Successive Isolation Rather Than Evolutionary Centres for the Origination of Indo-Pacific Reef Corals

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Successive isolation rather than evolutionary centres for the origination of Indo-Pacific reef corals

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Abstract. Biogeographic patterns are interpreted using relationships based on phylogenetic systematics in Indo-Pacific reef corals (Scleractinia). A cladistic biogeographic analysis of the genera *Symphyllia* (Milne Edwards & Haime. 1848) and *Coscinaraea* (Milne Edwards & Haime, 1848) yielded three patterns. (1) Indo-Pacific reef coral species ranges overlap in a west to east stepwise fashion with the closest biogeographic relationships occurring between adjacent areas. These area relationships show a marked congruence with the Cenozoic geologic history of the Indo-Pacific. (2) The region represented by southeastern and southwestern Australia appears to be biogeographically distinct from both the north and western Indo-Pacific and the eastern Indo-Pacific. In Western Australia, controls over the biogeographic distribution of species of the two genera studied appear to be a function of latitudinally related environmental parameters. (3) Species with relatively derived character states display a higher degree of endemism than species which show relatively primitive character states.

The relatively derived coral species showing the highest degrees of endemism exist at the periphery of Indo-Pacific reef coral distributions. Thus, many reef coral species must have originated far from the Indo-West Pacific centre of diversity. Congruence between the geologic history of the Indo-Pacific and the biogeographic area relationships suggest successive isolation as a working hypothesis for the origination patterns of Indo-Pacific reef corals. Species origination in reef corals was a response to geologic events that resulted in successive isolation of populations at various times and in various places during the Cenozoic history of the Indo-Pacific. It is suggested that future biogeographic studies do not confine themselves to diversity maps, but use species level phylogenetic information in constructing biogeographic hypotheses.

Key words. Coral, biogeography, phylogeny, centre-of-origin, Indo-Pacific.

INTRODUCTION

Study of the biogeographic distribution of reef corals has led to a considerable array of hypotheses concerning the evolutionary history of tropical reef biotas. In a recent review of reef-coral biogeography, Rosen (1988a) identified thirteen historical theories which attempt to explain the origin of Cenozoic to Recent distributions of reef corals and other associated reef organisms. Whereas these historical explanations did not consider phylogenetic relationships in the analysis of biogeographic patterns, some recent workers have incorporated phylogenetic relationships in biogeographic analyses of tropical marine biotas (Hoeksema, 1989; Reid, 1990; Springer, 1981, 1982; Springer & Williams, 1990; Wallace *et al.*, 1991).

Hoeksema (1989) recently reviewed the biogeographic distribution of Indo-Pacific Fungiidae and provided a species level phylogenetic analysis. He noted the lack of endemism in Fungiidae as the reason for not incorporating cladistic biogeographic methods. Sheppard (1987) provided a biogeographic analysis for Indian Ocean coral species using various similarity indices, but Rosen (1988b) has argued against the utility of such methods in constructing biogeographical hypotheses. Wallace *et al.* (1991), using cladistic biogeography, related the phylogenetic relationships of some *Acropora* species to their distribution patterns in the Indo-Pacific and Red Sea.

With the exception of the Fungiidae (Hoeksema, 1989), endemism in reef corals has only been evaluated at the generic level whereas species level endemicity is relatively unexplored. It is likely that a large portion of Indo-Pacific coral species span wide geographic ranges (Potts, 1985; Veron, 1985a), but there are many endemic coral species which may lend themselves to fruitful cladistic biogeographical analysis (J.E.N. Veron. pers. comm. 1989; Wallace & Pandolfi, unpubl. data). In addition, resolving cladistic relationships among taxa which are widespread may further our understanding of biogeographic patterns at broad geographic scales, such as the eastern versus the western Pacific Ocean, and the Red Sea versus the Indian Ocean.

In this paper I provide a cladistic biogeographic analysis of reef coral species from the two genera *Coscinaraea* (Milne Edwards & Haims, 1848) and *Symphyllia* (Milne Edwards & Haime, 1848). The area cladograms produced by the analysis are then utilized: (1) to interpret broad-scale Indo-Pacific coral distribution patterns in light of the geologic history of the Indo-Pacific, (2) to interpret Western Australia coral distribution patterns and their significance to reef coral speciation, and (3) to investigate the relationship between endemism and recency of ancestry. The hypotheses generated in this study will need testing with more phylogenetic analyses both within the Scleractinia and with other marine organisms.

Phylogenetic systematics and corals

Few modern studies of phylogeny in Scleractinia exist, though virtually all systematic studies of these organisms mention phylogenetic hypotheses. In fact, only four studies of Anthozoa have been based on cladistic hypotheses, three in the Scleractinia (Cairns, 1984; Hoeksema, 1989; Wallace *et al.*, 1991), and one in the Tabulata (Pandolfi, 1989a).

Several problems exist with determining phylogenetic relationships among corals: morphological variability within the group under study, lack of combined molecular/morphological data sets, and delimitation of species. Morphological variability among living corals is commonplace and has resulted in an enormous amount of effort to determine its genetic and environmental influences (Ayre, Veron & Dufty, 1991: Foster, 1979, 1980; Hunter, 1985; McMillan *et al.*, 1991; Veron, 1981; Willis, 1985; Willis & Ayre, 1985). Many corals inhabit a range of environments and respond morphologically to various environmental parameters. This morphological response often results either in variability in quantitative characters or variability in the presence or absence of qualitative characters. Within a single taxon, therefore, more than one character state for any character (polymorphism) may occur. This type of polymorphism is meant in a general sense and its usage is distinct from the polymorphism where different functional and/or morphological forms of polyp or zooid occur in colonial groups like corals and bryozoans.

There is very little genetic work available on modern hard corals, most of it constrained to descriptions of the genetic structure of populations (Stoddart, 1984a; Stoddart, Babcock & Heyward, 1988) and assessment of population or clonal relatedness (Ayre *et al.*, 1991; Ayre & Resing, 1986; Ayre & Willis, 1988; Hunter, 1985; Willis & Ayre, 1985; Stoddart, 1983, 1984b). Most of these studies are concerned with intra- and interpopulational variability and not relationships between species (but see Ayre *et al.*, 1991). There is presently only one coral group where molecular data are being analysed with respect to phylogeny (McMillan *et al.*, 1988, 1991). In groups as morphologically variable as scleractinians, a combined molecular/morphological approach is most desirable (Hillis, 1987) but there is at present a lack of combined molecular/morphological data sets. However the importance of phylogeny in constructing general biological and evolutionary hypotheses demands that phylogenetic analysis goes ahead even if only with morphological data. Hypotheses erected may later be modified in the light of new data, be they molecular or otherwise.

The taxonomy of corals has historically been riddled with overlapping species definitions. To a large degree this has been alleviated by the concentrated efforts of Australian workers on the Great Barrier Reef (Veron & Pichon, 1976, 1980, 1982; Veron, Pichon & Wijsman-Best, 1977; Veron & Wallace, 1984; Wallace, 1978) whose excellent monographs provide an ideal starting point for the gathering of morphological characters and character states among scleractinian species. However, there is a lack of knowledge of microstructural detail and of information about the internal details of coral skeletons in the literature on Recent corals. Clearly, there is much further work, including genetic, which needs to be undertaken before species limits are adequately determined. In general, however, these will represent refinements to an already workable scheme and so it is now timely to begin asking phylogenetic questions at the species level in scleractinians.

MATERIALS AND METHODS

Phylogenetic analysis

Phylogenetic trees were generated using the criterion of parsimony (Camin & Sokal, 1965; Edwards & Cavalli-Sforza, 1963, 1964). Phylogenetic analyses were conducted at two taxonomic levels. *Coscinaraea* is referred to the Siderastreidae (Vaughan & Wells, 1943) and *Symphyllia* is referred to the Mussidae (Ortmann, 1890). *Psammocora* is included in the Siderastreidae following Veron (1986). The first phylogenetic analysis was performed on the genera of each of the two families Siderastreidae and Mussidae using Lundberg rooting and the phylogenetic package HENNIG86 (Farris, 1988). Lundberg rooting (Lundberg, 1972), maximizes character congruence and utilizes an ontogenetic criterion of absence (primitive) to presence (derived). Primitive character states in the analysis were used to construct an outgroup. These initial analyses were performed to establish sister groups to be used as outgroups in the species level analyses; thus, from each of these cladograms an outgroup was chosen as the most nearly related confamilial genus to the genus under study.

Outgroup comparison (Farris, 1982; Lundberg, 1972; Maddison, Donoghue & Maddison, 1984; Stevens, 1980; Watrous & wheeler, 1981; Wiley, 1981) was used to root trees in the species cladograms. In the analyses at the species level in *Symphyllia* and *Coscinaraea*, the trees were rooted by an outgroup, which consisted of the set of all species of the sister group obtained in the phylogenetic analysis of the respective family. Data sets with characters and character states for genera of the Mussidae and Siderastreidae, and for species of *Coscinaraea* and *Symphyllia*, together with the options used in the HENNIG86 runs, can be found in Appendix I.

Due to the high degree of within-taxon polymorphism in the Scleractinia it was necessary to either split the original taxa into additional taxa which reflect the polymorphisms present within the original taxon or to break down the polymorphic characters into a series of nominal characters. Whilst Pimental & Riggins (1987) have cautioned against this approach, I chose the latter, as the former methodology resulted in an inordinate number of additional taxa analysed with a small number of characters. I coded quantitative characters by their numeric ranges to reflect the variability associated with corals. Because each taxon displayed a range of values for an individual quantitative character, the ranges were broken into a series of nominal characters which reflected the range occupied by the individual taxon over the range occupied by all taxa. This method was preferable to gap-coding (Archie, 1985; Goldman, 1988; Chappill, 1989) because population parameters were not estimated.

All characters except the taxonomic affinity character (see below) were equally weighted; therefore both polymorphic qualitative and quantitative characters which were split into a series of nominal characters were weighted such that when all the nominal characters of a single character were taken together, they were equivalent in weight to a single character with two character states. In no case was there any *a priori* reason to order the multistate characters (but see Mickevich, 1982; and Pimental & Riggins, 1987), and multistate characters were left unordered.

Characters and character states were determined through analysis of published monographs (Chevalier, 1975; Matthai, 1928; Nemenzo, 1959; Veron, 1985b, 1986; Veron & Pichon, 1980, 1976; Wells, 1956; Zlatarski & Estalella, 1982) and specimens housed at the Australian Institute of Marine Science. The character lists are not exhaustive but represent the amount of information that was known about all taxa at the time the data was gathered. As these groups come under further study it is anticipated a larger character matrix can be generated.

Because corals can be extremely morphologically similar, yet taxonomically distinct, it was necessary to use a heavily weighted taxonomic affinity character in each species level analysis. This allowed the ingroup to be separate from the outgroup in the resulting cladogram. The incorporation of this character also circumvented the additional task of investigating the apomorphic characters of the outgroup which did not occur in the ingroup.

Biogeography

Species distribution patterns found in Tables 1 and 2 were derived from Veron (in press) and Veron & Marsh (1988). Only the distributions marked in these tables were used in the biogeographic analysis. To derive biogeographic hypotheses of area relationships, area cladograms were produced for each genus based on the component species distribution patterns and phylogeny. Area cladograms were generated from taxon cladograms under three rules: Assumptions 0 (Zandee & Roos, 1987; Nelson & Ladiges, 1991), 1 and 2 (Nelson & Platnick, 1981; Nelson & Ladiges, 1991) using COMPONENT (Release 1.5, Page, 1989). Assumption 0 compels all area statements of a cladogram to be monophyletic; thus the areas inhabited by each widespread species represent indisputable components of the area cladogram (Zandee & Roos, 1987) and all the areas for a given taxon are equally relevant. Assumption 1 constrains areas to be mono- or paraphyletic. Assumption 2 'allows areas to be polyphyletic and allows an analytical escape from such accidental biological events as dispersal, extinction and failures by taxa to respond to vicariance' (Humphries, 1989; p. 101). Area cladograms were chosen on the basis of their commonality to the two genera under study.

CHARACTERS USED IN THE CLADISTIC ANALYSIS

Mussidae

I. Growth form. Growth form refers to the external shape of the living coral colony. In the Mussidae four growth forms occur: flattened, domed, cylindrical and phaceloid. The flattened state is taken as the pleisiomorphic state because an expected colony astogeny (Pandolfi, 1989b) would proceed from the expansion of a single or multiple corallites over a substrate (flattened) to a domed, then cylindrical, then branched phaceloid form (Coates & Oliver, 1973). *Acanthastrea* (Milne Edwards & Haime, 1848) and *Australomussa* (Veron, 1985b) are polymorphic, displaying both flattened and domed character states.

II. Corallite arrangement. This character describes the underlying architecture of the coral colony. The solitary state is taken as the pleisiomorphic state and an expected colony astogeny might proceed from solitary to phaceloid to the development of common walls in cerioid to subplocoid colonies to the loss of walls in meandroid and flabello-meandroid colonies (Coates & Oliver, 1973). Only *Scolymia* (Haime, 1852) is polymorphic for corallite arrangement, displaying both solitary and ceroid/subplocoid character states.

III. Septo-costae height. Septo-costae range in height in the Mussidae from less than 1 mm to 11 mm. Most genera have a height of either less than 4 mm or greater than 4 mm. The lower value is taken as the pleisiomorphic state because ontogenetically, continuous characters must pass through a lower value before attaining a higher value. Both *Symphyllia* and *Lobophyllia* (de Blainville, 1830) have a wide range of septo-costae heights and are therefore polymorphic for this character. Missing values are recorded for *Isophyllastrea* (Matthai, 1928) and *Isophyllia* (Milne Edwards & Haime, 1851) because only Indo-Pacific genera were studied microscopically and there is no report of the value of this character in the literature for these genera.

IV. Corallite diameter. Corallite diameter is divided into three character states, based on the range of values exhibited by each genus in comparison to the range exhibited by the family as a whole. As in all continuous characters the lowest value is the pleisiomorphic state. Both *Scolymia* and *Acanthastrea* are polymorphic for this character.

V. Columellae diameter. Genera of the Mussidae have columellae diameters either less than or greater than 5.5 mm. The pleisiomorphic state is less than 5.5 mm. A missing value is recorded for the non-Indo-Pacific genus *Mycetophyllia* (Milne Edwards & Haime, 1848), as no reports of columellae diameter could be found in the literature.

VI. Valley thickness. Corallites may be arranged in valleys in meandroid and flabello-meandroid Mussidae or such valleys may be the elongated corallites of solitary or cerioid/subplocoid Mussidae. The thickness of the valley is divided into three continuous character states, and the lowest value is the pleisiomorphic state. Polymorphism occurs in *Lobophyllia* and *Australomussa*. Missing values are recorded for genera without valley development (*Cynarina* (Bruggemann, 1877), *Blastomussa*, *Acanthastrea*, *Mussismilia* (Ortmann, 1890), and *Isophyllastrea*).

VII. Septal number per cm. The number of septa/cm varied widely in the Mussidae with a range from 4.5 to 16. This character has thirteen character states, reflecting the wide variability in many genera. It is unclear whether the lowest or highest value should be the pleisiomorphic state; thus, the outgroup is scored 0 for all thirteen nominal characters. Polymorphism occurs in *Lobophyllia*, *Scolymia*, *Acanthastrea*, *Symphyllia*, *Mussismilia*, *Isophyllia*, and *Mycetophyllia*.

VIII. Septal dentation shape. Four shapes are exhibited by Mussidae septal dentations (blunt, rounded, lobate, acute spiny) and it is unclear which state is plesiomorphic. Thus, the outgroup is scored 0 for all four nominal characters. *Lobophyllia* is polymorphic for this character.

IX. Epitheca. Epitheca is an extension of the basal plate which may or may not occur in Scleractinian corals. Ontogenetically, the basal plate pre-dates the epitheca and may exist without the development of the epitheca. It stands to reason then that the absence of epitheca predates the presence of epitheca in coral development. Thus, absence of epitheca is taken as the pleisiomorphic state.

X. Wall thickness. Wall thickness is divided into either less than 1 mm or greater than 1 mm. The lower value is the plesiomorphic state. Polymorphism occurs in *Lobophyllia* and *Isophyllastrea*. A missing value was recorded for *Mussismilia* because no reports of wall thickness in this genera have been published.

XI. Permanent number of stomodeal centres. The number of stomodeal centres varies in the Mussidae. Monocentricity is taken as the plesiomorphic state. *Scolymia* and *Isophyllastrea* are polymorphic for this character.

Symphyllia

I. Valley shape. Valley shape is either straight or sinuous in the species of *Symphyllia*. Three species *S. agaricia* (Milne Edwards & Haime, 1849), *S. radians* (Milne Edwards & Haime, 1849), and *S. wilsoni* (Veron, 1985b) are polymorphic for this character.

II. Valley arrangement. Valleys are either radially arranged or irregular. *Symphyllia agaricia* and *S. radians* are polymorphic for this character.

III. Valley width. Valley width is divided into three character states, based on the range of values exhibited by each species in comparison to the range exhibited by the genus as a whole.

IV. Septal orders. The number of septal orders is polymorphic in only *S. recta* (Dana, 1846).

V. Septal number per cm. The number of septa/cm varied widely in *Symphyllia* with a range from 6 to 13. This character has six character states. Polymorphism occurs in all species of the ingroup.

VI. Number of teeth on 1st order septa. This character also varied widely in *Symphyllia* having a range from 2 to 10. There are nine character states, reflecting the wide variability in many species. Both *S. valenciennesii* (Milne Edwards & Haime, 1849) and *S. wilsoni* show low variability for this character.

VII. Septal exsertness. Septal exsertness ranges from 0.5 mm to 12 mm in *Symphyllia*. *Symphyllia agaricia* and *S. radians* have low values, *S. recta* and *S. wilsoni* intermediate values, and *S. valenciennesii* high values for this character. The wide range in values resulted in ten character states for this character.

VIII. Colline thickness. Thickness of collines was divided into character states on the basis of whether they were less than or greater than 5 mm thick. No polymorphism was displayed for this character.

IX. Columellae. Columellae are either single or arranged in double rows in *Symphyllia*. No polymorphism occurs in the ingroup, but its occurrence in the outgroup warranted splitting of the character into two nominal characters.

X. Corallum shape. Colony shape is divided into four character states, flattened, hemispherical, subfoliaceous and phaceloid. *Symphyllia radians* shows extreme polymorphism, displaying the first three of these character states. Only *S. recta* displays strictly one of the character states (hemispherical).

XI. Columellae linkage. The structure of the columellae is either lamellar or trabecular in *Symphyllia*. Polymorphism occurs in *S. recta* and *S. wilsoni*.

XII. Columellae texture. Columellae are either compact or spongy. Polymorphism occurs in *S. agaricia*, *S. valenciennesii*, and *S. wilsoni*.

XIII. Valley length. The length of the valleys is the most variable of the presently studied characters in *Symphyllia*. This character ranged from 7 to 55 mm and is represented by ten character states. Valley lengths were not estimated for *S. agaricia* and *S. wilsoni*.

XIV. Taxonomic affinity. This character was used to weight the phylogenetic analysis such that ingroup species could not be grouped with outgroup species. Characters which occur only in *Lobophyllia* were not used in the phylogenetic analysis of *Symphyllia*. These characters would have separated the species of the two genera into two taxa (*Lobophyllia* and *Symphyllia*), but since only *Symphyllia* was under scrutiny, they were not investigated.

Siderastreidae

I. Growth form. In the Siderastreidae four growth forms occur: laminar, encrusting, massive, and columnar. The laminar state is taken as the pleisiomorphic state because an expected colony astogeny (Pandolfi, 1989b) would proceed from the expansion of a single or multiple corallites over a substrate (laminar) to an encrusting then massive form to a columnar form (Coates & Oliver, 1973). Only *Anomastrea* (von Marenzeller, 1901) and *Horastrea* (Pichon, 1971) are **not** polymorphic for growth form.

II. Corallite arrangement. The cerioid state is taken as the pleisiomorphic state in the Siderastreidae, as sub-meandroid implies the incipient loss of walls, and is treated as a derived character state. Because it seems to be equally likely to proceed from a cerioid state to either of the sub-meandroid states, this character was left unordered in the analysis. No polymorphism occurs for this character.

III. Septal arrangement. Septa may be fused in genera of the Siderastreidae. The pleisiomorphic state is taken as not fused, because fusion takes place later in corallite ontogeny. Only *Siderastrea* (de Blainville, 1830) has septa that are not fused.

IV. Wall composition. Corallite walls are made up entirely of the septa (septo-thecate), or, where the septa are perforate, synapticulotheca is formed. A synapticulothecate wall allows more inter-polyp communication than a septo-thecate wall and represents a higher degree of colony integration. High colony integration is considered as more derived than low colony integration (Coates & Oliver, 1973; Pandolfi, 1988, 1989b); thus, synapticulothecate is derived with respect to septo-thecate. Only *Horastrea* has septo-thecate walls.

V. Budding. Corals display either intra-tentacular budding, where the polyp divides into two or more daughter polyps or extra-tentacular budding where daughter polyps form on the side of the parent. Extra-tentacular budding is characteristic of colonies with low integration whereas intra-tentacular budding is characteristic of colonies with high integration (Coates & Oliver, 1973). Because low integration is considered primitive with respect to high colony integration (Coates & Oliver, 1973; Pandolifi 1988, 1989b), extra-tentacular budding is the plesiomorphic state. *Psammocora* (Dana, 1846) and *Coscinaraea* are both polymorphic for this character.

VI. Columellae. Columellae may be simple or compound. Simple is taken as the plesiomorphic state. Again, both *Psammocora* and *Coscinaraea* are polymorphic for this character.

VII. Valleys. Valleys may be absent or present in the Siderastreidae. Their presence implies higher colony integration and inter-polyp communication than their absence because walls are absent between individual polyps where valleys are developed. Thus, the absence of valleys is the plesiomorphic state.

VIII and IX. Septal granulations and petaloid septa. These two characters are modifications of septa and their presence is considered derived with respect to their absence. Polymorphism is absent in the Siderastreidae for these two characters.

X. Colony size. Small colony size (<20 cm) is the plesiomorphic state. Only *Pseudosiderastrea* (Yabe & Sugiyama, 1935) displays small colony sizes.

XI. Synapticular rings. Pronounced synapticular rings occur where septal synapticulae fuse to form a ring within the corallite. The absence of such well-developed synapticular structures is taken as the plesiomorphic state.

XII. Wall thickness. Thin colony walls is the plesiomorphic state.

XIII. Corallite size. Corallite size is divided into three character states. The lowest value is the plesiomorphic state.

Coscinaraea

I. Growth form. Four growth forms occur in *Coscinaraea*: columnar, explanate, branching and massive. Polymorphism occurs in *C. columna* (Dana, 1846) and *C. monile* (Forskål, 1775).

II. Corallite arrangement. Thamnasteroid species are characterized by the absence of a corallite wall and by confluent septa which join neighbouring corallites together in a pattern resembling lines of force in a magnetic field. Only *C. columna* and *C. exesa* (Dana, 1846) do **not** exhibit this character state.

III. Budding. Budding in *Coscinaraea* is either circumoral or marginal. *Coscinaraea crassa* (Veron & Pichon, 1980) displays both budding types.

IV. Superficial calices. *Coscinaraea* may possess corallites which remain at or below the corallum surface and these are referred to as superficial calices. Only *C. marshae* (Wells, 1962) does not possess such calices.

V. Corallite growth. Corallites may occur singly or may occur in series along the corallum. In *C. columna* and *C. exesa*, corallites occur both singly and in series.

VI. Concentric corallite rows. Corallites may or may not occur in concentric rows in *Coscinaraea.*

VII. Collines. Collines are protuberant ridges located between corallites on the colony surface. Only *C. wellsi* (Veron & Pichon, 1980) lacks collines.

VIII. Colline width. This character varied widely in *Coscinaraea* with a range from 0.5 to 7 mm. There are fourteen character states, reflecting the wide variability in many species. Missing values are assigned to *C. wellsi*, as this species lacks collines.

IX. Distance between calices of the same valley. This character also varied widely, has a range of 0.5 to 8 mm, and fourteen character states.

X. Corallite diameter. Corallite diameter was considered small if less than 6 mm and large if greater than 6 mm. Only *C. monile* had large corallites.

XI. Septal number. The number of septa had a range from 5 to 40, resulting in thirteen character states.

XII. Number of septa reaching columellae. This character was divided into two character states: <20 and >20. Only *C. crassa* had >20 septa reaching the columellae.

XIII. Colline height. This character has a range of 0.2 to 4 mm and seven character states. Again *C. wellsi*, due to its lack of collines, has missing values for this character.

XIV. Columella diameter. Only *C. monile* has a columella diameter greater than 1 mm.

XV. Wall texture. Wall texture is either perforate with synapticulothecal wall development or imperforate in *Coscinaraea.*

XVI. Taxonomic affinity. (see above discussion under *Symphyllia*).

RESULTS

I. Phylogeny

Symphyllia. Two trees were found (length = 290; consistency index {c.i.} = 0.45; retention index {r.i., Farris, 1989} = 0.58) for the Mussidae (Fig. 1). *Lobophyllia* is the sister group to *Symphyllia* in both trees (Fig. 1). All species of *Lobophjyllia* were chosen as the outgroup.

Phylogenetic analysis of *Symphyllia* resulted in six equally parsimonious trees (length = 315; c.i. = 0.60; r.i. = 0.70). Only two different topologies were found for the ingroup (Fig. 2). *Symphyllia valenciennesii* is the basal

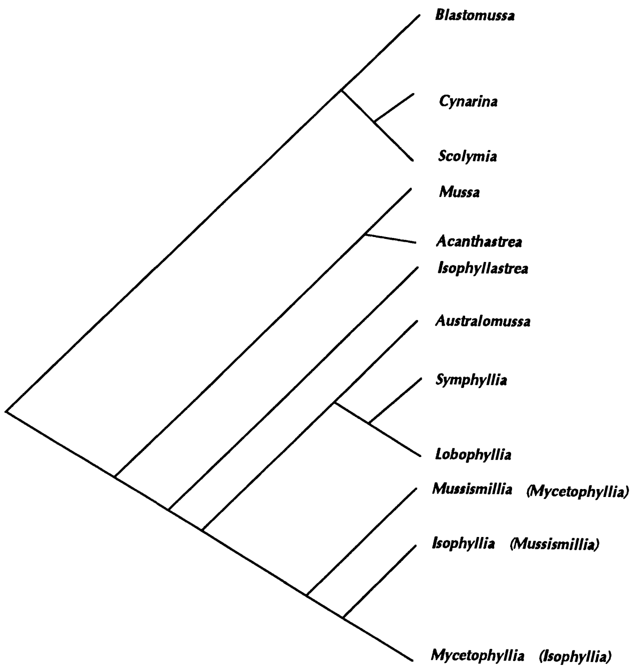

FIG. 1. Cladogram of the genera of the Mussidae (Ortmann, 1890). Two trees were obtained using Lundberg rooting; plesiomorphic states were assigned to the outgroup. The topology of the second tree is similar to the first except for the genera shown in parentheses alongside the lower part of the tree. In both trees, *Lobophyllia* (de Blainville, 1830) is more closely related to *Symphyllia* (milne Edwards & Haime, 1848) than either are to any other taxa. Characters and coding of their states, and HENNIG86 options used can be found in Appendix I.

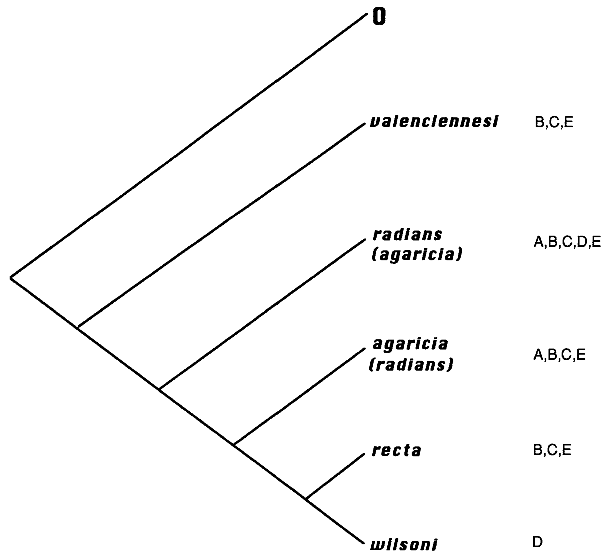

FIG. 2. Cladogram of the species of *Symphyllia* (Milne Edwards & Haime, 1848). Two different topologies for the ingroup were found; in the second tree, the position of *S. agaricia* (Milne Edwards & Haime, 1849) and *S. radians* (Milne Edwards & Haime, 1849) is reversed. Species of *Lobophyllia* (de Blainville, 1830) are the outgroup. *Symphyllia wilsoni* (Veron, 1985) and *S. recta* (Dana, 1846) are relatively derived with respect to other members of the clade. See text and Table 1 for explanation of biogeographic areas A, B, C, D and E. Characters and coding of their states, and HENNIG86 options used can be found in Appendix I.

taxon within the ingroup followed either by *S. radians* or *S. agaricia* and then *S. recta* and *S. wilsoni* (Fig. 2). It would appear that *S. wilsoni* and *S. recta* shared a common ancestor after the establishment of the rest of the species within the genus. These latter two species are considered relatively derived with respect to the other species within *Symphyllia* (Fig. 2). The relationships among the species of the outgroup, *Lobophyllia*, are not presented as they are determined only upon the basis of characters which were applicable to *Symphyllia*.

Coscinaraea. A single tree was found (length = 86; c.i. = 0.69; r.i. = 0.60) for the Siderastreidae (Fig. 3). *Psammocora* is the sister group to *Coscinaraea* and all species of *Psammocora* were chosen as the outgroup.

Phylogenetic analysis of *Coscinaraea* resulted in three equally parsimonious trees (length = 392; c.i. = 0.56; r.i. = 0.70). Only two different topologies were found for the ingroup (Fig. 4). Either *Coscinaraea wellsi* is the basal taxon or a branch uniting *C. exesa* and *C. columna* occupies the basal position. The four remaining taxa are fully resolved in both trees with *C. crassa* forming a sister group to the remaining resolved taxa *C. monile*, *C. marshae*, and *C. mcneilli* (Wells, 1962). Again, the relationships among the species of the outgroup are not shown because they were determined only on the basis of characters which were applicable to the ingroup.

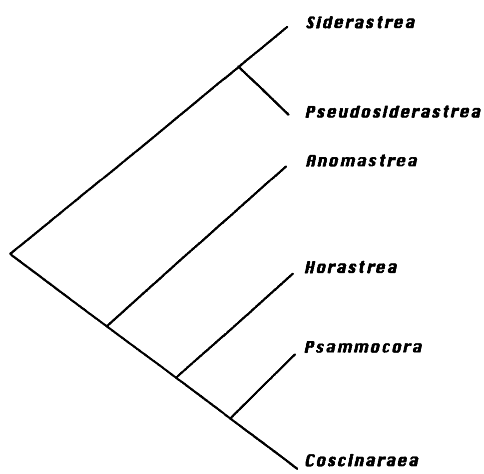

FIG. 3. Cladogram of the genera of the Siderastreidae (Vaughan & Wells, 1943). Tree obtained using Lundberg rooting; plesiomorphic states were assigned to the outgroup. *Coscinaraea* (Milne Edwards & Haime, 1848) is more closely related to *Psammocora* (Dana, 1846) than either are to any other taxa. Characters and coding of their states, and HENNIG86 options used can be found in Appendix I.

2. Endemism and character state evolution

Symphyllia wilsoni and *S. recta* are relatively derived with respect to the other species of *Symphyllia*. *Symphyllia wilsoni* also displays the highest degree of endemism in the genus (Fig. 2 and Table 1). Compared to the other species of *Coscinaraea*, *C. mcneilli*, and *C. marshae* are also rela-

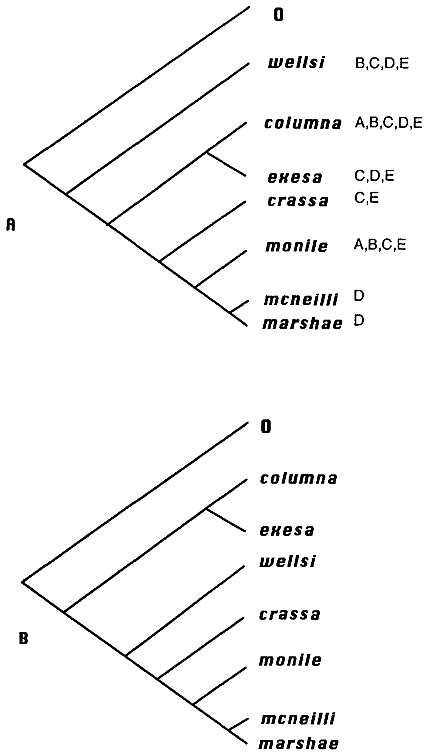

FIG. 4. Two equally parsimonious cladograms for species of *Coscinaraea* (Milne Edwards & Haime, 1848). Species of *Psammocora* (Dana, 1846) are the outgroup. *Coscinaraea marshae* (Wells, 1962), and *C. mcneilli* (Wells, 1962) are relatively derived with respect to the other members of the clade. See text and Table 1 for explanations of biogeographic areas A, B, C, D, and E. Characters and coding of their states, and HENNIG86 options used can be found in Appendix I.

tively derived and show the highest endemism (Fig. 4 and Table 1). (*C. columna* and *C. exesa*, however, also share a high number of derived character states and are more cosmopolitan in their distribution.) These two species have the most restricted ranges of any of the other species in the genus (Table 1). Thus, in both genera, the most derived taxa have the most restricted biogeographic distributions.

3. Biogeographic distributions

Western–Australia. Symphyllia and *Coscinaraea* both show clear intrageneric differences in latitudinal distribution along the west coast of Australia (Fig. 5 and Table 2). Of the five species of *Symphyllia*, only *S. wilsoni* occurs in the southwestern cool water and is mutually exclusive in distribution with the remaining four northwestern warm water species. Of the four species of *Coscinaraea* which occur in Western Australia, the southwestern cool water species *C. mcneilii* and *C. marshae*, are more closely related to each other than they are to the northwestern warm water species, *C. columna* and *C. exesa.* In both genera, taxa with relatively derived character states exist to the south of taxa with relatively primitive character states.

Red Sea and Indo-Pacific. Table 1 gives the Red Sea and Indo-Pacific distributions of the species from the two genera under study (Veron, in press). *Symphyllia wilsoni* is restricted to Western Australia, whilst the other four species of the genus have extremely cosmopolitan distributions, from the Red Sea to Vanuatu (Table 1) (Veron, in press). Note that *Symphyllia radians* is present in the cool southern waters of eastern Australia.

Coscinaraea columna, *C. exesa*, and *C. wellsi* have a widespread Indo-Pacific distribution including the cool

TABLE 1. Distribution of species of *Symphyllia* Milne Edwards & Haime, 1848) and *Coscinaraea* (Milne Edwards & Haime, 1848). Data from Veron (in press).

	Red Sea	East Africa	Kuwait	Aldabra	Maldives	Hong Kong	Malaysia	Vietnam	Thailand	Indonesia	NW Australia	Philippines	SW & SE Australia	Japan	PNG	Eastern Australia	Marshall Islands	Fiji	Tonga	Samoa	Vanuatu	Pitcairn Islands
Biogeographic area	A	B	B	B	B	C	C	C	C	C	C	C	D	E	E	E	E	E	E	E	E	E
S. agaricia	X	X					X	X	X	X	X	X		X	X	X				X	X	
S. radians	X	X					X	X	X	X	X	X	X	X	X	X		X			X	
S. recta		X			X		X	X	X	X	X			X	X	X	X			X	X	
S. valenciennesi				X			X		X	X	X	X		X	X	X			X		X	
S. wilsoni													X									
C. columna	X	X				X	X	X	X	X	X	X	X	X	X	X		X		X	X	X
C. crassa												X		X	X	X						
C. exesa								X		X	X		X	X	X	X		X			X	
C. marshae													X									
C. mcneilli													X									
C. monile	X		X				X		X					X								
C. wellsi		X						X	X	X		X		X	X	X	X					

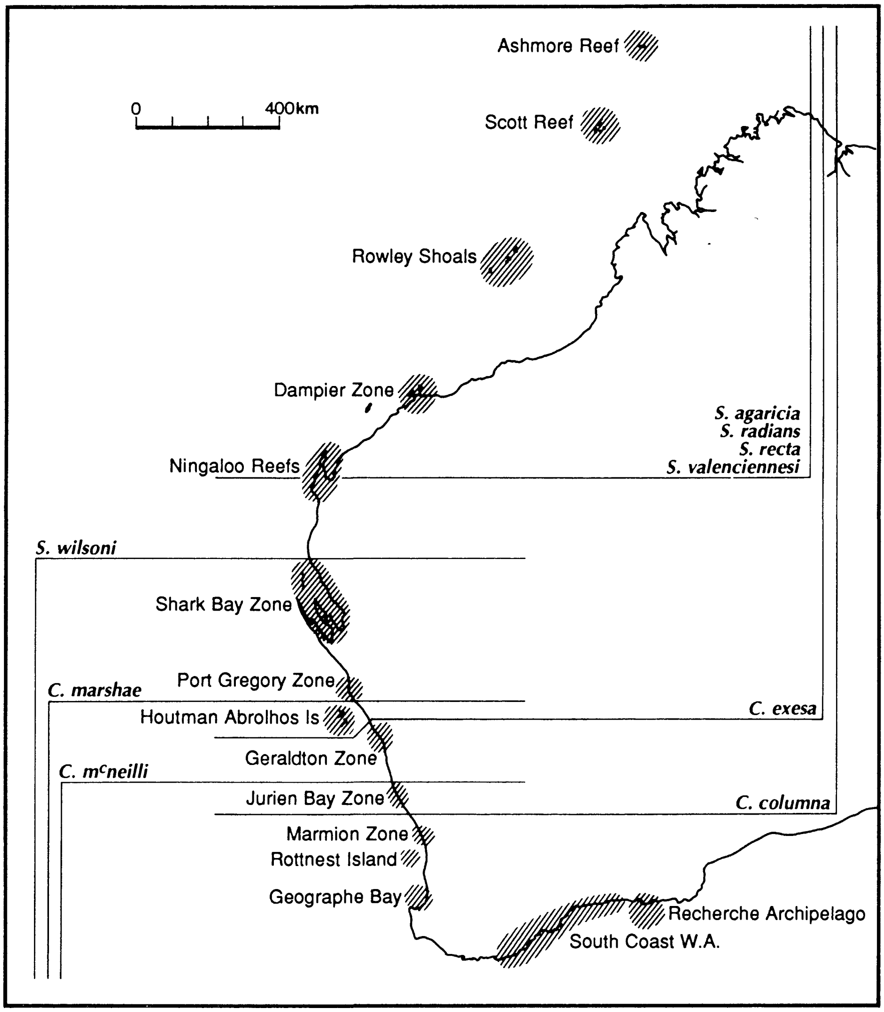

FIG. 5. Principal coral regions of Western Australia showing distribution of *Symphyllia* (Milne Edwards & Haime, 1848) and *Coscinaraea* (Milne Edwards & Haime, 1848). *Symphyllia wilsoni* (Veron, 1985) is found only at Shark Bay and south. All other species of *Symphyllia* are found at Ningaloo Reefs and north. With the exception of an occurrence at the Houtman Abrolhos Islands *C. marshae (Wells, 1962)* is found only from Rottnest Island south, and *C. mcneilli* (Wells, 1962) is found only from the Jurien Bay Zone south. *Coscinaraea columna* (Dana, 1846) and *C. exesa* (Dana, 1846) are found from the Houtman Abrolhos Islands north, with the exception of an occurrence of *C. columna* at the Jurien Bay Zone. Locality and species distribution information, and base map after Veron & Marsh (1988).

southern waters of eastern Australia. *Coscinaraea marshae*, as with *S. wilsoni*, is found only in the cool southern waters of Western Australia, and nowhere else in the world. *Coscinaraea mcneilli* is only found in the cool waters of southwestern and southeastern Australia. *Coscinaraea marshae* and *C. mcneilli* are in biogeographic contrast to *C. crassa* which occupies a more northern and eastern distribution of the Phillipines, Japan, PNG, GBR and the Marshall Islands. Lastly, *Coscinaraea monile* is found in all biogeographic areas except SW/SE Australia (Table 1).

On the basis of these distribution patterns five biogeographic areas are recognized (Table 1): A, the Red Sea; B, western to central Indian Ocean from the east African coast to the Ninetyeast Ridge; C, east Indian Ocean from the Ninetyeast Ridge to the Malay Archipelago and the Philippines; D, southwest (Shark Bay southeast to Reserche Archipelago) to southeast (Lord Howe and Solitary Islands and south) Australia; E, western to central Pacific Ocean (including E. Australia). These five areas are superimposed on the cladograms in Figs 2 and 4. Endemism occurs only in area D.

COMPONENT produced area cladograms under Assumptions 0 (Zandee & Roos, 1987), 1 and 2 (Nelson & Platnick, 1981). Because COMPONENT can only deal with fully resolved cladograms, both taxonomic cladograms generated in each genus were analysed. In *Symphyl-*

TABLE 2. Distribution of species of *Symphyllia* (Milne Edwards & Haime, 1848) and *Coscinaraea* (Milne Edwards & Haime, 1848) from Western Australia. Data from Veron & Marsh (1988).

	Ashmore Reef	Scott Reef	Rowley Shoals	Kimberly Coast	Dampier Zone	Ningaloo Reefs	Shark Bay Zone	Houtman Abrolhos Is.	Port Gregory Zone	Geraldton Zone	Jurien Bay Zone	Lancelin Zone	Rottnest I.	Marmion Zone	Geographe Bay	South Coast W.A.	Recherche Archipelago
S. agaricia	X	X	X		X	X											
S. radians	X					X											
S. recta	X	X	X	X	X												
S. valenciennesi	X	X	X		X												
S. wilsoni							X	X	X	X	X	X	X	X	X	X	
C. columna	X	X		X	X	X	X	X			X						
C. exesa			X		X	X		X									
C. marshae								X					X		X	X	X
C. mcneilli											X	X	X	X	X	X	X

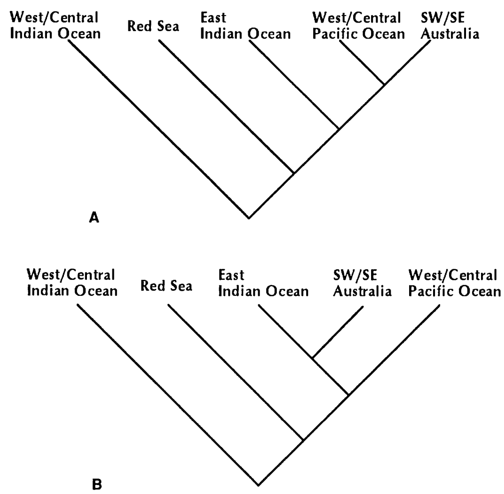

FIG. 6. Two five-area statements of relationships of biogeographic areas for Indo-Pacific reef corals derived from COMPONENT using the taxonomic cladograms presented in Figs 2 and 4. The area cladograms were produced by both taxonomic cladograms of *Symphyllia* (Milne Edwards & Haime, 1848) and one taxonomic cladogram of *Coscinaraea* (Milne Edwards & Haime, 1848) under Assumption 2. These area cladograms are considered as working hypotheses for Indo-Pacific reef coral biogeography.

lia, COMPONENT generated the same six area cladograms for each taxonomic cladogram under Assumption 0, the same four area cladograms for each taxonomic cladogram under Assumption 2, and all 105 possible area cladograms under Assumption 1. The number of items of error (the number of extra terms and components required to reconcile the original area cladogram with the reduced area cladogram (Page, 1989)) for all 105 trees is 30.

In *Coscinaraea*, COMPONENT generated the same area cladogram for each taxonomic cladogram under Assumption 0, and eleven area cladograms for each taxonomic cladogram under Assumption 2. Four area cladograms were common to both sets of eleven area cladograms; thus eighteen unique area cladograms were produced. All 105 possible area cladograms were produced under Assumption 1. The number of items of error for all 105 trees is 38.

No area cladograms were shared by the two taxa under Assumption 0. Under Assumption 2, two area cladograms were shared by *Symphyllia* and one of the *Coscinaraea* taxonomic cladograms (Fig. 4a). These two trees (Fig. 6a,b) are considered as working hypotheses for reef coral biogeography.

DISCUSSION

Comparison of the phylogenetic analyses with the distribution of species resulted in three patterns: (1) Indo-Pacific reef coral species ranges overlap predominantly in a west to east stepwise fashion with the closest biogeographic relationships occurring between adjacent areas; (2) Western Australia reef coral species show peripheral endemism and are distributed with respect to a North/South environmental gradient; and (3) species with relatively derived character states show a higher degree of endemism than species which show relatively primitive character states.

The first area cladogram used as a working hypothesis for reef coral biogeography (Fig. 6a) shows separation of a component A + C + D + E from area B (west to central Indian Ocean), then of a component C + D + E from area A (the Red Sea), then of a component D + E from area C (east Indian Ocean), then of area D (southwest to southeast Australia) from area E (western to central Pacific Ocean). The second area cladogram (Fig. 6b) is very similar to the first, except that the West Central Pacific Ocean separated from the East Indian Ocean and SW/SE Australia before SW/SE Australia separated from the east Indian Ocean. Overlap of species ranges occurs in mainly a west to east stepwise fashion, resulting in adjacent areas having the closest biogeographic relationships. A strikingly similar pattern is found in the Acroporidae (Wallace *et al.*, 1991), and congruence is noted with the geographical provinces outlined for the Fungiidae (Hoeksema, 1989).

In the scenario based on the area cladograms in Fig. 6, an ancestral taxon (or taxa) occupied a broad distribution from Africa through to the central Pacific. Vicariance events led to the breaking up of this distribution first along a line at the junction between the West/Central and East Indian Ocean, then between the East Indian Ocean and the West/Central Pacific Ocean at the Indonesian Arc. An additional vicariant event ensued between either the East Indian Ocean or West/Central Pacific Ocean and SW/SE Australia. The anomalous position of the Red Sea on the area cladogram is thought to represent a dispersal event as all the taxa in the Red Sea are found in the West/Central Indian Ocean. Speciation events tend to be either east or south of the vicariance line. As occurs in the Acroporidae (Wallace *et al.*, 1991) speciation events may or may not have been followed by migration to broaden the range of the taxa (corals have a wide ability to disperse during their life cycle (Jokiel, 1984, 1990; Fisk & Harriot, 1990; Richmond, 1987)), but with the exception of the Red Sea, neither migration nor extinction is needed to explain the biogeographical relationships.

The stepwise progression from west to east with adjacent biogeographic areas more closely related to each other than to areas further apart is consistent with past geologic events related to the submergence of the Ninetyeast Ridge in the Early Miocene, to the separation of the Indian and Pacific Oceans as a consequence of the great Mid-Miocene collision between Gondwanic Australia and Laurasian SE Asia, and to Quaternary sea level and temperature fluctuations associated with glacial intervals (Pandolfi, *in press*). Palaeocene or earlier ancestral taxa occupied a broad distribution in the Tethys Ocean from the present day Mediterranean Sea to the Pacific Ocean. The Ninetyeast Ridge in the central Indian Ocean (Kemp & Harris, 1975), emergent in the Eocene and Oligocene, became submerged and may have acted as a wide oceanic barrier between western and eastern Indian Ocean taxa whose populations had earlier used the Ninetyeast Ridge as a stepping stone for maintaining genetic continuity across the Indian Ocean. The great mid-Miocene collision between Gondwanic Australia and Laurasian SE Asia would have separated, either as a barrier or a strong filter, the east Indian Ocean fauna from the Pacific plate fauna (Audley-Charles, 1987; Pigram & Davies 1987). The separation of southwest and southeast Australia from either or both the East Indian Ocean and West/Central Pacific Ocean may have occurred in response to lower sea temperatures during Pleistocene glacial sea level minima. Such times were accompanied by an increase in upwelling, further depressing surface temperatures (Fleminger 1986) thus providing a thermal vicariant barrier. Springer & Williams (1990) believe that these lower sea levels with increased coastal upwelling and loss of marine habitats could have led to the extinction of continuously distributed Indo-Pacific marine populations and to the formation of widely separated Pacific Plate endemics.

Based on the congruence between the general area cladogram and the Cenozoic geologic history of the Indo-Pacific, an hypothesis of successive isolation provides an historical explanation of how and where Indo-Pacific reef coral species may have originated (Fig. 6). Species origination in reef corals was a response to geologic events that resulted in successive isolation of populations numerous times and places during the Cenozoic history of the Indo-Pacific (Pandolfi, *in press*). Individual speciation events may have been followed by dispersal to broaden the range of individual taxa. Thus, the presence of the Red Sea on the left side of the general area cladogram was probably due to dispersal of West/Central Indian Ocean taxa to the Red Sea when it opened to the Indian Ocean in the early Pliocene (Girdler & Styles 1974).

Both relatively derived taxa, *Symphyllia wilsoni* and *Coscinaraea marshae*, are endemic to the southern cool waters of the Western Australia coast. The vicariance event which segregated southeastern and southwestern Australia from the remaining Indo-Pacific could possibly be due to latitude-associated environmental variables. This environmental barrier would have divided the *Symphyllia* ancestral range somewhere between Shark Bay and Ningaloo Reefs and the *Coscinaraea* ancestral range somewhat further south between the Houtman Abrolohos Islands and the Jurien Bay Zone (Fig. 5, Table 2). If the speciation events which led to the formation of *S. wilsoni* and *C. marshae* occurred on the Western Australia coast, they may have resulted because new species were able to live at a latitude and/or climate where their congeneric species did not. Thus, environmental variables associated with latitudinal and/or Pleistocene sea level/temperatures change, including competition with macroalgae and/or lower temperatures (Johannes *et al*., 1983) may have played a role in the present Western Australia distributions of species of *Coscinaraea* and *Symphyllia*. Reid (1990) noted a similar association between more derived *Littorina* species with cooler habitats and also explained this in terms of latitude/climate induced vicariance. Valentine (1984) argued that speciation is likely when climate change alters species distributions and disrupts their ranges.

SW/SE Australia is peripheral to the high diversity centres for reef corals. It seems clear that this area, with two endemic species that possess relatively derived character states with respect to other congenerics, is an area where new species may have originated. Such peripheral endemicity indicates that the evolutionary history of reef corals is not solely dependent on an Indo- West Pacific evolutionary centre. McCoy & Heck (1983) noted that centre-of-origin biogeographers believe either (1) evolutionary centres are the site of derived faunas and more primitive taxa occupy the periphery of the range (Briggs, 1981) or (2) centres have the most primitive taxa with more derived taxa occurring at the periphery due to allopatric speciation (Brundin, 1981). The centre-of-origin hypothesis espoused for Indo-Pacific reef corals by Stehli & Wells (1971) predicted that the youngest and therefore most derived taxa should be located in the warm waters of the western Pacific Ocean where generic diversity is greatest. This is clearly not the case for *Symphyllia* and *Coscinaraea* because the endemic species which possess the most derived character states exist toward the periphery of Indo-Pacific reef coral distributions. In addition, peripheral endemicity, as occurs in *C. marshae* and *S. wilsoni*, might be more common than previously realized (e.g. Potts, 1985).

Because there are other geographical origins for Indo-West Pacific coral species, I suggest multiple geographical origins due to successive isolation of populations in response to the geotectonic and climatic history of the Indo-Pacific as a more appropriate hypothesis than centres of origin for characterizing the evolutionary history of coral reef scleractinians. Thus, models of reef coral speciation need not depend on the taxonomic richness of corals from the so-called Indo- West-Pacific centre of high diversity (Stehli & Wells, 1971). The warm seas of the western Indo-Pacific ocean may represent an optimal reef coral habitat and may have nothing to do with the mechanisms and biogeographic history of reef coral speciation. Alternatively, Jokiel (1990) argued that the migration of reef corals on pumice may indicate that the Indo-West Pacific is a centre of species accumulation rather than it being a centre of species origin. The present interpretation of successive isolation for speciation in reef corals casts doubt on extracting speciation mechanisms solely from modern diversity patterns in reef corals and highlights the utility of species level phylogenetic/biogeographic data, especially where congenerics show varying degrees of endemism.

In both *Coscinaraea* and *Symphyllia* species possessing the most derived character states have the most restricted distributions; thus, in the taxa under study, endemicity appears to correlate with recency of ancestry. This confirms a relationship previously established in the Acroporidae (Wallace *et al*., 1991), but not in the Fungiidae (Hoeksema, 1989). Endemic species exist within the Scleractinia in areas distinct from the high centres of tropical reef diversity. In addition such species may over time increase their ranges and coral species may have increased their ranges toward ecologically favourable environments. The hypothesis that reef coral species originated in a specific (and perhaps, limited) geographic area and subsequently increased their geographic range as a function of time has recently been raised in a general way by McManus (1985) and is discussed in Potts (1985). This hypothesis sets no restriction on the place where new species originate and regards their increased range throughout their duration not as a 'simple migration across environmental stress barriers which may require considerable adaptation' (Stehli & Wells, 1971, p. 125), but as a possible result of a variety of later processes acting alone or in combination, including sea level changes (Potts, 1984, 1985; Rosen, 1984), vicariance events (Rosen, 1984), or migration (Veron, 1985a).

The biogeographic patterns presented here are broad scale and intended to stimulate biogeographic questions beyond consideration of modern diversity maps. The results of the present study indicate that phylogenetic relationships provide information about distribution patterns in reef corals, that these distribution patterns are congruent with the geologic history of the Indo-Pacific, and that species level peripheral endemicity exists in the Scleractinia. By focusing on these issues we can come to a more global appreciation of how and where reef corals originated and subsequently came to be distributed the way they are.

CONCLUSIONS

1. From area cladograms derived from phylogenetic analysis of *Coscinaraea* and *Symphyllia,* Indo-Pacific species ranges overlap predominantly in a stepwise fashion from west to east. Areas adjacent to one another are biogeographically more closely allied than non-adjacent areas. In a scenario consistent with the area cladogram, vicariance events might have been an important control over initial distribution patterns in scleractinian corals. Support for vicariance lies in the congruence between major geologic events in the Indo-Pacific and the biogeographic area relationships obtained in the cladistic biogeographic analysis. Primitive widespread species however, may have distributions which reflect various processes, including migration, occurring over a long interval of time.

2. Taxa of both *Coscinaraea* and *Symphyllia* which display relatively derived character states have a higher degree of endemicity than those displaying relatively primitive ones. These derived species appear to have originated at or near the western Australian continental shelf, far from the reef coral centres of diversity. The position of their distributions on the area cladograms suggest they originated as a result of a thermal vicariant event caused by Quaternary sea level fluctuations.

3. The demonstration of peripheral endemicity of relatively derived reef coral species in conjunction with the congruence between cladistic biogeographic patterns and Indo-Pacific geologic history corroborate a successive isolation hypothesis (as opposed to evolutionary centres) for the evolutionary history of Indo-Pacific reef corals. Reef corals appear to have originated outside of the so-called Indo-Pacific centre-of-origin. The hypothesis put forward by Ladd (1960) 30 years ago of mid-Pacific island origins for molluscs is mirrored for reef corals in that both taxa appear to have origins outside of the Indo-West Pacific. Future studies should consider species level relationships and distributions as opposed to coral diversity maps in interpreting reef coral biogeography.

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APPENDIX I

A. Mussidae

Characters:

(I) 0-3*. Growth form: flattened; domed; cylindrical; branching;
(II) 4-8*. Corallite arrangement: solitary; phaceloid; cerioid to subplocoid; meandroid; flabello-meandroid;
(III) 9-10*. Septo-costae height: LE 4 mm; > 4 mm;
(IV) 11-13*. Corallite Diameter: 0-25 mm; 25-60 mm; > 60 mm;
(V) 14. Columellae Diameter: small (0.5 - 5.5 mm); large (> 5.5 mm);
(VI) 15-17*. Valley Thickness: < 1 cm; 1-2 cm; >2 cm;
(VII) 18-30#. Septal Number/cm: range from 4.5 - 16
(VIII) 31-34*. Septal Dentation Shape: blunt; rounded; lobate; acute spiny;
(IX) 35. Epitheca: absent; present;
(X) 36-37*. Wall Thickness: < 0.1 mm; > 0.1 mm;
(XI) 38-39*. Permanent number of stomodeal centres: mono-centric; polycentric;

Data:

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Outgroup	1000	10000	10	100	0	100	0000000000000	0000	0	10	10
Cynarina	0010	10000	01	010	1	???	1000000000000	0010	1	10	10
Blastomussa	1000	01000	10	100	0	???	0001000000000	0100	1	10	10
Lobophyllia	1100	01001	11	010	1	111	0111111110000	0011	0	11	10
Scolymia	1000	10100	01	011	1	100	0111111000000	1000	1	10	11
Acanthastrea	1100	00100	10	110	0	???	0111111100000	0001	0	01	10
Symphyllia	1100	00010	11	010	0	010	0000011111000	0001	0	10	01
Australomussa	1100	00100	01	001	0	110	0000000000010	1000	0	01	01
Mussismillia	0001	01000	10	100	0	???	0000000011000	0001	1	??	01
Isophyllastrea	0100	00100	??	100	0	???	0000010000000	0001	0	01	11
Isophyllia	1100	00100	??	100	0	010	0001111111111	0001	1	01	01
Mussa	0100	01000	10	010	0	001	0000010000000	0001	0	01	10
Mycetophyllia	1100	00100	10	100	?	010	0000011100000	0001	1	01	01

HENNIG86 Options:

```
ccode /1 18.30;
ccode /2.4 4.8;
ccode /3 0.3 31.34;
ccode /4 11.13 15.17;
ccode /6 9.10 36.39;
ccode /12 14 35;
mhennig;
ie;
```

B. *Symphyllia*

Characters:

(I) 0-1*. Valley shape: straight; sinuous;
(II) 2-3*. Valley arrangement: radiating; irregular;
(III) 4. Valley width: < 15 mm; 15-25 mm; > 25 mm;
(IV) 5-8*. Septal orders: none distinct; two; three; four;
(V) 9-14#. Septa/cm: range from 6-13;
(VI)15-23#. Number of teeth on 1st order septa: range from 2-10;
(VII) 24-33#. Septal exsertness: range from 0.5-12 mm;
(VII) 34. Colline thickness: < 5 mm; > 5 mm;
(IX) 35-36*. Columellae: two rows; single;
(X) 37-40*. Growth form: flattened; hemispherical; subfoliaceous; phaceloid;
(XI) 41-42*. Columellae linkage: lamellar; trabecular;
(XII) 43-44*. Columellae texture: compact; spongy;
(XIII) 45-54#. Valley length: range from 7-55 mm;
(XIV) 55. Taxonomic affinity: *Lobophyllia; Symphyllia;*

Data:

I II III IV V VI VII VIII X XI XIII XIV

IX XII

L. hemprichii
11 11 1 1101 111100 111111111 0111111110 ? 01 1100 11 11 1111111110 0
L. corymbosa
?? ?? ? 0101 011000 000000100 1111111100 ? 01 0100 01 11 0111000000 0
L. pachysepta
?? ?? ? 0001 100000 011111100 0000011100 ? 01 0001 01 01 0000011000 0
L. hataii
11 11 2 0010 110000 001111110 1111111000 1 11 0100 10 01 0001111111 0
L. diminuta
?? ?? ? 1000 ?????? 001111100 1111111000 ? 01 0001 ?? 11 ?????????? 0
S. agaricia
11 11 2 1000 001110 001111110 1111100000 0 10 1100 10 11 ?????????? 1
S. radians
11 11 1 0001 001110 011110000 1111100000 1 01 1110 10 01 0011111100 1
S. recta
01 01 0 0110 000110 000001110 0001100000 0 01 0100 11 01 0111110000 1
S. valenciennesii
10 10 2 1000 110000 000100000 0000001111 1 01 1100 10 11 0111100000 1
S. wilsoni
11 01 0 1000 000111 000000100 0001000000 0 01 1100 11 11 ?????????? 1

HENNIG86 Options:

outgroup = 0.4
ccode /1 15.23 24.33 45.54;
ccode /2 9.14;
ccode /3 5.8 37.40;
ccode /5 0.3 35.36 41.44
ccode /10 4 34;
ccode /50 55;
ie-;
bb;

C. Siderastreidae

Characters:

(I) 0-3*. Growth form: laminar; encrusting; massive; columnar;
(II) 4. Corallite arrangement: cerioid; sub-meandroid to cerioid; sub-meandroid to plocoid;
(III) 5. Septal arrangement: not fused; fused;
(IV) 6. Wall composition: septo-thecate; synapticulothecate;
(V) 7-8*. Budding: extra-tentacular; intra-tentacular;
(VI) 9-10*. Columellae: simple; compound;
(VII) 11. Valleys: absent; present;
(VIII) 12. Septal granulations: absent; present;
(IX) 13. Petaloid septa: absent; present;
(X) 14. Colony size; small; large;
(XI) 15. Pronounced synapticular rings: absent; present;
(XII) 16. Wall thickness: thin; thick;
(XIII) 17. Corallite size: <3 mm; 3-5 mm; > 5 mm;

Data:

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
Outgroup	1000	0	0	1	01	01	0	0	0	0	0	0	0
Anomastrea	0010	1	1	1	01	01	1	0	0	1	0	0	1
Siderastrea	0110	0	0	1	10	10	1	0	0	1	1	0	1
Psammocora	1111	1	1	1	11	11	1	1	1	1	0	1	0
Pseudosiderastrea	0110	0	1	1	10	10	0	1	0	0	1	0	1
Coscinaraea	1111	1	1	1	11	11	1	1	1	1	0	1	1
Horastrea	0010	2	1	0	01	01	1	0	0	1	0	1	2

HENNIG86 Options:

ccode /1 0.3;
ccode /2 7.10;
ccode /4 4.6 11.17;
ccode -4;
mhennig;
ie;

D. *Coscinaraea*

Characters:

(I) 0-3*. Growth form: columnar; explanate; branching; massive;
(II) 4. Corallite arrangement: thamnasteroid; non-thamnasteroid;
(III) 5-6. Budding: circumoral; marginal;
(IV) 7. Superficial calices: present; absent;
(V) 8.' Corallite growth: single; in series; singly and in series;
(VI) 9. Concentric corallite rows: absent; present;
(VII) 10. Collines: absent; present;
(VIII) 11-24#. Colline width: range from 0.5-7 mm;
(IX) 25-38#. Distance between calices (same valley): range from 0.5-8 mm;
(X) 39. Corallite diameter: small (< 6 mm); large (> 6 mm);
(XI) 40-52#. Septal number: range from 5-40;
(XII) 53. Septa reaching columellae: < 20; > 20;
(XIII) 54-60#. Colline height: range from 0.2-4 mm;
(XIV) 61. Columellae diameter: < 1 mm; > 1 mm;
(XV) 62. Wall texture: perforate (synapticulothecal); imperforate;
(XVI) 63. Taxonomic affinity: *Coscinaraea; Psammocora;*

Data:
I II III IV V VI VII VIII IX X XI XII XIII
XIV XV XVI
C. columna
1110 1 01 0 2 0 1 00011111111110 00000010000000 0 0000000001111 0 0000100
0 0 0
C. crassa
0100 0 11 ? 1 1 1 00000000000001 00000000001110 0 0000111111000 1 0011100
0 0 0
C. exesa
1000 1 01 0 2 0 1 00000100000000 00000011100000 0 0000011000000 0 0011100
0 0 0
C. marshae
0100 0 10 1 1 1 1 00000111110000 00000000000111 0 0000000000010 0 0000001
0 1 0
C. mcneilli
0100 0 10 0 1 1 1 00000111111100 00000000111110 0 0001111111111 0 0011110
0 1 0
C. wellsi
0100 0 01 0 0 0 0 ?????????????? 00000000000100 0 0011100000000 0 ???????
0 0 0
C. monile
0101 0 10 0 1 1 1 00011100000000 00000000011110 1 0001110000000 0 0011110
1 0 0
P. contigua
0010 0 ?? 0 1 0 1 01111111000000 11111110000000 0 1111111110000 0 0100000
0 0 1

I II III IV V VI VII VIII IX X XI XII XIII
XIV XV XVI

P. nierstraszi
0001 0 ?? 1 0 0 1 00011100000000 00001110000000 0 0001111000000 0 0011100
0 0 1
P. superficialis
0100 0 ?? 0 2 0 1 10000000000000 10000000000000 0 0110000000000 0 0010000
0 0 1
P. explanulata
0100 0 ?? 0 0 0 0 ?????????????? 00000011111000 0 0001100000000 0 ???????
0 0 1
P. digitata
1100 0 ?? 0 0 0 0 ?????????????? 00011111000000 0 0111000000000 0 ???????
0 0 1
P. haimeana
0100 0 ?? 1 0 0 1 01110000000000 ?????????????? 0 0000001000000 0 0011100
0 0 1
P. profundacella
0101 0 ?? 1 2 0 1 00110000000000 00011110000000 0 0001111000000 0 1110000
0 0 1
P. obtusangula
0010 0 ?? 0 0 0 0 ?????????????? 00000110000000 0 0110000000000 0 ???????
0 0 1
P. vaughani
0101 0 ?? 1 2 0 1 01110000000000 00111110000000 0 0011100000000 ? 0010000
0 0 1

HENNIG86 Options:

ccode /1 11.24 25.38 40.52;
ccode /2 54.60;
ccode /3 0.3
ccode /6 5.6;
ccode /12 4 7.10 39 53 61.62;
ccode /24 63;
mhennig;
ie;

*character states treated as nominal characters (0: absent; 1: present)
range coded character