., 1987; Frakes et al., 1992). Rapid subsidence rates, dispersal and recruitment factors, limiting chemical conditions of the water, including salinity, oxygen, and nutrients, and unfavourable speeds and directions of currents, might all have been contributory causes, but cannot be assessed easily in an ancient context.

Substrate control is more readily inferred, since some of the foraminifera-dominated carbonates represent shifting coarse-grained shoals (Fig.11d), perhaps comparable with ooid shoals today, and hence unfavourable for coral colonisation. Water depth is also an important factor, although the taxa and growth forms of the larger benthic foraminifera and other shallow marine bioclasts, such as coraline algae, within the Paleogene limestones studied, indicate a range of water depths within the photic zone (Adams, 1970; Ghose, 1977; Hottinger, 1983; Hallock and Glenn, 1986). Some of the limestones dominated by thin flat forms of larger benthic foraminifera were probably deposited below the depth of the most prolific z-coral growth (generally < 100 m, Fig.11e). However, in other deposits, the taxa and growth forms of foraminifera, which show little signs of reworking, indicate deposition in the upper part of the photic zone (Fig.11a-d). Perhaps coral facies were once more widespread but have been largely destroyed, though there are too few deposits with abundant coral clasts to support this.

Whatever the proximal causes, secondary feedback effects would also have been important if coral communities were too scattered in time and space to sustain frequent larval exchange and recruitment between areas within the region. This would have led to high rates of local extinction, and prevented longer-term development of z-coral facies. While the Paleogene paucity of z-corals in SE Asia appears to be a real phenomenon linked to lack of habitable areas, no clear set of ecological factors yet explains the paucity of z-corals in the few areas where they might be expected.

**Distributional change**

The factors of distributional change most relevant to the models in Table 1 are immigration rates. Low rates may have contributed to the Paleogene paucity of z-corals in SE Asia, and higher immigration rates to the subsequent surge in their abundance and diversity in the Neogene. There are as yet few data for addressing this, but Rosen and Smith (1988) used an indirect approach, analysing the history of endemcity patterns of corals and echinoids from different time slices. In the middle to late Eocene, and in the early Miocene, Pacific and Australasian faunas were relatively isolated from Tethyan and Indian Ocean faunas, and a pan-Indo-Pacific fauna in the modern sense did not exist until these more remote elements became fully integrated during or after the early Miocene.

Further support for this comes from the tectonic evolution of SE Asia and neighbouring regions (Schlanger, 1981; Rosen and Smith, 1988; Rosen, 1984, 1988; Paulay, 1997). Paleogene paucity of z-corals in SE Asia may reflect partial isolation of its carbonate environments from z-coral areas elsewhere, though the existence of modern examples of rich reefs in isolated settings (e.g., Chagos) suggests that the factors here may be more complex. Australia was not a reefal region as it is today, and lay over several thousand kilometres away to the southeast of the Asian margins, and outside the z-coral belt. To the east, on the Pacific plate, the Paleogene forerunners of the modern mid-Pacific archipelagos lay much further to the east than now. Apart from the Hawaii-Emperor chain, most of these archipelagos are broadly confined to the limits of the Darwin Rise/Superswell. Mid-plate oceanic islands are otherwise unusual features, and few suitable areas for corals may have occurred between the Darwin Rise/Superswell and the western Pacific convergence zones in the area which has been lost due to subduction. Thus, during the Paleogene, this intervening oceanic region may have been wide enough to have caused partial or intermittent isolation of Pacific areas now represented by the Eocene coral-bearing limestones underlying these islands.

To the west of SE Asia, the collision of the Indian continent with Eurasia in the Eocene eliminated the east-west trending Tethys seaway in that region, and initiated large-scale clastic input along the surrounding coastlines. In the tropical waters of the Indian Ocean, the few oceanic island ‘staging posts’ (Rosen, 1983),
such as the Ninetyeast Ridge, may have aided only intermittent larval exchange of benthic populations between SE Asia and the rich Eocene z-like coral regions on the western side of India, the Middle East and Europe (Fig.9). These palaeogeographical factors, combined with the great width of the Indo-Pacific gateway between the Asian and Australian continents, and scarcity of shallow areas in that gateway, must have limited immigration into this gateway area during the Paleogene. This did not completely prevent colonisation by z-corals since the biogeographical affinities of the Tonasa fauna indicate that biogeographical continuity between SE Asia (Sulawesi) and the western side of the Indian continent occurred at least once, perhaps via the Ninetyeast Ridge. The faunal affinities of the contemporaneous Enewetak z-corals (Wells, 1964) suggest an analogous pattern for mid-plate Pacific areas.
Cenozoic corals of SE Asia

The broadly contemporaneous collision of Australia with SE Asia and closure of Tethys in the Middle East during the latest Oligocene to earliest Miocene (Rosen and Smith, 1988; McCall et al., 1994, for the coral history) had a profound effect on the palaeogeographic setting of z-coral faunas in SE Asia. Taxa within the Indo-West Pacific centre from this time onward must have consisted of (1) pre-Neogene, but not necessarily Indo-Pacific, relicts, (2) those of local SE Asian origin and (3) taxa that originated elsewhere within the Indo-West Pacific but which immigrated into the centre (see below). It is unlikely any other taxa that had originated elsewhere could have then entered the Indo-West Pacific. Meanwhile, northern Australia and New Guinea had entered the reef coral belt, and the Pacific archipelagos of the Darwin Rise/Superswell had moved closer to Asia by over 3000 km (CGMW/UNESCO, 1990) since the late Eocene. These latter events have greatly increased the extent and variety of potential habitats for z-coral colonisation in SE Asia. During the Neogene, SE Asia became, in effect, a biogeographically cross-roads and meeting point for faunal convergence of shallow marine organisms from numerous different directions (Rosen, 1988; Pandolfi, 1992) perhaps enhanced by changes in oceanic current configurations at this time (Grigg, 1988).

Originations

Rates and locations of originations are crucial criteria of the different models in Table 1. Rigorous treatment however requires good knowledge of the phylogenetic relationships of taxa to each other and to their times and places of occurrences. However, such work is currently confined to studies of a few extant Indo-Pacific z-corals, and until now fossil data have not been incorporated. Stratigraphic distributions also offer important historical clues, but since the fossil record is incomplete and there is insufficient taxonomic knowledge, they mainly provide indications of the minimum limits of former distributions in time and space and evidence of changing patterns of faunal affinities. A third approach, age-and-area studies of modern taxa, has until recently dominated Indo-Pacific work. Stratigraphic distributions, age-and-area studies and cladistic biogeography are discussed in this order, below.

As emphasized already, endemic Eocene z-corals have yet to be recorded from SE Asia. Their affinities (above) cannot rule out SE Asian, European or Indian Ocean origins, although given the paucity of this fauna there is therefore no evidence for high endemic origination rates in SE Asia at this time. The Oligocene picture is less clear for taxonomic reasons. The main fauna (Tanjung, Table 3), comprises a mixture of European and apparently endemic taxa. Our initial work on the Boera corals of Papua New Guinea (Fig.12), reveals strong European affinities, even though they are dated uppermost Oligocene (Table 3). For a more complete picture however, revision and/or description is urgently needed of the important Paleogene faunas of Pakistan (Duncan, 1880; Gregory, 1930), together with those of the western Indian Ocean margins from Iran and the Arabian region, to eastern Africa. Currently, however, there is no reason to change Gerth’s (1925, 1930) view that relations between the corals of SE Asia during the Paleogene generally, were closer to that of the Indian and Mediterranean regions, than they were during the Neogene, and that exchange of species took place throughout these three regions during the Paleogene (see also Pandolfi, 1992). Hence palaeontological evidence of origination patterns give no support for SE Asia being a Centre of Origin (or part of one) during the Paleogene.

The fourfold surge in z-coral diversity in the Indo-West Pacific centre from around the early Neogene (Fig.9) must reflect, at least in part, the dramatic geological changes. Severance of Tethyan seaways in the Middle East at around this time would have confined subsequent originations either to the Atlantic-Mediterranean or to the Indo-Pacific, respectively, and this is reflected in their well-established post-Paleogene endemisms. Each region became an evolutionary entity, with the Indo-Pacific exhibiting the more marked taxonomic radiation (Fig.9). Independent Neogene evolution in the western Atlantic is shown by Agaricia species, and amongst such groups as the meandrinids, mussels and meandrid favids (Budd et al., 1994; Johnson, 1998). The important question is whether the Indo-Pacific radiation was particularly confined to the Indo-West Pacific centre.

The oldest record of the ecologically important and very diverse modern z-coral, Acropora, is in the Paleocene of Somalia (Carbone et al., 1994). It occurs in numerous European localities from the Eocene to Miocene, but it does not appear in either the Caribbean or the Indo-West Pacific centre until the Oligocene (Fritsch, 1878; Wells, 1964; Frost, 1972; Budd et al., 1992, 1994,
and Fig.10). It shows a very recent (/latest
Miocene or Pliocene) marked radiation in the
Indo-West Pacific but not in the Caribbean
(McCall et al., 1994; Budd et al., 1994). This his-
tory has parallels with the fungiids whose most
primitve genus Cylcoerosis, occurs in the Paleo-
ecologic of Somalia and western Pakistan, and in
the Eocene (Tonsawa) of SE Asia (Fig.10,b,c) and
Europe (Hoeksema, 1989; Carbone et al., 1994).
Subsequent radiation occurred during the
Neogene in SE Asia and fungiids are now richest
in the Indo-West Pacific center, though in con-
trast to Acropora they are not known from the
Caribbean. These two cases show that the Indo-
West Pacific center has not been the location of
their origins, although it has been important in
the evolutionary history of z-corals from the
Neogene onwards. Even so, it is still question-
able on other grounds (see below) whether or
not the region then acted as a Centre of Origin for
these corals from that time.
Perpetuation of the idea that the Indo-West
Pacific locus was a Centre of Origin for z-corals
can be largely attributed to the landmark age-
and-area study by Stehli and Wells (1971). In
this particular context, however, such analyses
are flawed because they give the illusion that
the age of a modern taxon found in a particular
area indicates that it has been in that area
throughout that time. Admittedly, Stehli and
Wells did not claim this, but by plotting average
ages for different areas on global maps, they
provided a visually powerful synthesis which
compounded the illusion, leading others to in-
terpret such analyses in this way. For example,
of the 18 extant Indonesian z-genera which are
of Eocene age (Rosen, 1984), only 6 actually oc-
cur in the Eocene of SE Asia, and a further one
(Astrocoenia) is extinct (present data). None of
the genera appear to have been local Eocene
endemics, so the bulk of the 18 corals must have
arrived in the region from elsewhere. Although
this line of argument assumes that the fossil
record is reliable (cf., Briggs, 1992), it is equally
clear that the record does not support a Centre
of Origin in SE Asia at this time. Parallel argu-
ments apply to Eocene corals of the Pacific.
Age-and-area information alone cannot be
used to infer origination patterns, but is best
combined with phylogenetic work as in elistic
biogeography. Paradoxically though, Stehli and
Wells (1971), used their age-and-area data to

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Fig.10. Representative fossil scleractinian corals of Eocene and Oligocene age from the Tonsawa Formation in South Sulawesi.
Specimen numbers, prefixed AZ, are those of The Natural History Museum, London. Details of inferred zooxanthellate status
are also given. Ages of Pakistan occurrences revised according to Adams (1970). So far, the upper Eocene fauna from the
Tonsawa Formation consists of 12 species, 7 of which are z-like and 5 are z-like? In addition to those illustrated here, are: fungiid
sp. (z-like), Stylocoenia sp. (z-like?), and a solitary or phacelloid species (z-like?) A-C: Basal beds of the Tonsawa Formation,
lowermost upper Eocene (Tb), Dori doi locality. A: Tetroacyathus mummiformis (Duncan, 1880). Transverse thin section, x1.5 (AZ
1188). Patellate to discoidal solitary coral. Modern Tiroacothyathus is azooxanthellate, but Tonsawa specimens and Duncan's coral
may not belong to this genus. Present species is z-like? on facies occurrence only, previously known from lower to mid-
Oligocene (Te-c) of Pakistan. B: Cyclosersis (Cyclolites) crenulata (Duncan, 1880) syn. Funginellastraea (Cyclolites) beberti
(Tournouer, 1872). A: Aboral surface, x1.5, B: polished transverse section, x1.5 (AZ 1202). Discoidal solitary 'mushroom coral'.
Modern genus is a soft-substrate dweller, usually but not always zooxanthellate. Present species is z-like? on facies occurrence
only; previously known from upper Paleocene of Pakistan (Ta1) and (?) various Eocene localities in southern Europe (P. beberti).
D-E: Bulo Bunting locality, lower part of Tonsawa Formation, but stratigraphically above Dori doi locality, upper Eocene (TB).
D: Trachypbyllia (Montivallia) indica (Duncan, 1880). Transverse thin section, x1.2 (AZ 1182). Filabellid pedunculate form,
consistently four-lobed in mature examples. Modern genus is a zooxanthellate soft-substrate dweller. Present species is z-like on
generic and morphological grounds; previously known from middle Eocene (Ta3) of Pakistan. E: Caulstrea (Calmopyllia) indica
(Duncan, 1880). Transverse thin section, x2 (AZ 1179). Phaceloid branching colony. Modern genus is zooxanthellate. Present
species is z-like on generic grounds; previously known from middle Eocene (Ta3) of Pakistan. F: Paturis sp. Transverse
thin section, x2 (AZ 1193). Geroid colony. Modern genus is zooxanthellate. Present form is z-like on generic grounds. G:
Diploastrea r?d Rhizangiidae aggmensa Fritsch, 1878. Transverse thin section, x2 (AZ 1191). Astroid colony. Modern genus is
zooxanthellate. Present species is z-like on generic and morphological grounds; previously known from mid-Oligocene (Td) of
Kalamanta (Table 3). H: Favia (Phyllocoenia) conferta (Duncan, 1864). Transverse thin section, x4 (AZ 1178). Plocoid colony.
Modern genus is zooxanthellate. Present species is z-like on generic and morphological grounds; previously known from
uncertain Tertiary horizon in Pakistan, possibly upper Oligocene to middle Miocene (Te - lower Tb). I: Astrocoenia biestellata
(Cuttolo, 1896). Transverse thin section, x6 (AZ 1177). Geroid colony. Extinct genus. Present species is z-like? on facies
occurrence only; previously known from Eocene of Italy, J: Favia pliculata Duncant, 1880, J (AZ 1192) weathered calcal
surface, x0.5, K: Favia (1187) Transverse thin section, x2. Plocoid pedunculate colony. Modern genus is zooxanthellate. Present
species is z-like on generic and morphological grounds; previously known from middle Eocene to lower Oligocene (Ta3-Td) of
Pakistan. L: Tonsawa II Quarry locality, upper Oligocene (Te-c) middle part of the Tonsawa Formation. Acropora sp. Polished
longitudinal section through ramose branch, x2 (AZ 1213). Ramose branching colony with plocoid corals. Modern genus is
zooxanthellate, widespread, and an abundant reef contributor in both Indo-West Pacific and Caribbean. Present form is z-like on
generic and morphological grounds.
Fig. 11. Thin section photomicrographs of Tertiary limestones dominated by larger benthic foraminifera and deposited in different environments in the photic zone. All were photographed in plane polarized light at x10 magnification. Samples and thin sections are held at Royal Holloway London University. A: Imperforate foraminifera bioclastic packstone (MTR114) containing soritids, miliolids, alveolins (Borelli sp.), Austerotrettilia sp. and other fragmented bioclasts. Oligo-Miocene sample from the Tabular Limestone, Tabular River, Mangkalihat peninsula, East Kalimantan. The foraminifera are all typical of the shallower parts of the photic zone and can tolerate some fluctuations in salinity. B: Probable lower Oligocene (Tc) Nummulites bioclastic pack/grainstone (GU6) from Gua Unguk, Bengalon River area, north Kutai, East Kalimantan. Contains robust Nummulites and other fragmented and often abraded marine bioclasts and is inferred to have been deposited in moderate to high energy in the upper part of the photic zone. C: Lower Oligocene (Tc) Nummulites and Heterostegina bioclastic packstone (GB45) from Gua Bunga, Bengalon River area, north Kutai, East Kalimantan. Contains moderately robust Nummulites and thin forms of Heterostegina in a micritic matrix inferred to have been deposited under moderate to low energy conditions in moderate depths in the photic zone. D: upper Eocene (Tb) Discocyclina and Biplanispira bioclastic packstone (BR81) from the Bengalon River area, north Kutai, East Kalimantan. Contains abundant whole and sometimes fragmented larger benthic foraminifera, including Discocyclina sp., Biplanispira sp., Pellatispira sp., Nummulites sp., and other fragmented marine bioclasts such as coralline algae and echinoid plates. The species of foraminifera, their growth forms and the nature of the surrounding sediment suggests deposition in a moderate to high energy setting in shallow to moderate depths in the photic zone, possibly as a foraminiferal shoal. E: Upper Oligocene (Td/Tc1-4) Lepidocyclina and heterostegind packstone (MTR100) from the Tabular Limestone, Tabular River, Mangkalihat peninsula, East Kalimantan. Includes Eudiplina sp., Nephelepidina sp., Heterostegina sp. and possible Spirochyes sp. Large, thin forms of these species of larger foraminifera are typical of development towards the base of the photic zone.
**Fig. 12.** Representative fossil scleractinian corals from the upper Miocene part of the Tacipi Formation, Sungai Pesing, Ujunglampur, south Sulawesi (A-B), and from the uppermost Oligocene to lower Miocene (Te1-5) Boera Formation, Boera Head, south Papua (C-D; see Table 3). A: *Hydnogorgia australoides* (Martin, 1880). Calical surface, x2 (AZ 1212). Continuously meandroid colony with vestigial walls reduced to isolated monticules. Modern genus is zooxanthellate. Present species is z-like on generic and morphological grounds; previously known from Miocene of Indonesia. B: *Platygyra daedalea* (Ellis and Solander, 1786). Calical surface, x2 (AZ 1211). Meandroid colony. Modern species is zooxanthellate; so same is inferred for present occurrence. Extant, widespread and important reef contributor, previously recorded from numerous fossil and modern Indo-West Pacific localities from Miocene onward. C: *Favites* *prionastreaeal borneensis* (Gerth, 1925). Polished transverse section, x3 (AZ 1209). Ceroid colony. Modern genus is zooxanthellate. Present species z-like on generic grounds; previously known from Neogene of Indonesia. D: *Asteropora* cf. *meneghinii* (D’Achiardi, 1866). Polished transverse section, x2 (AZ 1210). Plocoid colony. Modern genus is zooxanthellate. Present species z-like on generic and morphological grounds; previously known from Oligocene of Italy.

Support the widely held notion that Centres of Origin have an intrinsic evolutionary characteristic in which continuous emergence of more successful taxa pushes older taxa out from the focal region. This predicts a pattern of continuous evolutionary turnover, in which (1) older faunas, prior to their displacement, should share the same central origin, and be more or less as rich, as younger faunas, and (2) a given fauna of one time slice should comprise numerous taxa that were subsequently displaced. There is as yet no evidence however that Tonasa and Enewetak Eocene genera originated in the Indo-West Pacific centre, and all but two of them still occur in the modern Indo-West Pacific centre. Therefore most of these genera were not displaced from the centre, or if they were, they evidently returned. This, as well as the paucity of the fauna is incompatible with Centre of Origin notions.

Moreover, sympatric speciation modes aside, the very commonly observed overlapping patterns of sibling species (and sister genera) amongst modern z-corals species in the Indo-Pacific, especially the central region (e.g., Hoeksema, 1989, 1993; Veron, 1995; Wallace *et*
al., 1991; Wallace, 1998; Pandolfi, 1992) suggest that siblings must have originated in different areas and subsequently migrated into their observed overlapping distributions (see also Paulay, 1997). Hence, whatever the evolutionary characteristics of Centres of Origin, competitive displacement, in this case, does not appear to be one of them. Since average longevity estimates for z-coral species are about 10 Ma (Veron, 1995), many of these numerous overlapping species must be post-Paleogene in origin, suggesting that distribution patterns in and around the centre are predominantly Neogene or younger. This is again incompatible with a Centre of Origin model, though it is also likely that some species originated through geographical isolation within and around the Indonesian archipelago (Pandolfi, 1992; Wallace, 1998).

Evidence for heterogeneous geographical origins of Indo-Pacific z-corals, including peripheral sources, has come not just from their overlapping distribution patterns but also from cladistic studies of the fungids (Hoeksema, 1993), the siderastreids and mussids (Pandolfi, 1992), and some species of Acropora (Wallace et al., 1991). These studies do not include estimates of ages of origination from fossil evidence but Pandolfi infers these from the timing of geological events whose associated features correspond geographically to his area cladograms. Parallel studies in other groups (cf., Pandolfi, 1992; Palumbi, 1996; Paulay, 1997) give similar indications of widespread heterogeneous origins for the common marine organisms of the Indo-West Pacific centre. Reef fishes, for example, apparently evolved rapidly during the first 20 Ma or so of the Cenozoic and then remained in relative stasis (Choat and Bellwood, 1991; Bellwood 1996). Cladistic analysis of reefal parrotfish (Scaridae) by Bellwood shows that the labroid lineage which gave rise to this group, was already present by the latest early to earliest middle Eocene of Europe (i.e., most recent date of Monte Bolca fish fauna from J. Pignatti, pers. comm., 1997), a pattern that has parallels with Acropora and the fungids.

Plate tectonics and the implications of the Mesozoic coral record

It is instructive to view the Cenozoic coral record in the longer-term context of the Mesozoic coral record and its plate tectonic setting. During the Triassic and Jurassic, the large tropical ocean of Meso-Tethys separated blocks such as Sibumasu and Indochina in the north, from those Gondwana blocks to the south which would later form Borneo, Sulawesi, Nusa Tenggara and Australia (Metcalfe, 1996). Around the margins of Meso-Tethys, z-coral facies developed in shallow marine waters and have been preserved today in Upper Triassic (Stanley, 1988) and Upper Jurassic limestones in Burma, Thailand and eastern Indonesia. Rifting during the Jurassic and Cretaceous separated blocks, such as west Burma and west Sulawesi, from the northern part of the Australian craton by a seaway. Australia lay too far south of the z-coral belt to support coral growth. In contrast, the rifted blocks were drifting northwards across tropical latitudes to be juxtaposed against mainland SE Asia during the Jurassic to Late Cretaceous and the few known Cretaceous scleractinian corals from Borneo and Sumatra reflect this. However, as with the Paleogene, z-corals are rare in the rest of the region during the Cretaceous. Thus the ‘Paleogene data gap’ for z-corals is the continuation of an earlier pattern which goes back into the Cretaceous, and presumably had similar causes.

The underlying issue of interest is the relative importance of plate tectonics as an evolutionary influence compared with intrinsic evolutionary processes. In general, development and diversity of both Mesozoic and Cenozoic scleractinian z-corals in SE Asia have been ultimately controlled by the plate tectonics of the region. For the Paleogene in particular, Flessa and Jablonski (1996) gave three criteria (above) by which plate tectonics might be judged to be of greater importance than intrinsic evolutionary factors in the Paleogene history of SE Asian coral paratums. Firstly, the lack of latitudinal diversity gradients is effectively fulfilled in our study because the zooxanthellate occurrences are so few that there is no gradient to speak of. Secondly, the lack of endemics of Eocene age in particular, and the European-Indian affinities of SE Asian Paleogene corals in general, suggest, as predicted, that their average age cannot be much younger, if at all, than that of corals in these other regions.

Thirdly, Flessa and Jablonski predict that recovery from the K-T extinction would also have been a significant influence on SE Asian distributions if plate tectonics were important. In fact, the paucity of both Cretaceous and Paleogene coral records within the region means that K-T extinctions and recovery were largely witnessed elsewhere. Extensive development of z-coral faunas and communities did not really occur in
SE Asia until around the earliest Neogene, whereas elsewhere in the tropics its earliest signs begin only 3-5 Ma into the Paleocene, with quite rich faunas established by the Thanetian (Fig.9; Schuster, 1996; Rosen, 1998). Thus while Flessa and Jablonski’s third prediction is not fulfilled in their precise terms, the absence of K-T coral evidence in SE Asia, clearly reflects the influence of plate tectonics. This also suggests that the idea that the Indo-West Pacific centre is largely a vestige or derivation of Cretaceous patterns (McCoy and Heck, 1976; Table 1) is at best an oversimplification. More generally therefore, there is no need to suppose that SE Asia was endowed with special evolutionary processes, as Centres of Origin models imply. It has been a region in which the potential to develop rich communities has been controlled by the way in which suitable areas for them have been continually created, reorganized and lost, especially according to the timing and movements of blocks which have broken away from Gondwana, their northward passage across Tethys into tropical waters, and their eventual accretion to the Eurasian continent.

**Plate tectonics or Centre of Origin?**

Two contrasting major patterns can be discerned: a Paleogene one in which diversity, endemicity and origination rates of z-corals in SE Asia were low, and a post-Paleogene one which is effectively the opposite. The change coincides with tectonic events, especially the collision of Australia with SE Asia. During the Paleogene, the marine region between the continental margins of SE Asia and Australia was about 3000 km wide and, compared with the post-Neogene, there were few shallow water areas suitable for z-corals. A much more extensive, but now largely inaccessible area of shallow water carbonates existed in the mid-Pacific (on the Darwin Rise/Superswell) especially during the Eocene. However, the z-coral faunas of both regions appear to have been low diversity outposts of the very much richer faunas of Europe, eastern Tethys and the western Indian Ocean margins.

The modern high diversity pattern in SE Asia and the Indo-West Pacific centre began to emerge around the earliest Neogene with an apparent regional radiation of z-corals. However, detailed studies are revealing that relicts, and migrations of taxa into the region were both as qualitatively important as originations within the region. Local originations derived, at least in part, from these antecedent elements. The geographical complexity of the region since the Neogene favoured all three processes through increasing habitat heterogeneity and potential allopatric speciation amongst fragmented shallow water areas, further enhanced in the last 10 Ma or so by the effects of glacio-eustasy and increased climatic fluctuation.

Our fossil patterns show that a Centre of Origin model (Table 1) is completely inapplicable to Paleogene z-corals of the SE Asian region, since there was only a small non-endemic fauna here. In fact, it is misleading to think of it as a ‘centre’ of any kind during this time. This contrasts with the Neogene onwards, which superficially accords with a Centre of Origin model, albeit very short duration compared with species turnover timescales. Moreover, the combined patterns from a range of different studies show that a more appropriate model requires a combination of all three of the possibilities in Table 1. A longer-term perspective suggests that the above contrast in Paleogene and post-Paleogene patterns represents a cyclical sequence which has occurred at least twice before with strong z-coral developments in the late Triassic and late Jurassic in SE Asia, coincident with times when rifted Gondwanan blocks docked against the Asian continent in the tropics. Thus plate tectonic processes rather than intrinsic evolutionary processes (like Centres of Origin, competitive displacement, etc.) have been a major control on regional diversity patterns of z-corals, and presumably also numerous other shallow marine organisms.

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