Indo-Pacific Coral Biogeography:
a Case Study from the *Acropora selago* Group

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Abstract

We develop species-level biogeographic hypotheses for *Acropora*, the largest extant coral genus and the dominant scleractinian coral of Indo-Pacific reefs, based on morphometric and phylogenetic analyses of the *Acropora selago* group. Fourteen morphometric characters differentiated species from this group with an accuracy of 95%. When the Tukey test was administered, 11 of these characters displayed non-overlapping subsets. The most resolved phylogenetic tree resulted from an analysis based on both morphometric and qualitative characters. Cladistic–biogeographic analysis using this tree and areas derived from species-distribution patterns showed that species with the greatest degree of endemism within the *A. selago* group possess the most derived character states, while the most primitive species (*A. yongei*) is the most widespread.

Within the range of the group, four areas are recognised: (1) the Red Sea, (2) western to central Indian Ocean, (3) eastern Indian Ocean and (4) western to central Pacific Ocean. Species ranges overlap in a stepwise fashion from west to east. Areas adjacent to one another are biogeographically more closely related than non-adjacent areas. Whilst we offer a scenario for the history of distribution patterns of the *A. selago* group, we propose that biogeographical hypotheses based on *Acropora* be tested using a number of different species-groups. Similar distributional ranges for other *Acropora* species-groups, as well as separate distributional ranges for further groups, suggest that *Acropora* will provide an appropriate taxon to examine the biogeography of the tropical marine realm.

Introduction

Reef building scleractinian corals are distributed throughout the tropical and subtropical regions of the world. Distribution patterns are usually expressed in terms of numbers of genera or subgeneric groups present in different regions. The most obvious feature of these patterns is a radial decrease in numbers from a high in the Indo-West Pacific, with smaller centres in the West Indian Ocean and Caribbean (e.g. see Stehli and Wells 1971). Rosen (1988) summarises 13 hypotheses regarding the origins of coral distribution patterns. We note among these the papers of McCoy and Heck (1976, 1983), who attempt to break the run of untestable hypotheses about coral distributions. Hoeksema (1989) reconsiders these hypotheses with species of Fungiidae and concludes that patterns may be explained by a combination of dispersal, vicariance and refugiality. Common to these works is a conclusion that biogeographic analysis will be better facilitated when more species-level data are available. Towards this end,

we are embarking upon a species-level study of the phylogeny and distribution of the coral genus *Acropora*. This genus is distinguished from all other coral genera by its possession of an axial corallite. Because this feature is shared by all of its species, and by no other scleractinian genera, we consider *Acropora* to be monophyletic. *Acropora* is the largest extant coral genus (Wells 1987), occurs in all three oceans (Fig. 1) and is the most obvious component of most Indo-Pacific reefs. Despite this, it has often been omitted from taxonomic revisions, or summarised in non-taxonomic terms in distributional studies. It has always presented problems of identification, because of bewildering within- and between-species variability combined with absence of some skeletal elements used traditionally in coral taxonomy (Wells 1956; Wallace and Dallwitz 1981).
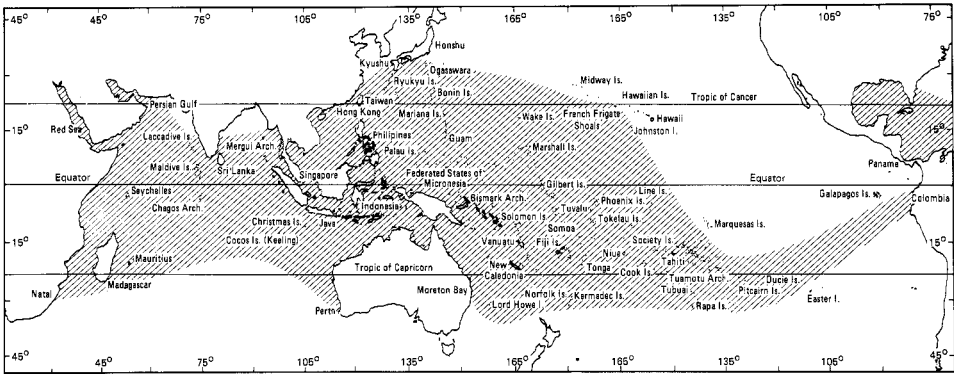

Fig. 1. Distribution of *Acropora* worldwide.

Several factors have contributed to making *Acropora* more accessible to phylogenetic and biogeographic study in recent years. Firstly, the genus has been revised twice (Wallace 1978; Veron and Wallace 1984), species limits being interpreted by observations of variability in the field as well as by microscopic characters. Although Veron and Wallace (1984) presented no phylogenetic analysis, they identified 13 species-groups in which species were thought to be more closely related than species from different groups. Secondly, the mode of reproduction and a mass-spawning phenomenon have been discovered and investigated (e.g. Bothwell 1981; Harrison *et al.* 1984; Wallace 1985; Harrison and Wallace 1990), providing further sources of phylogenetic characters. In particular the sperm has provided ultrastructural characters and nucleotide sequences that vary between species (Harrison 1985, 1988; McMillan and Miller 1988, 1989, 1990).

We report here an investigation of phylogenetic relationships and biogeography of the *Acropora selago* group of Veron and Wallace (1984). The phylogenetic analysis was based on a series of morphometric characters measured from field populations, providing morphological characters independent from those used by Veron and Wallace (1984) to separate *Acropora* species. The morphometric characters, along with some qualitative characters of the *A. selago* group, are used to present the phylogeny.

The objective of the biogeographic study was to develop hypotheses about the relationships amongst areas within the known distribution of the *Acropora selago* group. Our future aim is to test the biogeographic hypotheses generated from this study with a data set drawn from a larger set of *Acropora* species groups.

Methods

Samples comprised 10 colonies each of five species of the *Acropora selago* group (*A. selago, A. tenuis, A. yongei, A donei* and *A. dendrum*) and an outgroup species, *A. millepora*. These colonies were collected from a single reef (Britomart Reef on the Great Barrier Reef) to minimise interpopulation variability. For the two rarest species, *A. donei* and *A. dendrum*, some specimens were obtained from nearby reefs. We did not consider this to present a major problem, since populations of *Acropora* are thought to recruit predominantly externally: fertilisation is external and a precompetency time of 4–7 days is the norm (Harrison and Wallace 1990). Thus, these coral populations may be continuous over scales larger than a single reef.

A further species, *A. striata*, is regarded by CCW as belonging to the *A. selago* group. As this species does not occur on the Great Barrier Reef, it was not included in the morphometric and phylogenetic analyses, but its distribution was plotted for comparison with the other *A. selago* group-species.

In the process of examining specimens for this study, a taxonomic decision had to be made for *Acropora yongei*. Wallace (1978) included this species in *A. haimei*, an apparently broadly distributed species. This decision was revised by Veron and Wallace (1984) who described *A. yongei* as a new species with a known distribution of only the Great Barrier Reef and the Philippines. Subsequent examination of specimens collected by Y. Loya in the Red Sea, as well as Sheppard's interpretation (1987) indicate that they are probably the same species throughout a range extending from the Red Sea and W. Indian Ocean to Johnson Atoll in the Central Pacific. Thus, the two species are herein combined as *A. yongei*, a name which may prove to be a junior synonym of *A. haimei*.

Morphometric Analyses

Fourteen morphological characters were measured to determine whether species that were previously described on the basis of qualitative variation could be differentiated by quantitative morphometrics. Nine describe the branching of the coral ($n = 20$ per colony). These were length of the first order branch (*sensu* Cheetham *et al*. 1980), length of the second order branch, top, middle and bottom diameter of the first-order branch, middle diameter of the second-order branch, the number of radial corallites per mm of first-order branch, the angle the first-order branch makes with its parent branch, and the average distance from the axial corallite to its five nearest neighbours. Five characters were measured from the axial corallites ($n = 40$ per colony). These were the inside and outside diameters of the axial corallites, the length of axial septa, the axial corallite wall thickness and the exertness of the axial corallite. In the analyses presented here, only colony means for each character were used. Thus in analyses of all species, $n = 60$, and in analyses performed only on the *A. selago* group, $n = 50$. Data on the radial corallites are currently being gathered but are not included in the present study.

Two discriminant function analyses (DFA) were performed on two data sets, 'ingroup plus outgroup' and 'ingroup only'. The first analysis, a canonical DFA, was used to investigate species separation and gave Mahalanobis distances (Mahalanobis 1930) between species. Group centroids representing the class means on each canonical variable were plotted for each species for the first two canonical variates.

Because the species seemed to be well separated in the canonical DFA, a second 'classification' DFA was done on the first data set to determine whether the suite of morphometric characters selected for measurement was useful in classifying (in the sense of diagnosing) species of the *A. selago* group and *A. millepora*. Thus we were interested in how our pre-assigned species were classified on the basis of the new morphometric characters. The morphometric analyses were conducted using the SAS software package (SAS 1989).

Phylogenetic Analyses

To investigate whether the measured quantitative characters were sufficiently different among taxa to be useful as phylogenetic characters, we conducted a multivariate analysis of variance (MANOVA) and a Tukey multiple comparisons test on the entire 60 species' means. Quantitative characters were coded using a modification of the Tukey test as suggested in Farris (1990). Each character was weighted equally, regardless of range (ie. number of character states) (Farris 1990). As an outgroup we used *A. millepora*, which occurs in one of the two species-groups placed by Veron and Wallace (1984) closest to the *A. selago* group.

We present phylogenetic results from a data matrix of quantitative character states obtained from the Tukey multiple comparison procedure, and qualitative characters obtained from Veron and Wallace (1984). The phylogenetic analyses used Hennig86 (Farris 1988). Three analyses were made, one using the quantitative data only (characters 0 through 10, Appendix 1), one using the qualitative data only (characters 11 through 21, Appendix 1), and one using a combined data set. The ie option in Hennig86 was used. In the case of the quantitative characters, the nelsen option was used to build a consensus tree. Multistate characters (characters 17, 20 and 21, see Appendix 1) were left unordered (non-additive).

Biogeographic Analyses

Distribution patterns of the *A. selago* group and of *A. millepora* were compiled by interpreting presence/absence data in distributional papers (Hoffmeister 1925; Wells 1954; Rosen 1971, 1979; Jones *et al*. 1972; Pillai *et al*. 1973; Pillai and Scheer 1976; Pillai 1977; Faure 1982; Randall 1983; Scheer and Pillai 1983; Hamilton and Brakel 1984; Sheppard 1985, 1987; Sheppard and Sheppard 1985; Latypov 1986; Maragos and Jokiel 1986; Sheppard and Salm 1988; Veron 1988, 1990*a*, 1990*b*; Veron and Marsh 1988; Best *et al*. 1989; Veron and Hodgson 1989), as well as from specimens lodged in the Museum of Tropical

Queensland, unpublished uncollected site records from Lombok, Indonesia, 1989 by CCW, and records in an unpublished manuscript by the late Jan Verwey on corals collected from the Bay of Batavia (now Jakarta). Taxonomic agreement between species cited in the literature and the study species was interpreted in terms of present and past usage and synonymies. When the interpretation was doubtful, the record was registered by a question mark on the distribution map. The compilation represents a summary of records available to date and is part of an ongoing study to which many further records are to be added before distributional maps can be said to be complete.

To derive an hypothesis of biogeographic area relationships we produced an area cladogram based on the distribution patterns and our phylogenetic analysis for the *A. selago* group. This area cladogram was analysed under Assumptions 0 (Zandee and Roos 1987), 1 and 2 (Nelson and Platnick 1981) using COMPONENT (Release 1·5, Page 1989) to obtain reduced area cladograms.
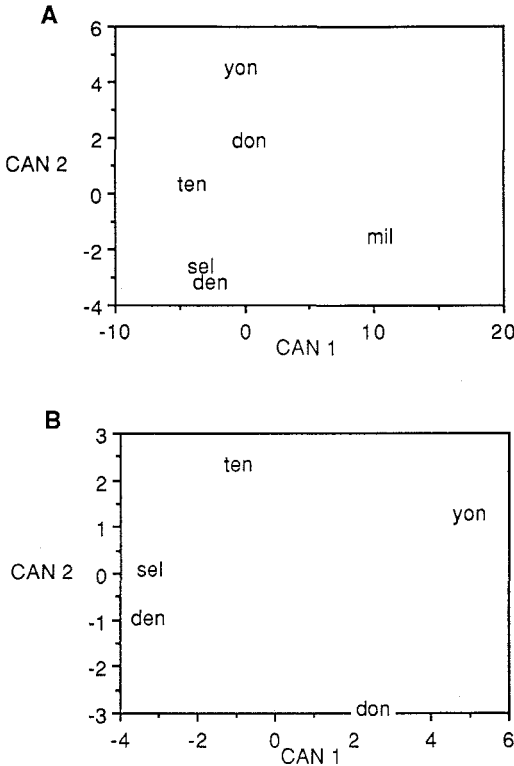

Fig. 2. (*A*) Plot of the group centroids of the discriminant function analysis for all species of the *A. selago* group and for *A. millepora*, the outgroup. *Acropora millepora* plots well away from the other species, especially along canonical variate 1. *Acropora selago* and *A. dendrum* plot very close together. (*B*) Plot for the group centroids for only species of the *A. selago* group. The ingroup species are more separated in the absence of the outgroup. The *A. selago/A. dendrum* pair is still apparent, with the other species plotting well away from each other. ten, *A. tenuis*; sel, *A. selago*; yon, *A. yongei*; den, *A. dendrum*; mil, *A. millepora*; don, *A. donei*. (Note variations in scale.)

Results

Morphometrics

In the first canonical DFA in which both the ingroup and the outgroup were included, the first canonical variate explained 67%, the first two canonical variates 88%, and the first three canonical variates 94%, of the total sample variance. In a plot of the group centroids of all species for canonical variates 1 and 2 (Fig. 2*a*), *Acropora millepora*, the outgroup, plots well away from the ingroup along canonical variate 1. *Acropora selago* and *A. dendrum* plot close to one another. Mahalanobis distances were also least between these two species and greatest between *A. millepora* and the ingroup species. When the outgroup *A. millepora* is excluded from the analysis greater separation occurs among the ingroup species (Fig. 2*b*) than occurs when *A. millepora* is included in the analysis (Fig. 2*a*). *Acropora selago* and *A. dendrum* still plot closely, and their Mahalanobis distances are the shortest of any between species. The other three species plot well away from each other and from the *A. selago/A. dendrum* pair.

Out of 60 possible misclassifications, the classificatory DFA only misclassified three colonies. Two *A. selago* colonies were misclassified as *A. dendrum* and one *A. dendrum* colony was misclassified as *A. selago*. This represents a correct classification rate of 95%.

Phylogenetic Analysis

The MANOVA on the entire 60 species means showed a significant species effect ($P <$ 0·0001 using Wilk's Criterion) and significant differences in population means ($P < 0·0001$) for all but one variable among the six species. Only the length of the second-order branch was not signficantly different among species. Thus 13 of the 14 morphometric characters were subsequently analysed to determine character states. When we used the Tukey test on these 13 characters, only six contained wholly non-overlapping homogenous subsets. A further five characters, however, showed little enough overlap to be useful as characters with one, two or three of the species scored as unknown (i.e. missing data).
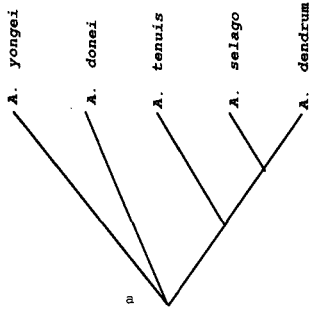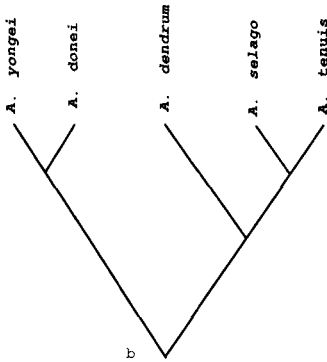

Fig. 3. (*a*) Phylogenetic analysis using only quantitative characters. (*b*) Phylogenetic analysis using only qualitative characters. See Appendix 1 for characters and data matrix.

In the first phylogenetic analysis using only the quantitative data, two trees were obtained with a tree length of 23 and consistency index of 0·91. Fig. 3*a* shows the consensus tree, which contains a trichotomy between *A. yongei*, *A. donei* and a resolved branch comprising *A. tenuis* as a sister-group to the sister-taxa *A. selago* and *A. dendrum*.

In the second analysis using only the qualitative characters, one tree was obtained with a length of 14 and consistency index of 1·00 (Fig. 3*b*). *Acropora dendrum* is here the sister-taxon to the group *A. tenuis* and *A. selago*, and *A. yongei* and *A. donei* are resolved as sister-species.

Fig. 4 shows the tree obtained from the combined analysis. *Acropora tenuis, A. selago*, and *A. dendrum* form a clade as in the cladogram based on the analysis using morphometric data (Fig. 3*a*), and the *A. yongei/A. donei* branch is resolved as in the analysis using only the qualitative characters (Fig. 3*b*). The tree length for the combined analysis is 38 and the consistency index is 0·92.

Biogeographic Analysis

All taxa of the *Acropora selago* group occur in the western and central Pacific Ocean (Fig. 5). *Acropora dendrum* occurs only in this region, while *A. selago* and *A. donei* occur in this region and the eastern Indian Ocean. *Acropora tenuis* and *A. yongei* occur in these regions and also the central to western Indian Ocean. *Acropora yongei*, the most widespread species, also occurs in the Red Sea.

On the basis of these distribution patterns we recognise four geographic areas (Fig. 6): (*a*) The Red Sea, (*b*) western to central Indian Ocean, (*c*) eastern Indian Ocean and (*d*) western to central Pacific Ocean.

The areas occupied by the species are displayed directly above the names of the terminal taxa in the cladogram in Fig. 4. COMPONENT gave reduced area cladograms under Assumptions 0 (Zandee and Roos 1987), 1 and 2 (Nelson and Platnick 1981) (Fig. 7). Assumption 1 generated 15 trees from the four areas: i.e. all possible trees for four areas were found. Assumption 0 gave just one tree (Fig. 7*a*) whereas Assumption 2 gave two trees (Fig. 7*a*, *b*).

Discussion

The discriminant function analyses show that morphometric characters analysed are useful in differentiating species within the *A. selago* group. Whilst *A. selago* and *A. dendrum* are phenetically similar (Fig. 2), colonies were only misclassified in very low numbers. None of the other four species was misclassified. Thus the qualitative species evaluations previously made (Veron and Wallace 1984) are corroborated by quantitative morphometric analysis and the present morphometric characters appear to represent taxonomic characters in so far as they differentiate among species.
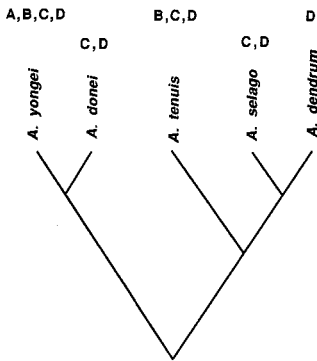

Fig. 4. Phylogenetic tree based on both quantitative and qualitative characters. Biogeographic areas defined in text are shown above terminal taxa. See Appendix 1 for characters and data matrix. A, Red Sea; B, western to central Indian Ocean; C, eastern Indian Ocean; D, western to central Pacific Ocean.

The results of the MANOVA suggest that 13 of the 14 quantitative characters were sufficiently different among species of the *Acropora selago* group to justify using them as characters in a phylogenetic analysis. The Tukey multiple comparisons test, however, resulted in only 11 characters with enough species subsets to be useful in this phylogenetic analysis.

A resolved tree was obtained from a combination of quantitative and qualitative characters. It appears both sets of information are essential for deciphering relationships within this subgroup of *Acropora*. We have yet to add to our quantitative characters another set of morphometric characters, derived from the radial corallite skeleton.

From the relationships between the phylogenetic tree and the distribution of species (from Figs 4 and 5), two patterns are evident: (1) taxa which show the greatest degree of endemism display character states that are the most derived; (2) species ranges overlap in a west to east stepwise fashion with the closest biogeographic relationships occurring between adjacent areas.

Whereas only one area (D, eastern to central Pacific) has an endemic species, the broadest areas are occupied by taxa displaying the least derived character states. *Acropora tenuis* and *A. yongei* have the most cosmopolitan distributions. *Acropora selago* and *A. donei* are more restricted in their distributions than the above taxa, and *A. dendrum* is the most restricted biogeographically. Thus on each branch of the cladogram, taxa possessing more derived character states appear to be more restricted in their distributions. A similar pattern has been found in some other non-*Acropora* coral species (Pandolfi, unpublished data) and is taken as evidence against the centre-of-origin hypothesis proposed in Stehli and Wells (1971).

Assumption 0 gave one reduced area cladogram (Area Cladogram I, Fig. 7*a*), Assumption 1 gave all 15 possible reduced area cladograms for 4 areas, and Assumption 2 gave Area Cladogram I (Fig. 7*a*) and an additional cladogram (Area Cladogram II; Fig. 7*b*).
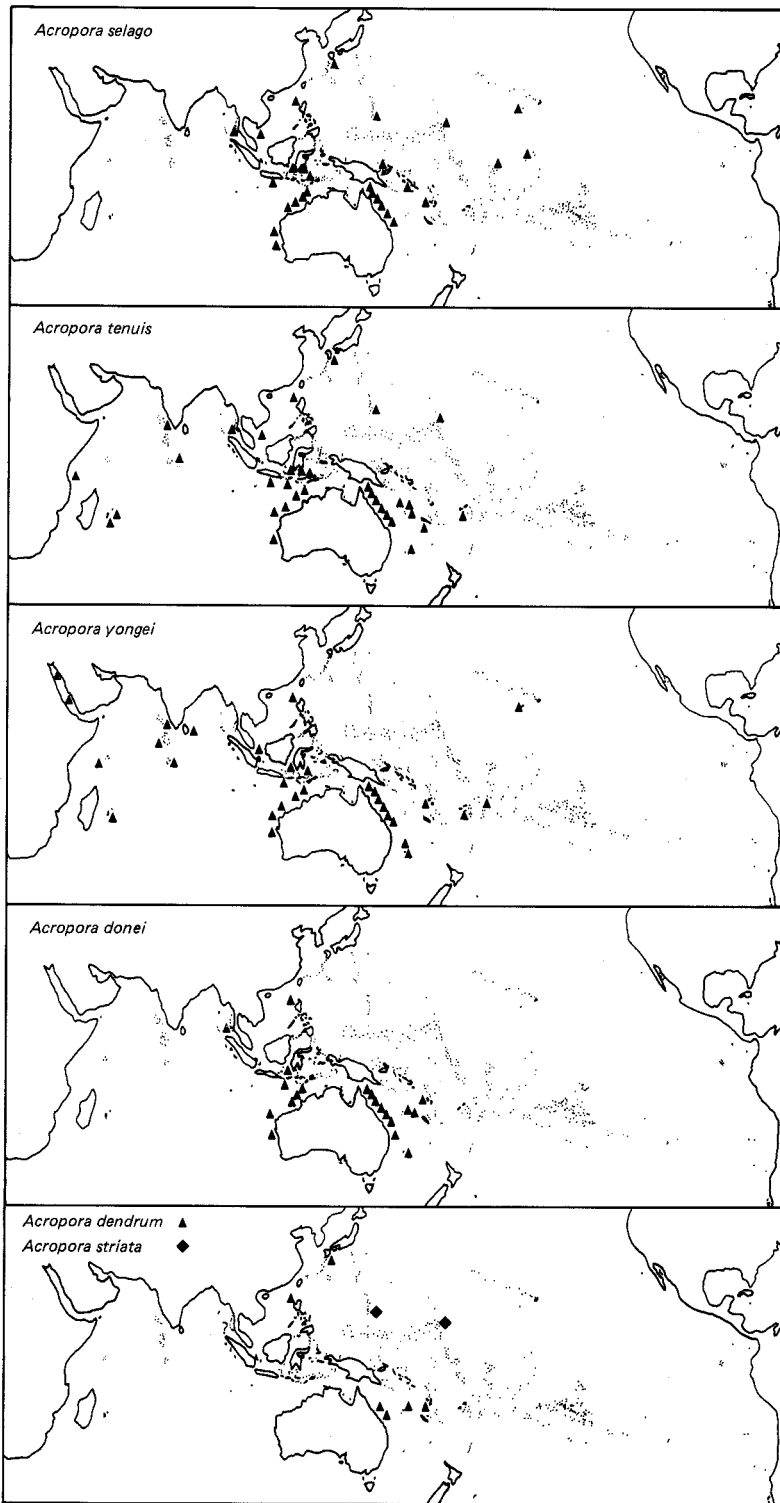
Fig. 5. Distribution of species from the *A. selago* group. (See text for basis of site records.)

To measure the degree of parsimony of the 15 possible area cladograms under Assumption 1, we calculated 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 (Nelson and Platnick 1981) using the FIT option in COMPONENT. We found that Area Cladogram I (Fig. 7*a*) required 6 fewer items of error than Area Cladogram II (Fig. 7*b*). In fact, the former singularly displayed the fewest items of error of any of the 15 possible trees, and is the most acceptable reduced area cladogram.
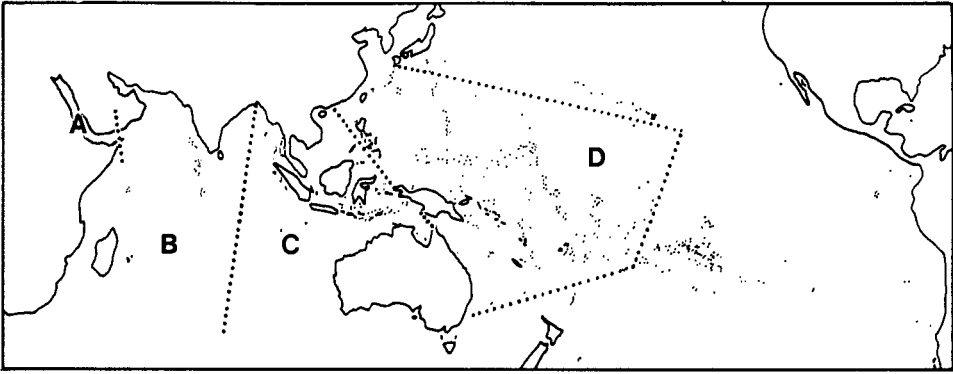

Fig. 6. Biogeographic areas recognised within the distribution patterns of the *Acropora selago* group.
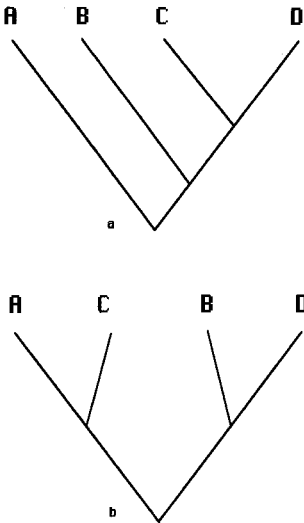

Fig. 7. Reduced four-area statement of relationships of areas A, B, C and D given the phylogeny presented in Fig. 4. Area cladogram (*a*) is the only possibility under Assumption 0. Under Assumption 2 area cladograms (*a*) and (*b*) are possible. Under Assumption 1 all 15 possible trees were obtained (not shown).

When considered under Assumption 2, we believe Area Cladogram I to be more parsimonious than Area Cladogram II. Reduced Area Cladogram I (Fig. 7*a*) shows stepwise separation of a component B + C + D from area A (the Red Sea), then component C + D from area B (western to central Indian Ocean), then of area D (western to central Pacific Ocean) from area C (eastern Indian Ocean). Reduced Area Cladogram II shows the biogeographic closest relationships between non-adjacent areas (Red Sea more closely related to eastern Indian Ocean than to western to central Indian Ocean; western to central Pacific Ocean more closely related to western to central Indian Ocean than to eastern Indian Ocean). It thus requires a number of explanations (dispersals, and/or extinctions) to interpret the species composition of related areas. We also note here that Area Cladogram I shares congruence with the geographical provinces outlined for another group of scleractinians, the fungiids (Hoeksema 1989).

A scenario based on Area Cladogram I for the history of the *A. selago* group is: an ancestral taxon (or taxa) occupied a broad distribution from the Red Sea to the central Pacific. Vicariance
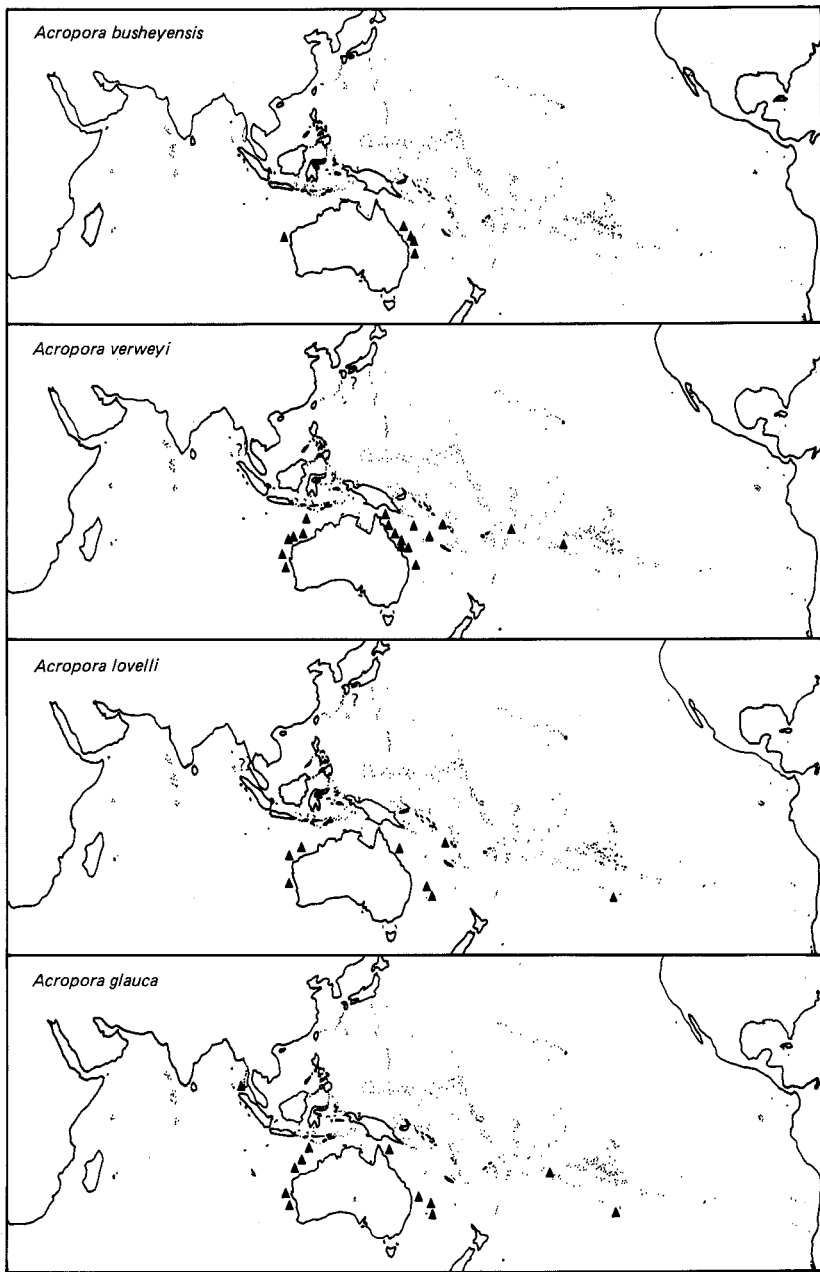
Fig. 8. Distribution of another *Acropora* subgroup, the *A. lovelli* group, for comparison with distribution patterns of the *A. selago* group. (See text for basis of side records.)

events led to the breaking up of this distribution at the mouth of the Red Sea, then west of the Western Australian continental shelf, and then at the Indonesian arc. Speciation events are always to the east of the vicariance line. Under this scenario, speciation events may or may not have been followed by dispersal to broaden the range of the taxa, but no dispersal or extinction need be invoked to explain the area cladogram.

Because this study is based on only a single *Acropora* species-group, we do not further speculate on possible physical, oceanographic, or biological explanations for our scenario. Similar analyses on further *Acropora* species-groups from Veron and Wallace (1984), with subsequent comparative analyses of area cladograms, are needed. Many of these *Acropora* species-groups comprise four or more species and occur within the set of areas A to D derived in this paper, thus they should readily lend themselves to component and consensus analysis

of cladistic biogeography (Humphries *et al.* 1988). Other *Acropora* species-groups, however, fall outside the areas A to D posed here. For example, when we plotted distribution records for species of the *Acropora loveli* group, we found them to have a mainly southern tropical to Austral distribution (Fig. 8) and no members present west of the Western Australian continental shelf. In addition, the Caribbean coral fauna includes three species of *Acropora* that do not occur in the Pacific. We are confident that as further groups are included and further areas come under scrutiny, *Acropora* will prove to be an appropriate taxon to examine the biogeographic history of the tropical marine realm.

Acknowledgments

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Appendix 1.

Characters and character states for three analyses: quantitative characters only, qualitative characters only, and all characters

0   Length of 1st order branches: range 18·9–28·6 mm

1   Top diameter of 1st-order branch: range 2·9–4·6 mm

2   Middle diameter of 1st-order branch: range 5·3–10·3 mm

3   Bottom diameter of 1st-order branch: range 5·7–11·1 mm

4   Middle diameter of 2nd-order branch: range 7·1–12·3 mm

5   Number of radials/cm on 1st-order branch: range 1·6–7·0

6   Angle of 1st-order branch: range 29·0–51·5 degrees

7   Distance to axial corallite nearest neighbour: range 13·7–27·4 mm

8   Inner axial corallite diameter: range 0·8–1·4 mm

9   Outer axial corallite diameter: range 1·8–3·7 mm

10   Axial corallite exertness: range 1·1–1·9 mm

11   Colony symmetry: symmetrical; not symmetrical

12   Colony growth: determinate; indeterminate

13   Recognisable attachment site in mature individual: present; absent

14   Upper colony surface: planar; not planar

15   Colony branching: arborescent; corymbose or caespito-corymbose

16   Contribution of radial corallites to branch thickness: > 50%; < 50%

17   Radial corallite shape: predominantly lipped without upper wall; predominantly lipped with some upper wall development

18   Coenosteal homogeneity: same on and between radial corallites; different between radials *versus* on radials

19   Radial corallite walls: costate or 'broken costate'; dense arrangement of spinules

20   Axial corallite walls: costate or 'broken costate'; reticulate with spinules; dense arrangement of spinules

21   Spinules: mostly single-tipped and slender; mostly multiple-tipped; mostly blunt-tipped

A. tenuis	0?1?1212121 0100101000?
A. selago	122222?223? 01001010000
A. yongei	?1111200010 10110111010
A. dendrum	??2?22?2232 01001120122
A. millepora	00000001101 01001101000
A. donei	?1111101012 01000111011