

Biogeography of Southeast Asia and the West Pacific

H. Turner^{1*}, P. Hovenkamp² and P. C. van Welzen² ¹*Institute of Evolutionary and Ecological Sciences, Section G7 Theoretical Biology and Phylogenetics, University of Leiden, PO Box 9516 and* ²*Nationaal Herbarium Nederland, Leiden Universiteit Branch, PO Box 9514, 2300 RA Leiden, The Netherlands*

Abstract

The biogeography of Southeast Asia and the West Pacific is complicated by the fact that these are regions on the border of two palaeocontinents that have been separated for a considerable period of time. Thus, apart from any patterns of vicariance, two general patterns relating to dispersal can be expected: a pattern of Southeast Asian elements, perhaps of Laurasian origin, expanding into Australian areas, and a reverse pattern for Australian elements, perhaps of Gondwanan origin. On top of this, both Australian and Southeast Asian elements occur in the Pacific. They dispersed there as the Pacific plate moved westward, bringing the different islands within reach of Southeast Asia and Australia. In order to reconstruct the biotic history of these areas, two large data sets consisting of both plants and animals were generated, one for each pattern, which were analysed using cladistic methods. The general patterns that emerged were weakly supported and do not allow general conclusions.

Keywords

Dispersal, Gondwana, Laurasia, unrooted area network, vicariance.

INTRODUCTION

The regions of Southeast Asia and the West Pacific have long attracted the attention of biogeographers. Already in the 19th century Alfred Russell Wallace noted that the biota of the Malay archipelago consisted of Asian and Australian elements, with the former predominant in the western part, and the latter towards the east. His explanation was that the different groups of organisms had originated in Asia and Australia, and subsequently dispersed. Also, he assumed that these continents had at one time been larger, and became fragmented as a result of sea level fluctuations. He (Wallace, 1860) drew a line demarcating where the Asian biota is separated from the Australian one, later called Wallace's line. Mayr (1944) showed that Wallace's line actually separates a region with a typically continental Asian biota from a region with an impoverished island biota. Other biogeographers, such as Weber, drew a line indicating where the two biotas are in balance (see Fig. 1), while still others [e.g. Lydekker, De Beaufort (Mayr, 1944)] considered the eastern equivalent of

Wallace's line (usually taken as the 100 m depth line) as the border between the Australian and Asian biotas. Mayr used the name Wallacea for the region between Wallace's and Lydekker's lines. Actually, this region is characterized by a more monsoonal climate than other parts of Malesia, with a pronounced dry period (Mayr, 1944; van Steenis, 1979).

Van Steenis (1935, 1964), investigating the mountain flora of Malesia, postulated that the Asian elements had used two different pathways into the archipelago. Lowland taxa dispersed from Southeast continental Asia to the islands of the Sunda plateau and beyond, while alpine taxa (mostly with close relatives in temperate climates) would in addition have originated more northward, using Taiwan and the Philippines as stepping stones. For some flora elements, he later (1979) postulated an additional pathway, assuming that there has been early contact between rafting India and the western part of the Malesian area.

More recently, the region has once more attracted the attention of many investigators, both geologists and biogeographers. The geologists are interested because of the complex geological history of the region, while the biogeographers are now employing cladistic methodologies to unravel the biogeographic history of the Malay archipelago and the West Pacific. This paper is a further attempt in this direction.

*Correspondence: H. Turner, Institute of Evolutionary and Ecological Sciences, Section G7 Theoretical Biology and Phylogenetics, University of Leiden, PO Box 9516, 2300 RA Leiden, The Netherlands. E-mail: turner@rulsfb.leidenuniv.nl.

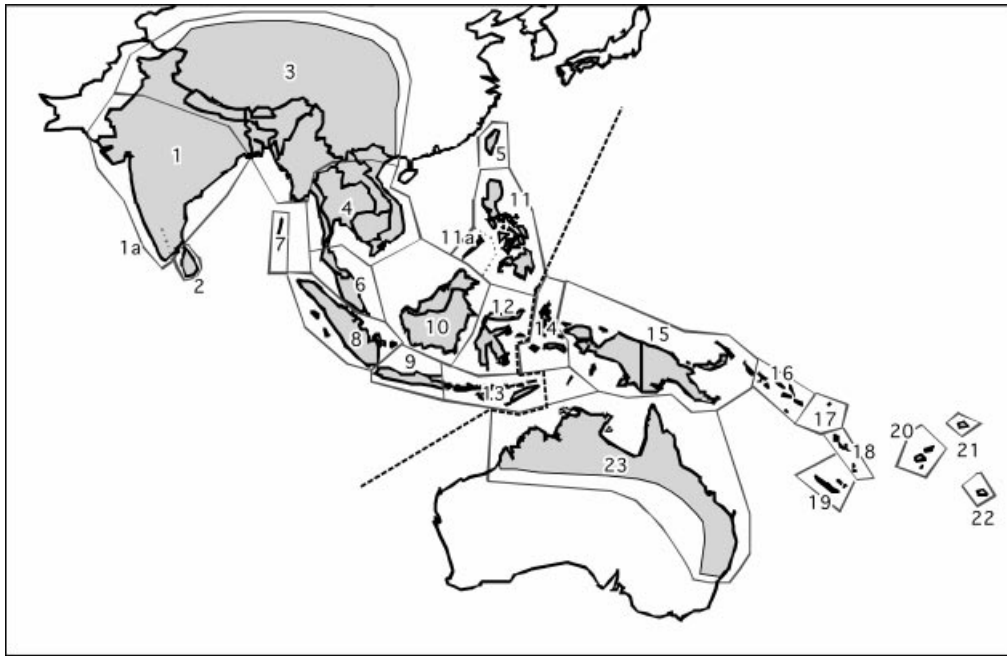


Figure 1 The areas of endemism employed. The dashed line is Weber's line (Mayr, 1944). (1) India, (1a) Kerala, (2) Sri Lanka, (3) Himalayas, (4) Southeast Asia, (5) Taiwan, (6) Malay Peninsula, (7) Andaman and Nicobar Islands, (8) Sumatra, (9) Java, (10) Borneo, (11) Philippines, (11a) Palawan, (12) Sulawesi, (13) Lesser Sunda Islands, (14) Moluccas, (15) New Guinea, (16) Solomon Islands, (17) Santa Cruz Group, (18) Vanuatu, (19) New Caledonia, (20) Fiji, (21) Samoa, (22) Tonga, (23) Australia.

GEOLOGICAL HISTORY OF THE MALAY ARCHIPELAGO AND THE WEST PACIFIC ISLANDS

The collisions between several ocean plates (Pacific, Indian, Philippine) and land plates (Eurasian, Indian, Australian) have created an intricate geological history for Southeast Asia and the West Pacific islands. Good summaries of the geological history (and all still existing controversies) can be found for the West Malay Archipelago in Ridder-Numan (1996 and references therein), and for the East Malay Archipelago and the West Pacific Islands in de Boer (1995 and references therein). A pictorial summary of the last 50 Ma can be found on the Internet (Hall, 1995). The following account is based on these sources.

The West Malay Archipelago (West Malesia, i.e. the area west of Wallace's line) and most of Southeast Asia consists mainly of fragments which broke off from Australia and which rifted northwards and collided with the Eurasian Plate. This process may already have started in the early Palaeozoic (c. 400 Ma). This means that most of Southeast Asia, although of Australian origin, was already in place before many recent plant and animal taxa evolved (but most plant families existed as early as the late Cretaceous, c. 70 Ma). Thus the plants and animals present in West Malesia will be mainly of Southeast Asian origin. The history of the plants and animals may still reflect part of the geological history of this region as many microplates remained separate for a long time, or after collision created

barriers like mountain ranges. Moreover, large parts of Southeast Asia and West Malesia were submerged several times, not only during the more recent interglacial periods, but high sea levels were for instance also present during the Late Eocene (c. 40 Ma).

India separated from Gondwanaland c. 195 Ma, and finally collided with Asia in the Late Eocene. India could have acted as a raft, carrying taxa from Africa to Asia, which could spread over Southeast Asia and West Malesia after collision. During its rift it came in close contact with still northward moving Sumatra, which means that an earlier exchange of floral and faunal elements could have taken place. Possibly, during the close contact between Sumatra and India, India became populated by Southeast Asian elements, still existing in the forests of Kerala and Sri Lanka (as suggested by most cladograms in this study).

The East Malay Archipelago (East Malesia, i.e. the area east of Wallace's line) also consists of small fragments of Australian–New Guinean origin, which broke off at c. 50 Ma. These include East Sulawesi, the Moluccas and the Lesser Sunda Islands. With the arrival of these slivers and after their emergence from sea, several island arcs were formed between Southeast Asia and Australia.

New Guinea has a very special history. The southern part (south of the central mountain ranges) has always been attached to Australia. The northern edge is an amalgamation of more than 30 terranes of various origin: island arcs, pieces of broken off Australian or New Guinean continent and even parts of trapped sea floor.

Table 1 Clades used for the biogeographic analyses

Clade	Reference
1. East–west pattern	
Sapindaceae	
<i>Arytera</i>	Turner (1995)
<i>Cnesmocarpon</i>	Adema & van der Ham (1993)
<i>Cupaniopsis</i>	Adema (1991)
<i>Guioa</i>	van Welzen (1989)
<i>Jagera</i>	Adema & van der Ham (1993)
<i>Lepidopetalum</i>	van Welzen <i>et al.</i> (1992)
<i>Mischarytera</i>	Turner (1995)
<i>Rhysotoechia</i>	Etman (1994)
Homoptera	
Chlorocystini	de Boer & Duffels (1996); Moulds (1990)
Cosmopsaltriaria*	de Boer & Duffels (1996); Duffels (1977, 1982, 1983, 1989, 1990a, b, 1997); Duffels & Turner, unpublished data
Hemiptera	
<i>Haloveloides</i>	Andersen (1989a, 1991, 1992)
<i>Halobates regalis</i> group	Andersen (1991, 1998); Andersen & Foster (1992); Andersen & Weir (1994)
<i>Halobates princeps</i> group	Andersen (1991, 1998); Andersen & Foster (1992); Andersen & Weir (1994)
<i>Halovelia malaya</i> group	Andersen (1989b, 1991, 1998)
<i>Xenobates</i>	Andersen (1991)
Reptilia	
Carphodactylini	Bauer (1990)
Coleoptera	
<i>Casnoidea</i>	Baehr (1996)
<i>Megarthus</i>	Cuccodoro (1998)
2. West–east pattern	
Asclepiadaceae	
<i>Genianthus</i>	Klackenberg (1995)
Euphorbiaceae	
Erismantheae	van Welzen (1995)
<i>Neoscortechinia</i>	van Welzen (1994)
Fabaceae	
<i>Fordia</i>	Buijsen (1988); Dasuki & Schot (1991); Schot (1991)
<i>Parkia</i>	Hopkins (1994); Luckow & Hopkins (1995)
<i>Spatholobus</i>	Ridder-Numan (1996)
Orchidaceae	
<i>Bromheadia</i>	Kruizinga <i>et al.</i> (1997); Repetur <i>et al.</i> (1997)
Rubiaceae	
<i>Xanthophytum</i>	Axelius (1990)
Coleoptera	
Hydrophilidae	Bameul (1997a, b)
Homoptera	
<i>Dundubia jacoona</i> assemblage	Beuk (1996)
Soricidae	
<i>Crocidura</i>	Corbet & Hill (1992); Hutterer (1993); Ruedi (1995, 1996)

* For the separate analysis of the east–west pattern, the outgroup taxa (*Orientopsaltria padda* and *Meimuna iwasakii*) and the outgroup node were not included.

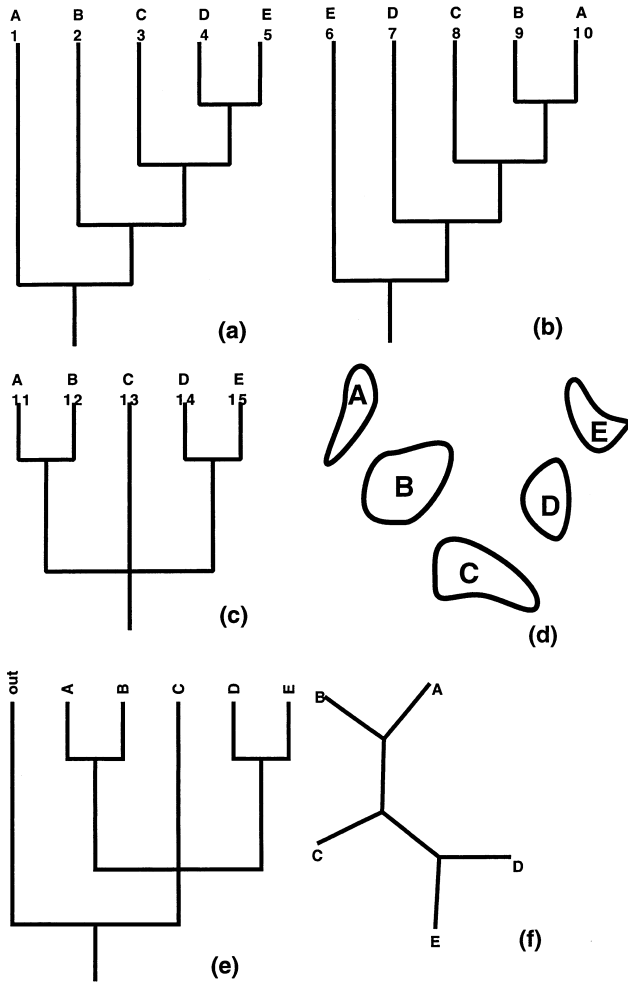


Figure 2 (a–c) Three clades with species in areas A–E, each displaying a different biogeographic pattern. (d) Areas A–E form a linear sequence. (e) Cladogram resulting from BPA. (f) BPA with the outgroup excluded, thus resulting in an unrooted network.

MATERIALS AND METHODS

Data

The data consisted of the distribution patterns and phylogenies of 29 monophyletic groups. The monophyletic groups were selected according to the following criteria: (1) availability of a phylogenetic hypothesis at species level, constructed using parsimony; (2) availability of detailed information on the distribution patterns of the terminals; (3) exclusively or at least predominantly occurring in the region of interest; and (4) a certain degree of confidence in the cladogram. Admittedly, the latter criterion is rather vague, but was used nevertheless to exclude some studies in which the researchers themselves expressed doubt as to the reliability of the cladogram.

The unit areas (usually referred to as ‘areas of endemism’ in the literature) used are shown in Fig. 1. We delimited areas on

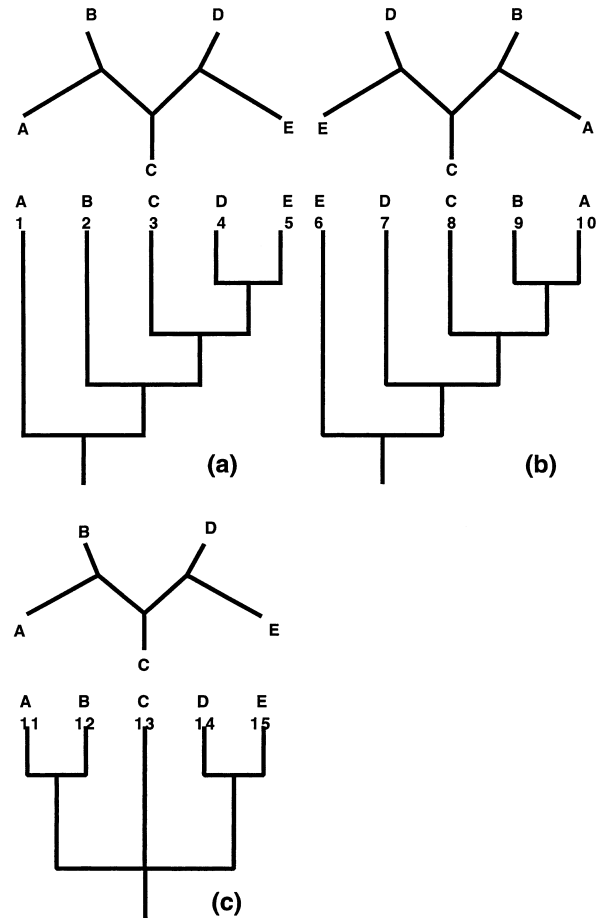


Figure 3 The unrooted network of Fig. 2(f) mapped onto the different taxon area cladograms (Fig. 2a–c), showing perfect fit in all three cases.

the basis of the presence of a unique combination of taxa (Axelius, 1991); in fact, most areas are also characterized by the occurrence of one or more endemic taxa. Initially, many of the areas were divided more finely, using knowledge of the geology (see references in van Welzen, 1989; de Boer, 1995; Turner, 1995; Ridder-Numan, 1996). However, because many taxa are known from only a limited number of collections, the analyses suffered greatly from the large amount of missing information, as well as from suspected undersampling. To overcome this, we decided to group small areas together into larger areas even when geological information was available to indicate that such areas are geologically composite areas (e.g. New Guinea, Sulawesi and Borneo).

We realize that the terms ‘unit area’ and ‘area of endemism’ for the terminal units in the analysis are somewhat misleading, because essentially the terminals are the biotas of particular areas, not the geological areas themselves. Entire biotas may migrate across the earth’s surface without changing their composition, e.g. not only because of climatic but also as a result of geological changes. For example, during the glacial periods arctic biotas had a much wider

distribution than at present and temperate biotas in Australia once extended well into Queensland when the continent occupied a more southerly position.

Table 1 gives a list of the clades used. Whenever a clade occurred outside the region of interest (e.g. *Cupaniopsis* on the Caroline Islands, Adema, 1991), these occurrences were omitted. In a few cases this resulted in species occurring in none of the designated areas. Such species and their hypothesized direct ancestors were deleted from the data set. In some cases, exact data on the distribution of species was not available. In such cases species were coded as unknown for those areas for which there was uncertainty (e.g. *Rhombosternum index* Bameul, 1997a on Java, Borneo and the Philippines), and where necessary their ancestors were coded likewise. The data set is available from the journal's website, <http://www.blackwell-science.com/products/journals/suppmat/jbi/jbi526/jbi526sm.htm>

Methods

The data were analysed by Brooks Parsimony Analysis (BPA), a method that uses standard parsimony analysis to construct a cladogram of the areas on the basis of the occurrences of the species and their reconstructed ancestors (Brooks, 1990). The data were coded using Assumption 0 (Zandee & Roos, 1987). Analyses were performed with and without an all-zero outgroup, using simple addition for the analyses of the separate patterns and 1000 random addition sequences for the final analyses, TBR branch swapping, and saving all most-parsimonious trees. For the analyses, we used PAUP* (vs. 4.0b2, Swofford, 1999). Bremer support values were also estimated using PAUP*, and AutoDecay 4.0.1 (Eriksson, 1998) to construct the input file. Most results were confirmed using Nona (Goloboff, 1997) with the following parameters: hold/20; mult*15; max;. Under Assumption 0, each terminal taxon in the data set is coded as present/absent for the unit areas, and the hypothetical ancestors (internal nodes in the taxon cladograms) are coded as present for those areas in which a descendant occurs. For each clade, the areas from which it is not recorded are coded as unknown data ('?') to avoid assuming spurious extra steps by extinction when in fact the clade is primitively absent from an area, and also to avoid artefactual placement of areas from which few clades are known close to the root of the area cladograms. Using BPA, we hoped to be able to detect common patterns of vicariance events (allopatric speciation mode I, Brooks & McLennan, 1991) as well as dispersal events (peripheral isolates allopatric speciation via sequential dispersal, Brooks & McLennan, 1991). In addition, the cladograms and distribution maps were inspected for traces of vicariance following a protocol (Vicariance Analysis) modified from Hovenkamp (1997 and in preparation). This method searches for allopatric sister-groups and attempts to identify vicariance events by finding multiple instances of allopatry in a similar geographical location. Because BPA is known to occasionally produce highly resolved cladograms even in the absence of strongly supporting evidence, we used the Vicariance Analysis to

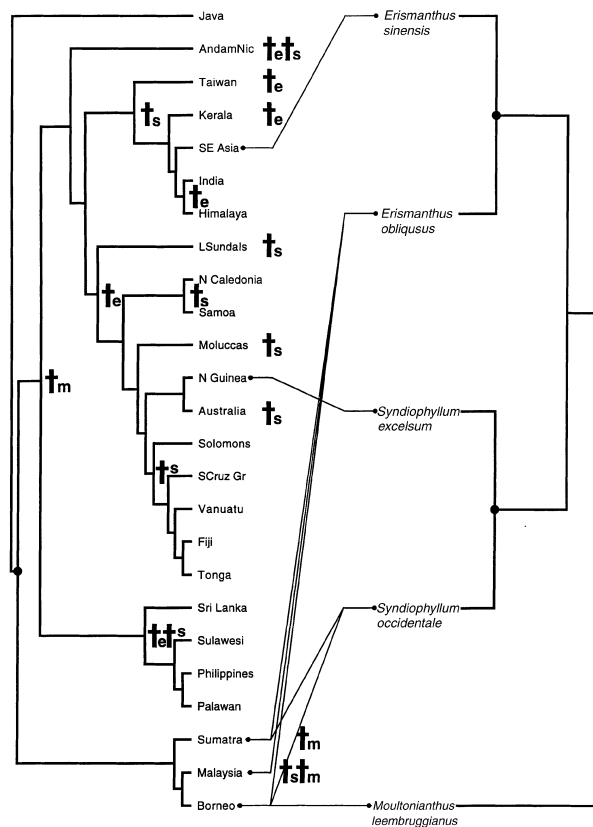


Figure 4 The cladogram for Erismanteae mapped (using Tree-Map) onto the area network rooted at Java. Bold dots indicate the nodes in the cladogram and the area network that can be mapped onto each other (vicariance events). Extinctions are indicated by crosses with letters to denote the particular subclade. Thus, the genus *Erismanthus* goes extinct at the node uniting the Lesser Sunda Islands with all areas to the east.

assess the confidence with which the nodes can be explained by vicariance events.

Separation of the different patterns

A peculiarity of the region studied is that it consists essentially of a linear sequence of areas, rather than a reticulate pattern. Thus, in order to disperse from, e.g., Sri Lanka to Tonga, it is almost unavoidable to pass through India, Himalayas, Southeast Asia, the Malay Peninsula, Sumatra (or Java or Borneo), Sulawesi (or the Lesser Sunda Islands), the Moluccas, New Guinea, the Solomon Islands, the Santa Cruz Group, Vanuatu and Fiji. If the dispersal barriers separating adjacent areas are older than a clade, and if, moreover, the barriers are sufficiently severe to make dispersal across them unlikely, clades might be expected to display patterns of peripheral isolates allopatric speciation via sequential dispersal (Brooks & McLennan, 1991). And because the areas of endemism lie in a concatenated pattern, clades starting in different areas will display the same pattern, if the area cladogram is unrooted.

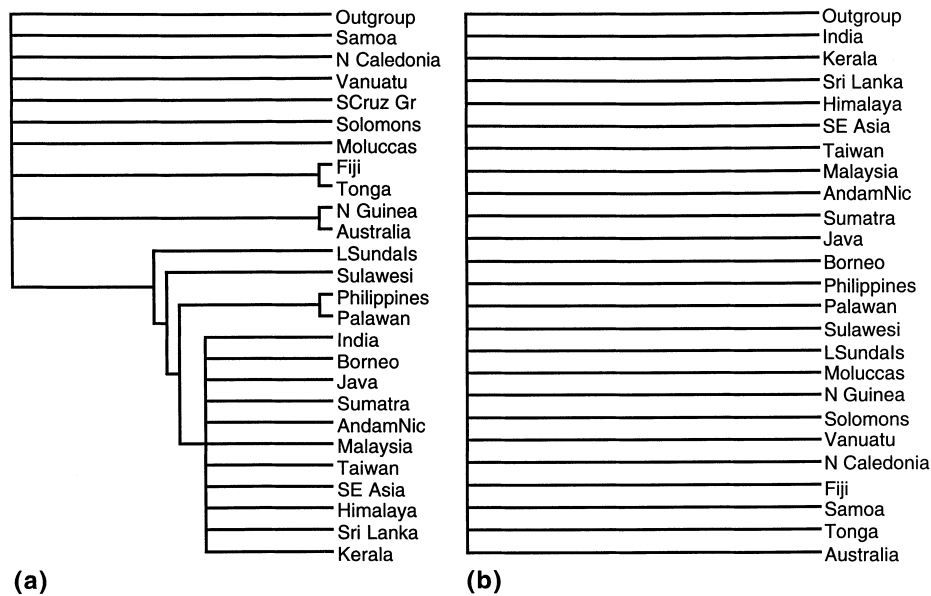


Figure 5 Strict consensus trees of the MPTs resulting from analysis of the two initial data sets. (a) East–west pattern. Consensus of > 90,000 trees, $l = 847$, $CI = 0.787$, $RI = 0.646$. The analysis was not completed; instead it was checked by branch-and-bound analysis that no shorter trees exist, nor any equally short trees incompatible with this consensus tree. (b) West–east pattern. Consensus of > 10,000 trees, $l = 480$, $CI = 0.667$, $RI = 0.587$. This analysis was not run to completion either, but it was checked that no trees exist that are shorter than 480 steps.

This principle is illustrated in Fig. 2 for three clades (consisting of taxa 1–15, Fig. 2a–c) and five areas A–E (Fig. 2d). The clades display different biogeographic patterns, but are all fully compatible with dispersal from the area of origin to a neighbouring area followed by speciation before further dispersal takes place. Upon analysis of the data set, two most parsimonious area cladograms result ($l = 14$, $CI = 0.786$, $RI = 0.700$), of which the consensus is almost completely unresolved (Fig. 2e). If the analysis is carried out without the outgroup (which serves to root the character-state trees) one single, fully resolved area network is recovered (Fig. 2f, $l = 8$, $CI = 1.0$, $RI = 1.0$). As can be seen by mapping the taxon cladograms onto the area network, they all fit the same pattern perfectly, as long as the network is not rooted (Fig. 3a–c).

Thus, in analysing the biogeography of the Malesian area, we may expect to find common patterns not only because of vicariance, but also as the result of dispersal-with-speciation following common ‘dispersal pathways’. It has been suggested that poorly resolved results from BPA may be caused by including two or more contradictory patterns in a single analysis. The standard solution for this phenomenon is to analyse the data for the different patterns separately (or to separate each area artificially for each pattern). Our initial assumption was that the biotic history of the region would display two patterns, namely (1) a pattern of East Malesian clades that either speciated as a consequence of the break-up of Gondwana or at some stage managed to disperse westward across the Malesian archipelago towards continental Asia, speciating along the way and (2) a pattern of West Malesian clades that eventually dispersed eastward

towards Australia and the Pacific. Therefore, the clades were divided into two sets according to their cladograms.

We feel that parsimony analysis (which looks for evidence of vicariance, rather than of dispersal) may still be useful in this case, especially when supplemented with a Vicariance Analysis, because such an analysis may be expected to reveal the importance of permanent splits in lineages for the genesis of the observed biogeographic patterns. Only on the basis of that knowledge it is possible to assess the relative importance of vicariance and dispersal in the history of each taxon.

All cladograms in which one of the subclades resulting after the first split was restricted to the Pacific/East Malesian core areas (all areas east of Weber’s line, see Fig. 1) were separately analysed (‘east-to-west pattern’). The remaining clades, which all displayed a pattern with the basal subclade(s) confined to the Sunda plateau and/or the Asian continent, were analysed together in the ‘west-to-east pattern’.

In addition, the separate taxon cladograms were mapped (using TreeMap 1.0b, Page, 1995) onto the generalized area network obtained from the unrooted parsimony analysis, to find out if a subdivision into more than two groups based on different ‘entry pathways’ could be detected. To achieve this, we developed the following procedure.

Because TreeMap can as yet only handle fully dichotomous trees, for each clade the cladogram was resolved into all possible dichotomous solutions. One was chosen when there were very many dichotomous resolutions possible. Usually the exact choice made no difference to the result, but in cases where it did, we attempted to select the optimal resolution. Subsequently, the dichotomous cladograms were optimized

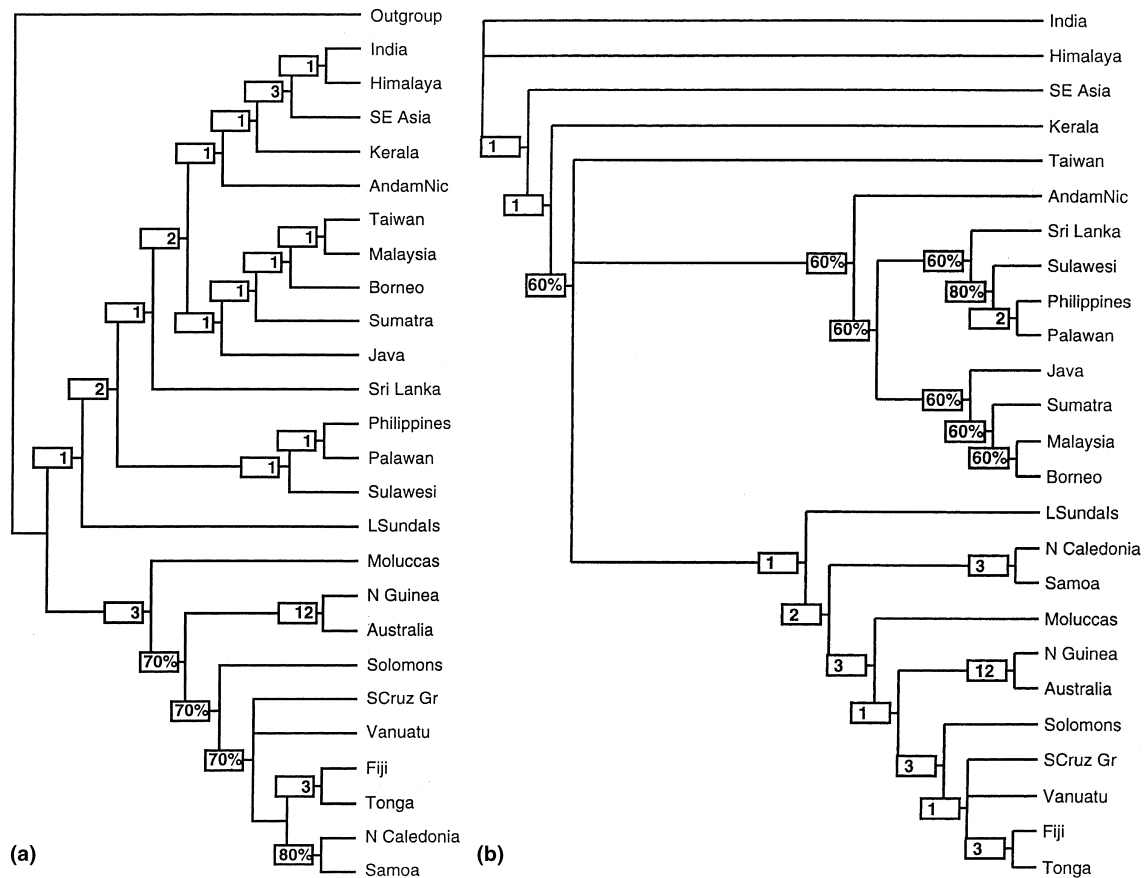


Figure 6 Majority rule consensus from (a) 10 most parsimonious rooted trees ($l = 1343$, $CI = 0.736$, $RI = 0.606$) and (b) 15 most parsimonious unrooted area networks ($l = 1240$, $CI = 0.752$, $RI = 0.605$). Values on each node are Bremer support for nodes present in the strict consensus tree or percentage of trees in which the node appears for the other nodes.

onto the area network, which in turn was rooted on all possible branches, resulting in 47 different area cladograms for each clade. In each case, the combination of resolved taxon cladogram and rooted area network was accepted that displayed the best fit in terms of number of vicariance events (termed cospeciation events in TreeMap). When several trees ended in a tie, the best combination was selected amongst them in terms of minimum number of sympatric speciations (duplications) or extinctions (sorting events). Dispersal (host switching, the fourth process that can be invoked as an explanation for the pattern observed) was not included, because it is not at all clear when a dispersal event is more parsimonious than a vicariant speciation accompanied by a number of extinctions. Using the selected combinations, note was taken of the amount of the support for each node as cause for speciation and the support for each branch as location of the root of the generalized area network.

Example

For the Euphorbiaceae tribe Erismantheae the number of vicariant speciations is either 0 (with four sympatric speciations) or 2 (with two sympatric speciations). Amongst the

trees allowing two vicariant speciations, the number of local extinctions postulated varies from 34 when the network is rooted on the branch leading to New Guinea to 18 when it is rooted at Java (Fig. 4). The support for the location of the root is unambiguous (in this case), because rooting the area network at, e.g., the Andaman and Nicobar Islands would be costlier in terms of extinctions postulated (20), although neither the Andaman and Nicobar Islands nor Java harbour a representative of the clade. TreeMap then shows that the node uniting *Syndiophyllum excelsum* and *S. occidentale* is best mapped onto the node uniting Sumatra/Malaysia/Borneo with all other areas (excluding Java). However, because not all areas are occupied by a representative of the Erismantheae, actually the node in the cladogram supports the branches leading from the smallest clade including Sumatra and Borneo (where *S. occidentale* occurs) to New Guinea (home of *S. excelsum*). Thus, support is counted for all branches connecting these two nodes. The node uniting *Erismanthus obliquus* and *E. sinensis* is mapped onto the same node in the area cladogram. In this case support is counted for all branches connecting the clade Sumatra/Malaysia/Borneo with Southeast Asia.

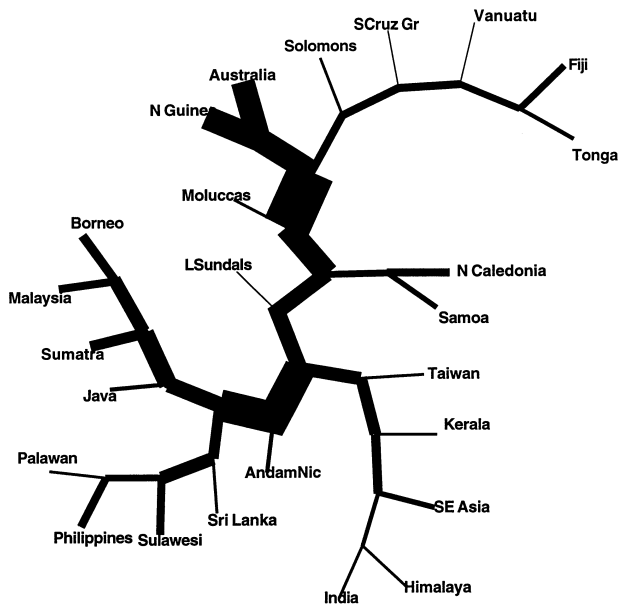


Figure 7 Support for the different branches in the unrooted area network. The thickness of the different branches is proportional to the total amount of support. See text for further explanation.

RESULTS

The BPA analyses of the east-to-west and west-to-east patterns separately resulted in many thousands of equally parsimonious trees, of which the strict consensus trees were almost completely unresolved (Fig. 5). Analysis of the entire data set with an all-zero outgroup included yielded 10 most parsimonious trees ($l = 1343$, $CI = 0.736$, $RI = 0.606$), without the outgroup 15 MPTs ($l = 1240$, $CI = 0.752$, $RI = 0.605$). Again, the strict consensus trees were poorly resolved. Therefore, the majority rule consensus trees are shown in Fig. 6. However, in both cases Bremer support for most fully resolved branches is weak compared with the length of the cladogram, not exceeding 3 except for the best supported clade (Australia + New Guinea). For the clades not represented in the strict consensus tree (hence with a Bremer support of 0), the frequency with which it appears in the complete set of MPTs is given.

A direct search for evidence of vicariant speciation reveals that few cladograms have retained evidence for vicariant speciation in the form of fully allopatric (renamed 'paralogy-free', Nelson & Ladiges, 1996) nodes, and that the majority of these nodes are near the tips of the tree, rendering most cladograms uninformative about the historical sequence of the vicariance events. The cladograms that are informative do not clearly specify a single pattern, but merely allow us to suggest a number of common elements.

The best-supported pattern is a sequence of vicariant events in East Malesia, traceable in the cladograms of *Arytera*, *Mischarytera*, *Cupaniopsis*, *Guioa* and *Rhysotoechia*. In this sequence, vicariance between Peninsular Papua New Guinea and more westerly parts of New Guinea is

followed by vicariance across the mountain range, involving the Markham and Fly River valleys, then by vicariance across Torres Strait and finally between New Guinea and more westerly parts of Malesia. Additionally, there are indications that in West Malesia vicariance between Malesia and Continental Asia is relatively basal with regard to vicariance on the Sunda shelf, which may be relatively recent. The results of the complete analysis of vicariant nodes are presented in the Appendix.

Figure 7 shows how frequently the different branches of the unrooted area network were compatible with the nodes in the different taxon cladograms when these were mapped onto the network as explained above, summed over all clades in the analysis. The branches between New Guinea and Australia on one hand, and the Greater Sunda Islands on the other, are best supported in these terms, but there is support for almost all branches in the network, with the exception of some of the terminal ones. Table 2 gives the most parsimonious location(s) of the root, together with the corresponding number of vicariant and sympatric speciation events and extinctions implied, for each clade. Figure 8 shows how often each branch in the area network could function as location of the root when the different taxon cladograms are mapped in turn onto the network.

DISCUSSION

The BPA analyses of the complete data set indicate weak support for a pattern that seems to reflect predominantly geographical proximity. The strict consensus of the trees from the unrooted analysis is fully resolved for the areas east of Weber's line (Fig. 6b), with the exception of the position of Vanuatu. For the western areas the resolution is much less: most nodes are only present in nine of the cladograms. Remarkably, the relationships that are fully resolved among the western areas are areas that are ordered linearly, namely India, Himalayas and Southeast Asia. The fuzzy patterns in West Malesia are possibly because of the (geological pattern destructive) glacial periods, which created a vast Sunda shelf, allowing different dispersal routes. This is also shown when the unrooted area network is mapped onto Malesia in Fig. 9. It shows an almost linear sequence for especially the East Malesian areas, and a branching pattern consisting of three sequences (which in turn are almost linear) for West Malesia. From Fig. 9 it will also be obvious that taxa originating in different areas will still display (partly) the same patterns, as explained in Figs 2 and 3. Therefore, an unrooted area network seems to be the best solution to show the BPA results.

Several areas have a place on the cladogram not directly compatible with their geographical position. For some of these, the explanation might be sought in a lack of data. Thus, Taiwan, Sri Lanka and Kerala are inhabited by only a few clades (three, six, and six, respectively). On the other hand, the Pacific islands are also occupied by few clades, but most of these are placed on the area cladogram in agreement with their physical position on the globe. Only Samoa and New Caledonia are placed oddly. But here, the lack of clades

Table 2 Optimal location of the root of the majority rule consensus area network for each clade, according to the number of vicariant speciations, sympatric speciations and extinctions implied (see text). A dichotomous resolution was used for each taxon cladogram (either the best, or a more or less arbitrarily selected one amongst many). The root is indicated by the smallest clade arising from the basal split. Alternative nodes where the root can be placed are given in parentheses

Clade	Root of tree	Vicariant speciations	Sympatric speciations	Extinctions
<i>Arytera</i>	N_Caledonia	4	19	34
<i>Bromheadia</i>	AndamNic	2	20	106
Carphodactylini	SolomonsSCruz_GrVanuatuFijiTonga	2	17	35
<i>Casnoidea</i>	PhilippinesPalawanSulawesi	5	11	77
Chlorocystini	Australia	3	25	41
<i>Cnesmocarpon</i>	Not Australia, not N_Guinea	0	3	3
Cosmopsaltriaria	SCruz_GrVanuatuFijiTonga	9	88	124
<i>Crocidura</i>	Sumatra	4	15	40
<i>Cupaniopsis</i>	N_Caledonia	7	49	88
<i>Dundubia jacoona</i> assemblage	Java	0	3	25
Erismantheae	Java	2	2	18
<i>Fordia</i>	Sumatra	3	13	43
<i>Genianthus</i>	AndamNic	4	10	46
<i>Guioa</i>	EMalxLSundalsWMal	5	48	132
<i>Halovelina malaya</i> group	N_CaledoniaSamoa (LSundaIs, Moluccas, N_Caledonia, Samoa)	3	2	21
<i>Halobates princeps</i> group	Samoa	2	2	22
<i>Halobates regalis</i> group	Australia	1	6	24
<i>Haloveloides</i>	N_GuineaSolomonsSCruz_Gr VanuatuFijiTongaAustralia	3	3	37
Hydrophilidae	Malaysia	4	10	51
<i>Jagera</i>	SolomonsSCruz_GrVanuatuFijiTonga (SCruz_GrVanuatuFijiTonga, VanuatuFijiTonga, FijiTonga, Fiji, Tonga, Aus)	0	2	4
<i>Lepidopetalum</i>	Australia	1	4	17
<i>Megarthus</i>	LSundals	3	9	29
<i>Mischarytera</i>	Not Australia, not N_Guinea	0	2	2
<i>Neoscortechinia</i>	MalaysiaSumatraBorneo (Java, SriLanka)	1	4	24
<i>Parkia</i>	AndamNic	2	5	43
<i>Rhysotoechia</i>	SolomonsSCruz_GrVanuatuFijiTonga (SCruz_GrVanuatuFijiTonga, VanuatuFijiTongaTonga, FijiTonga, Solomons, SCruz_Gr, Vanuatu, Fiji, Tonga)	2	13	37
<i>Spatholobus</i>	Taiwan	1	30	122
<i>Xanthophytum</i>	Borneo	3	25	34
<i>Xenobates</i>	N_GuineaSolomonsSCruz_GrVanuatuFiji TongaAustralia (SCruz_GrVanuatuFijiTongaTonga, VanuatuFijiTongaTonga, FijiTongaTonga, SCruz_Gr, Vanuatu, Fiji, Tonga)	1	4	4

cannot fully account for the anomalies: Samoa harbours six clades and New Caledonia seven, but the Santa Cruz Group, Vanuatu, Fiji and Tonga, which all occupy expected positions, are inhabited by only two, seven, seven, and five clades, respectively. The West Pacific island arcs were invaded from New Guinea (e.g. cicadas, de Boer, 1995; Sapindaceae: *Arytera*, Turner, 1995) and from New Caledonia (Sapindaceae: *Cupaniopsis*, Adema, 1991; van Balgooy *et al.*, 1996). Apparently the lack of definite data is not the only, or even sufficient, reason for anomalous placement

of particular areas. Analyses in which each clade was omitted from the data set in turn showed that *Cupaniopsis* caused this result. Only the analysis with *Cupaniopsis* omitted gave a different result: now Samoa grouped at the basis of the Pacific areas excluding the Solomon Islands. Using only the *Cupaniopsis* data resulted in a network with New Caledonia and Samoa branching from the same node. The only other clades containing a representative in Samoa are *Arytera* (Fiji, Samoa, Tonga), Chlorocystini (Solomons, Santa Cruz, Vanuatu, Samoa, Tonga), *Halobates princeps*

group (Samoa ((Vanuatu, New Caledonia) (Fiji, Tonga))) and *Cosmopsaltria* (Samoa (Tonga (Fiji, Vanuatu))) in parentheses the partial tree topologies resulting from analyses of each clade separately).

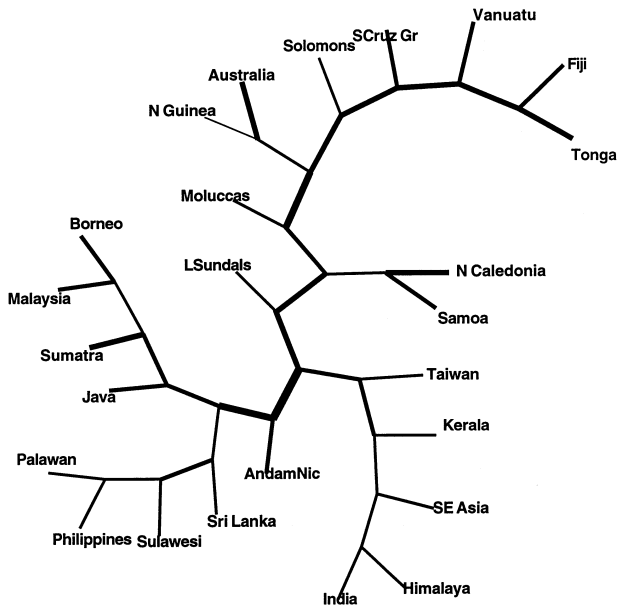


Figure 8 Support for the location of the root of the network. The thickness of the different branches is proportional to the total amount of support. See text for further explanation.

For the rooted analysis (Fig. 6a), most of the resolution is present in the Western part of the region. The area cladogram resembles the unrooted network, with a few exceptions: Taiwan is placed as sister to Malaysia in all the area cladograms, New Caledonia is still most closely related to Samoa, but now the pair is placed as sister area to Fiji and Tonga. The root is placed between the Moluccas and the Lesser Sunda Islands, i.e. on Weber's line.

Inclusion of a root has resulted in a number of changes in the cladogram, but not notably involving additional conflict. The weak Bremer support figures for the branches in both patterns probably indicate that the resolution of both cladograms is not very strongly supported, and that the apparent differences in resolution are probably not significant.

A curious discrepancy is present between the area cladogram resulting from BPA and the evidence for vicariance that can be detected in the cladograms. In the area cladogram, the most basal dichotomy is between East and West Malesia, followed by a dichotomy between Continental Asia and the islands of West Malesia. In the cladograms, both these dichotomies can be traced in six allopatric nodes. However, a basal position relative to vicariance on the Sunda shelf is more often taken by the second pattern, and one cladogram even specifies that the first pattern is predated by vicariance across the Torres Strait. Even if it is taken into account that the evidence for this sequence of events is very weak and often based on a single cladogram only, it remains curious that the two events appear to be so decisively placed in another sequence by BPA. This supports our conjecture

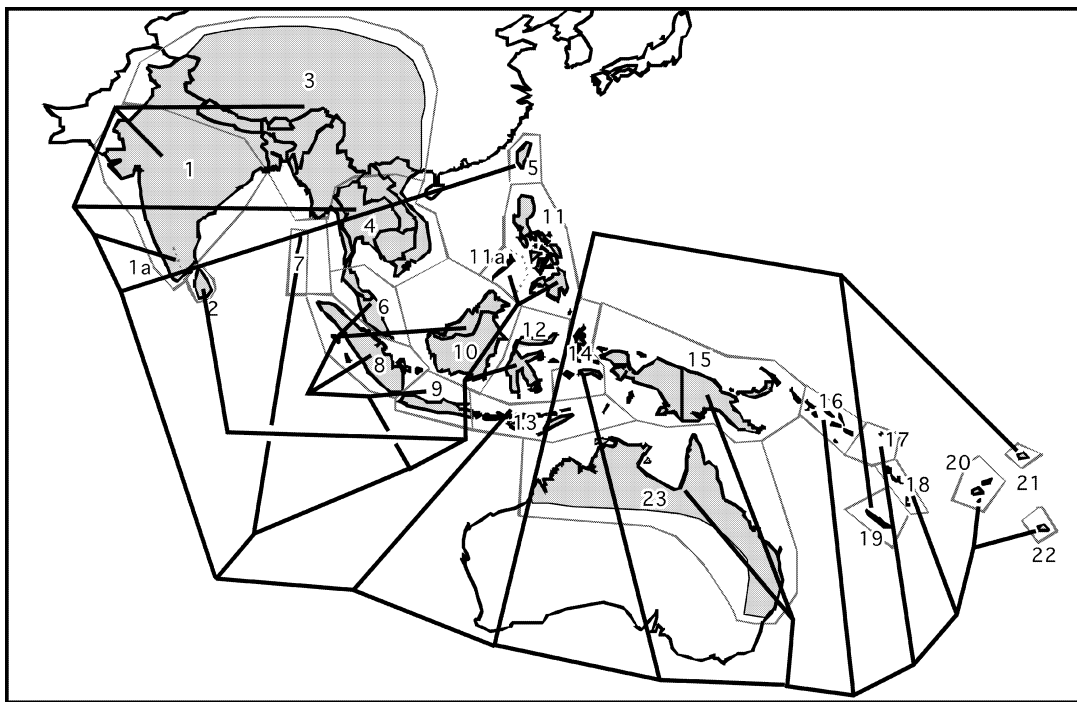


Figure 9 The majority rule consensus tree from the unrooted analysis mapped onto the topology of the region.

that the BPA-results reflect geographical proximity more than historical events.

Division of the data into two sets did not eliminate conflict from the data; instead, for each of the two subsets, resolution was much lower than for the complete analysis. It seems that each data set still contains clades displaying different biogeographical patterns. For the west–east data set, one reason might be that the two dispersal patterns recognized by van Steenis conflict. We do not consider this very likely, because the alternative pathway via Taiwan and the Philippines was described by van Steenis (1935, 1964) for montane taxa, which are not included in our analysis. However, clades predominantly adapted to a monsoonal climate might be secondarily absent from the Sunda plateau and could, therefore, cause conflict (van Steenis, 1979). Moreover, for the east–west data set, different patterns might be the result of some clades reacting to vicariance events as parts of the Australian plate broke away and drifted northward, while other clades display a dispersal pattern. One obvious way to distinguish between these possibilities would be by dating the different nodes in the cladograms using molecular data and the molecular clock hypothesis (Hillis *et al.*, 1996; Holloway, 1998). This would also distinguish possibly incompatible dispersal patterns of different age.

Because we did not have comparable molecular data available for the different clades in the total data set, we attempted to define other criteria with which to group together clades displaying similar biogeographic patterns. Amongst other things, we compared the consistency and retention indices of all clades when optimized onto the general area cladograms. Not surprisingly, some clades performed better than others, but we were unable to construct a satisfying, objective criterion to decide which clades are too different from the others to remain in the same data set. Next to vicariance and concerted dispersal along a newly available pathway, random (secondary) dispersal is an important process generating observed distribution patterns. Because of this, it is not very likely that two characters for the terminal units (i.e. two clades) will display fully compatible patterns. This in contrast to phylogenetic data, where horizontal transfer of character states is unlikely and where many consistent characters can be expected with accordingly high values for the consistency and retention indices.

When the individual cladograms were mapped onto the unrooted network, the rootings thus induced did not notably group around a limited number of branches. Inspection of Fig. 8 shows that the strongest support lies on the same branches as selected in Fig. 7, confirming to some extent our initial hypothesis that there are two patterns discernible in the distributions of clades occurring in the region.

CONCLUSION

Earth and life evolve together, but if there were a perfect correspondence, life would show a single pattern which would at the same time be the common pattern and a unique

one. That biogeography consists of the search for common patterns in different parts of the tree of life illustrates that processes like dispersal, extinction and non-vicariant (sympatric) speciation have disrupted a single pattern. Earth history does not determine life's pattern; it merely constrains it, to a degree that is variable both across time and across space. Our results indicate that in Southeast Asia we are dealing with an area where these constraints seem to be low. We have not been able to trace common patterns of biotic history with any confidence.

REFERENCES

- Adema, F. (1991) *Cupaniopsis* Radlk. (Sapindaceae): a monograph. *Leiden. Bot. Ser.*, **15**, 1–190.
- Adema, F. & van der Ham, R.W.J.M. (1993) *Cnesmocarpon* (gen. nov.), *Jagera*, and *Trigonachras* (Sapindaceae–Cupaniaceae): phylogeny and systematics. *Blumea*, **38**, 173–215.
- Andersen, N.M. (1989a) The coral bugs, genus *Halovelina* Bergroth (Hemiptera, Veliidae). I. History, classification, and taxonomy of species except the *H. malaya*-group. *Ent. Scand.*, **20**, 75–120.
- Andersen, N.M. (1989b) The coral bugs, genus *Halovelina* Bergroth (Hemiptera, Veliidae). II. Taxonomy of the *H. malaya*-group, cladistics, ecology, biology, and biogeography. *Ent. Scand.*, **20**, 179–227.
- Andersen, N.M. (1991) Cladistic biogeography of marine water striders (Insecta, Hemiptera) in the Indo-Pacific. *Austr. Syst. Bot.*, **4**, 151–163.
- Andersen, N.M. (1992) A new genus of marine water striders (Hemiptera, Veliidae) with five new species from Malesia. *Ent. Scand.*, **22**, 389–404.
- Andersen, N.M. (1998) Marine water striders (Heteroptera, Gerromorpha) of the Indo-Pacific: cladistic biogeography and Cenozoic paleogeography. *Biogeography and geological evolution of SE Asia* (eds R. Hall and J.D. Holloway), pp. 341–354. Backhuys Publishers, Leiden.
- Andersen, N.M. & Foster, W.A. (1992) Sea skaters of India Sri Lanka, and the Maldives, with a new species and a revised key to Indian Ocean species of *Halobates* and *Asclepios* (Hemiptera, Gerridae). *J. Nat. Hist.*, **26**, 533–553.
- Andersen, N.M. & Weir, T.A. (1994) The sea skaters, genus *Halobates* Eschscholtz (Hemiptera, Gerridae), of Australia: taxonomy, phylogeny, and zoogeography. *Invert Tax.*, **8**, 861–909.
- Axelius, B. (1990) The genus *Xanthophytum* (Rubiaceae). Taxonomy, phylogeny and biogeography. *Blumea*, **34**, 425–497.
- Axelius, B. (1991) Areas of distribution and areas of endemism. *Cladistics*, **7**, 197–199.
- Baehr, M. (1996) The ground beetle genus *Casnoidea* Castelnau: taxonomy, phylogeny and zoogeography (Insecta: Coleoptera: Carabidae: Odacanthinae). *Invert. Taxon.*, **10**, 1041–1084.
- van Balgooy, M.M.J., Hovenkamp, P.H. & van Welzen, P.C. (1996) Phytogeography of the Pacific – floristic and historical distribution patterns in plants. *The origin and evolution of Pacific island biotas, New Guinea to Eastern Polynesia: patterns and processes* (eds A. Keast and S.E. Miller), pp. 191–213. SPB Academic Publishing, Amsterdam.

- Bameul, F. (1997a) A revision of *Protosternum* Sharp (Coleoptera, Hydrophilidae). *Nouv. Rev. Ent. (N.S.)*, **14**, 17–41.
- Bameul, F. (1997b) A revision of *Mucetum* D'Orchymont and *Rhombosternum* Balfour-Browne (Coleoptera: Hydrophilidae) with a phylogenetic analysis of Protosternini. *Ann. Soc. Entomol. Fr. (N.S.)*, **33**, 375–403.
- Bauer, A.M. (1990) Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonner zoological monograph* 30. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.
- Beuk, P.L.Th. (1996) The *jacoona* complex of the genus *Dundubia* Amyot & Serville (Homoptera: Cicadidae): a taxonomic study of its species and a discussion of its phylogenetic relationships. *Contr. Zool.*, **66**, 129–184.
- de Boer, A.J. (1995) Islands and cicadas adrift in the west-Pacific. Biogeographic patterns related to plate tectonics. *Tijdschr. Entomol.*, **138**, 169–244.
- de Boer, A.J. & Duffels, J.P. (1996) Biogeography of Indo-Pacific cicadas east of Wallace's line. *The origin and evolution of Pacific island biotas, New Guinea to Eastern Polynesia: patterns and processes* (eds A. Keast and S.E. Miller), pp. 297–330. SPB Academic Publishing, Amsterdam.
- Brooks, D.R. (1990) Parsimony analysis in historical biogeography: methodological and theoretical update. *Syst. Zool.*, **39**, 14–30.
- Brooks, D.R. & McLennan, D.A. (1991) *Phylogeny, ecology, and behavior. A research program in comparative biology*. University of Chicago Press, Chicago.
- Buijsen, J.R.M. (1988) Revision of the genus *Fordia* (Papilionaceae: Millettieae). *Blumea*, **33**, 239–261.
- Corbet, G.B. & Hill, J.E. (1992) *The mammals of the Indomalayan region: a systematic review*, pp. 39–46. Natural History Museum Publications, Oxford University Press, Oxford.
- Cuccodoro, G. (1998) Revision and phylogeny of *Megarthrus* Curtis 1829 from New Guinea, New Caledonia and Fiji (Coleoptera, Staphylinidae, Proteininae). *Trop. Zool.*, **11**, 103–137.
- Dasuki, U.A. & Schot, A.M. (1991) Taxonomy of *Fordia* Hemsley (Papilionaceae: Millettieae). *Blumea*, **36**, 191–204.
- Duffels, J.P. (1977) A revision of the genus *Diceropyga* Stål, 1870 (Homoptera, Cicadidae). *Monogr. Ned. Entomol. Ver.*, **8**, 1–227.
- Duffels, J.P. (1982) *Brachylobopyga decorata* n. gen., n. sp. from Sulawesi, a new taxon of the subtribe Cosmopsaltriaria (Homoptera, Cicadoidea: Cicadidae). *Entomol. Ber.*, **42**, 156–160.
- Duffels, J.P. (1983) Taxonomy, phylogeny and biogeography of the genus *Cosmopsaltria*, with remarks on the historic biogeography of the subtribe Cosmopsaltriaria (Homoptera: Cicadidae). *Pac. Insects Monogr.*, **39**, 1–127.
- Duffels, J.P. (1989) The Sulawesi genus *Brachylobopyga* (Homoptera, Cicadidae). *Tijdschr. Entomol.*, **132**, 123–127.
- Duffels, J.P. (1990a) *Dilobopyga janstocki* n. sp., a new cicada endemic to Sulawesi (Homoptera, Cicadidae). *Bijdr. Dierk.*, **60**, 323–326.
- Duffels, J.P. (1990b) Biogeography of Sulawesi cicadas (Homoptera: Cicadoidea). *Insects and the rain forests of South East Asia (Wallacea)* (eds W.J. Knight and J.D. Holloway), pp. 63–72. Royal Entomological Society, London.
- Duffels, J.P. (1997) *Inflatopyga*, a new cicada genus (Homoptera: Cicadoidea: Cicadidae) endemic to the Solomons Islands. *Invertebr. Taxon.*, **11**, 549–568.
- Eriksson, T. (1998) AutoDecay 4.0.1. Program and documentation. Available from the author at <http://www.bergianska.se/personal/TorstenE/>.
- Etman, B. (1994) A taxonomic and phylogenetic analysis of *Rhysotoechia* (Sapindaceae). *Blumea*, **39**, 41–71.
- Goloboff, P. (1997) Pee-wee, Nona. Programs and documentation. Distributed by the author.
- Hall, R. (1995) S.E. Asia Reconstructions 50–0 Ma. http://glsun2.gl.rhnc.ac.uk/seasia/html/plate_tect.html.
- Hillis, D.M., Mable, B.K. & Moritz, C. (1996) Applications of molecular systematics: the state of the field and a look to the future. *Molecular systematics*, 2nd edn (eds D.M. Hillis, C. Moritz and B.K. Mable), pp. 515–543. Sinauer Associates, Inc., Sunderland, MA.
- Holloway, J.D. (1998) Geological signal and dispersal noise in two contrasting groups in the Indo-Australian tropics: R-mode analysis of pattern in Lepidoptera and cicadas. *Biogeography and geological evolution of SE Asia* (eds R. Hall and J.D. Holloway), pp. 291–314. Backhuys Publishers, Leiden.
- Hopkins, H.C.F. (1994) The Indo-Pacific species of *Parkia* (Leguminosae: Mimosoideae). *Kew Bull.*, **49**, 181–243.
- Hovenkamp, P. (1997) Vicariance events, not areas, should be used in biogeographic analysis. *Cladistics*, **13**, 67–79.
- Hutterer, R. (1993) Order Insectivora (Family Soricidae, subfamily Crocidurinae, genus *Crocidura*). *Mammal species of the world. A taxonomic and geographic reference*, 2nd edn, pp. 81–98 (eds D.E. Wilson and D.M. Reeder). Smithsonian Institution Press, Washington.
- Klackenberg, J. (1995) Taxonomy and phylogeny of the SE Asian genus *Genianthus* (Asclepiadaceae). *Bot. Jahrb. Syst.*, **117**, 401–467.
- Kruizinga, J., van Scheindelen, H.J. & de Vogel, E.F. (1997) Revision of the genus *Bromheadia*. *Orch. Monogr.*, **8**, 79–118.
- Luckow, M. & Hopkins, H.C.F. (1995) A cladistic analysis of *Parkia* (Leguminosae: Mimosoideae). *Am. J. Bot.*, **82**, 1300–1320.
- Mayr, E. (1944) Wallace's line in the light of recent zoogeographic studies. *Q. Rev. Biol.*, **19**, 1–14.
- Moulds, M.S. (1990) *Australian cicadas*. New South Wales University Press, Kensington.
- Nelson, G. & Ladiges, P.Y. (1996) Paralogy in cladistic biogeography and analysis of paralogy-free subtrees. *Amer. Mus. Novitat.*, **3167**, 1–58.
- Page, R.D.M. (1995) *TreeMap 1.0b*. Computer program and documentation. Distributed by the author, Glasgow.
- Repetur, C.P., van Welzen, P.C. & de Vogel, E.F. (1997) Phylogeny and historical biogeography of the genus *Bromheadia* (Orchidaceae). *Syst. Bot.*, **22**, 465–477.
- Ridder-Numan, J. (1996) Historical biogeography of the Southeast Asian genus *Spatholobus* (Legum. – Papilionoideae) and its allies. *Blumea Supplement*, **10**, 1–144.
- Ruedi, M. (1995) Taxonomic revision of shrews of the genus *Crocidura* from the Sunda Shelf and Sulawesi with description of two new species (Mammalia: Soricidae). *Zool. J. Linn. Soc.*, **115**, 211–265.

- Ruedi, M. (1996) Phylogenetic evolution and biogeography of Southeast Asian shrews (genus *Crocidura*: Soricidae). *Biol. J. Linn. Soc.*, **58**, 197–219.
- Schot, A.M. (1991) Phylogenetic relations and historical biogeography of *Fordia* and *Imbralyx* (Papilionaceae–Millettieae). *Blumea*, **36**, 205–234.
- van Steenis, C.G.G.J. (1935) On the origin of the Malaysian mountain flora. Part 2. Altitudinal zones, general considerations and renewed statement of the problem. *Bull. J. Bot. Buitenzorg Sér. III*, **13-3**, 289–417.
- van Steenis, C.G.G.J. (1964) Plant geography of the mountain flora of Mt. Kinabalu. *Proc. R. Soc. B*, **161**, 7–38.
- van Steenis, C.G.G.J. (1979) Plant-geography of east Malesia. *Bot. J. Linn. Soc.*, **79**, 97–178.
- Wofford, D.L. (1999) PAUP*. *Phylogenetic analysis using parsimony (*and other methods)*, Version 4.0b2a. Sinauer Associates, Sunderland, MA.
- Turner, H. (1995) Cladistic and biogeographic analyses of *Arytera* Radlk. & *Mischarytera* gen. nov. (Sapindaceae) with notes on methodology and a full taxonomic revision. *Blumea Supplement*, **9**, 1–230.
- Wallace, A.R. (1860) On the zoological geography of the Malay Archipelago. *J. Proc. Linn. Soc. Lond.*, **4**, 172–184.
- van Welzen, P.C. (1989) *Guioa* Cav.: taxonomy, phylogeny, and historical biogeography. *Leident Bot. Ser.*, **12**, 315.
- van Welzen, P.C. (1994) Taxonomy, phylogeny, and geography of *Neoscortechinia* Hook.f. ex Pax (Euphorbiaceae). *Blumea*, **39**, 301–318.
- van Welzen, P.C. (1995) Taxonomy and phylogeny of the Euphorbiaceae tribe Erismantheae G.L. Webster (*Erismantus*, *Moultonianthus*, and *Syndyophyllum*). *Blumea*, **40**, 375–396.
- van Welzen, P.C., Piskaut, P. & Windadri, F.I. (1992) *Lepidopetalum* Blume (Sapindaceae): taxonomy, phylogeny, and historical biogeography. *Blumea*, **37**, 439–465.
- Zandee, M. & Roos, M.C. (1987) Component-compatibility in historical biogeography. *Cladistics*, **3**, 305–332.

Appendix Analysis of vicariant nodes

Vicariant nodes in the cladograms were identified on the basis of distribution maps (where necessary, reconstructed from distributional data), and grouped into common patterns, representing putative vicariance events with a more or less clearly identified location. The nodes are named by species branching off in each daughter lineage. Nodes involving only areas outside Malesia are omitted.

Pattern A: vicariance between Continental Asia and Malesia

Identified on the basis of six nodes involving Continental Asia and Malesian (partial) areas

Genianthus – (*ellipticus* – *hastatus*)

Spatholobus – (*acuminatus* – *albus*) (*auricomus* – *gyrocarpus*), (*dubius* – *harmandii*)

Fordia – (*leptobotrys* – *albiflora*)

Hydrophilidae – (*Rhombosternum minutum* – *wagneri*)

Pattern B: vicariance between New Guinea and various more Westerly areas

Guioa – (*patentinervis* – *melanopoda*)

Cupaniopsis – (*celebica* – *platycarpa*)

Rhysotoechia – (*congesta* – *grandifolia*)

Neoscortechinia – (*forbesii* – *kingii*)

Lepidopetalum – (*micans* – *montanum*)

Haloveloides – (*browni* – *sundaensis*)

Pattern C: vicariance across Torres Strait

Arytera – (*foveolata* – *novaebritanniae*), (*pauciflora* – *musca*)

Rhysotoechia – (*elongata* – *flavescens*)

Cupaniopsis – (*wadsworthii* – *hypodermatica*), (*newmannii* – *macropetala*)

Pattern D: vicariance between the Southwestern margin of the Indian subcontinent and Malesia

Based on five nodes involving Sri Lanka/Kerala/Goa and a more easterly area.

Spatholobus – (*crassifolius* – *purpureus*)

Bromheadia – (*srilankense* – *coomansii*)

Casnoidea – (*celebensis* – *ceylonica*)

Hydrophilidae – (*Protosternum obscurum* – *Pr. abnormale* + *hammondi*)

Haloveloides – (n. sp. Goa – *malaya*)

Pattern E: vicariance involving Sumatra and a more easterly area

Sumatra is present in all three, but a different sister-group distribution is involved in each of these patterns.

Fordia – (*brachybotrys* – *stipularis*) (*ngii* – *nivea*)

Crocidura – (*butanis* – *orientalis*) (*lepidura* – *musseri*)

Appendix *continued***Pattern F:** vicariance involving Peninsular Papua New Guinea and more western parts of New Guinea*Rhysotoechia* – (*bilocularis* – *flavescens*)*Guioa* – (*hospita* – *scalariformis*)*Arytera* – (*densiflora* – *musca*)**Pattern G:** vicariance involving Borneo and a more northerly area*Xanthophytum* – (*borneense* – *fruticosum*)*Genianthus* – (*valvatus* – *rectinervis*)*Spatholobus* – (*apoensis* – *latistipulus*) (slight amount of back-dispersal)**Pattern H:** vicariance involving an endemic group on Andamans/Nicobars and a more easterly area*Genianthus* – (*nicobarensis* – *maingayi*)*Lepidopetalum* – (*montanum* – *perrottetii*)Hydrophilidae – (*Protosternum hanseni* – *longicarinatum*)**Pattern I:** vicariance involving Malay Peninsula and a more easterly area containing at least Borneo*Bromheadia* – (*rupestris* – *crassiflora*)*Spatholobus* – (*dubius* – *viridis*)**Pattern J:** vicariance involving west Java and a more Northerly area*Xanthophytum* – (*fruticosum* – *ferrugineum*)*Genianthus* – (*macrophyllus* – *maingayi*)**Pattern K:** separating east from west New Guinea*Guioa* – (*membranifolia* – *contracta*), (*pseudoamabilis* – *pteropoda*)**Pattern L:** separating Fly and Markham River areas in New Guinea*Mischarytera* – (*macrobotrys* – *lautereriana*)*Arytera* – (*morobeana* – *musca*)**In the cladograms the nodes occur in the following order:**

Cladogram	Ordered nodes	Event sequence
<i>Arytera</i>	F–L–C	F–L–C–B
<i>Cupaniopsis</i>	C–B	F–L–C–B
<i>Fordia</i>	A–E	A basal
<i>Genianthus</i>	A–G	A basal
	H–J	
<i>Lepidopetalum</i>	B–H	
<i>Rhysotoechia</i>	F–C	F–L–C–B
<i>Spatholobus</i>	A–I	A basal
<i>Xanthophytum</i>	G–J	
Hydrophilidae	D–I	