

Geological signal and dispersal noise in two contrasting insect groups in the Indo-Australian tropics: R-mode analysis of pattern in Lepidoptera and cicadas

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Abstract

Biogeographic methodology and philosophy are reviewed within the context of obtaining an objective means of identifying geological signal in a complex archipelagic system where dispersal has played a major role in the development of biogeographic pattern. A method of R-mode analysis is explored that associates phylogenetically related groups of species (clades) which share common features in terms of geographical representation of endemics and more widespread species. Such associations of clades, perhaps compatible with the panbiogeographic concept of generalised tracks, can provide the basis for an independent analysis of area relationships, facilitating the identification of contrasting patterns in the associations which may reflect spatially or temporally different episodes in the past geography of the archipelago. The method is applied to data for Lepidoptera and cicadas on the basis of areas of endemism recognised for the former and illustrates both the differences in pattern between the two, due to much more restricted powers of dispersal of cicadas, and common features that probably have a geological basis. A second analysis for cicada data, based on their much smaller areas of endemism, reveals a lack of clear groupings similar to that of the Lepidoptera at a grosser geographical scale, indicating that similar stochastic pattern generation through dispersal over the geological template may occur, but in a more localised fashion. The results are assessed in relation to geological events, in particular, the independent evolution of groups in the regions of Sundaland, the Sulawesi area and inner and outer Melanesian archipelagos. Evidence is presented for association of such groups on broader northern (Philippines and outer Melanesian archipelagos) and southern (Sundanian, Banda arc, inner Melanesian archipelago and Australia) axes. Sulawesi (or its components) appears to have interacted with both axes in a complex fashion.

Introduction

Geologists investigating the tectonic history of

the Indo-Australian tropics would probably be aware of the interest shown by biogeographers in the results of their work and the possibility for some mutual benefit to be gained by the sharing of ideas and data. They might also be puzzled at the frequent lack of agreement amongst biogeographers on the best way to approach data on plant and animal distributions, particularly where the objective was to derive from them information on Earth history.

Indeed there has been a danger in the not too distant past that biogeographers would polarise into two or three extreme groups. One rather traditionalist group was accused by the other, more iconoclastic groups of embracing biological dispersal to explain all biogeographic pattern. Each dispersal event was unique and therefore did not generate scientifically testable hypotheses. Such scenarios were condemned as story-telling, and dispersal was dismissed as random and therefore uninformative.

In attempts to secure biogeography on a sound methodological basis of hypothesis testing and falsification, there developed a counter-tendency to reject any notion of biological dispersal and veer to another extreme where modern biogeographic pattern was considered to have developed by a process of fragmentation, or vicariance, of both Earth and life together, with the potential to discover, using the new methodology, one unique set of area relationships from biological data that would encapsulate earth history. Conflicting biogeographic patterns in even very small archipelagos led some biogeographers, who might be termed geologi-

cal dispersalists, to postulate complex scenarios of island or terrane integration that would, if taken to their limits, rival the story-telling of the biological dispersalists. Page and Lydeard (1994) have reviewed the debate in relation to biogeography in the Caribbean archipelago.

The philosophies of three different biogeographic schools: cladistic/vicariant, dispersalist/migrationist and panbiogeographic, have been contrasted by Wilson (1991) in relation to a number of criteria, such as methods of analysis used, assumptions about dispersal, evolution and other process factors, attitudes to fossil evidence, non-structural physical factors such as climate, and the explanatory and predictive powers of the models. From these philosophies has emerged a general consensus on the need to separate as far as possible the analysis of biogeographic pattern from considerations of the processes that have led to development of such pattern. But disagreement has remained on the means whereby this may best be done, eliminating the likelihood of circularity of argument, yet not introducing such constraints in the cause of methodological rigour that the results foreclose on some process option in subsequent interpretation. Crisci *et al.* (1991) stated, "Although it is valid to investigate the existence of a unique pattern of interrelationships among areas of endemism, it cannot be accepted as an *a priori* assumption of the analysis".

Arguments with much of the middle ground excluded are never ultimately very productive in a real and messy world, and there are signs of a welcome return to a more pragmatic approach to analysis of biogeographic pattern in relation to earth history (*e.g.*, Page, 1989; Page and Lydeard, 1994; Wagner and Funk, 1995). There are still many potential pitfalls in the interpreting of biogeographic pattern: for example, the types of distribution patterns in the New Zealand biota that have been related to tectonic arc structures in the islands (*e.g.*, Craw, 1989) are also manifest in the distributions of plants introduced by Europeans, and suggested for these to have a climatic basis by Wilson *et al.* (1992).

There are a number of problems in attempting to investigate biogeographic pattern in relation to geological history in the Indo-Australian tropics. If the geological hypotheses current today for the history of the archipelago are taken at face value, then biological dispersal is likely to be the primary means whereby ancestral ranges of higher taxa (natural groupings of species) are established. Thereafter, fragmentation and vicariance can lead to biogeographic pattern in-

formative about the juxtaposition of land at the time when that dispersal occurred. But subsequent dispersal events equally will obscure such pattern, possible overlaying it with pattern reflecting a more recent juxtaposition of lands. Any methodology of pattern analysis must therefore optimise the possibility of recognising sequential, overlaid patterns. Also, terrane accretion in areas such as the Sunda shelf and New Guinea may lead to biotic assemblages that are disharmonic and of diverse affinity (Polhemus, 1996).

Dispersal, though random, stochastic, need not be uninformative (see also Jong, 1998 this volume). Its frequency will relate to factors such as distance and area among the islands existing at any point in geological time. This was modelled for island systems by MacArthur and Wilson (1967), shown to hold in the establishment of the biota of Norfolk Island where the source areas are unambiguous (Holloway, 1977, 1996), and thence applied to help understand the biological enrichment of Sulawesi (Holloway, 1991) and to highlight anomalies in the biogeographical affinities of elements of the biota of Lord Howe Island (Holloway, 1977, 1979).

This stochastic basis for interaction between island biotas, with likelihood of dispersal from one to another based on their distance and respective areas, offers one means whereby biogeographic pattern in dispersive groups of organisms can provide pointers to geological history in complex archipelagic systems. But this is realised through the methods of phenetic, rather than cladistic biogeography. There is the additional prospect, discussed by Roger Butlin at the meeting that led to this book, of modelling dispersal and speciation processes over different geological scenarios for the region, contrasting the resulting distribution patterns with actual ones. Again, phenetic methods of analysis may be as appropriate for this as cladistic ones. Such modelling has yet to be undertaken in a biogeographic context, but has been deployed to help understand Polynesian colonisation of the Pacific and options for coconut dispersal across it (Levison *et al.*, 1969; Ward and Brakefield, 1992).

Phenetic methods have been applied to data sets for mobile animal groups in the Indo-Australian tropics. Holloway and Jardine (1968) derived distance measures between major islands in terms of their faunal (species-level) similarities using data for butterflies, birds and bats. They used non-metric multidimensional scaling to find two-dimensional plots of points repre-

senting the islands that best summarised this array of 'faunal distances'. The plots for butterflies and birds showed high correlation with current geography, support for the predominance of a stochastic, dispersal mode of pattern generation within the group.

The authors went on to suggest that, where the plots departed from such correlation, this might reflect some aspects of past geography, particularly where plots for different groups of organisms showed the same trends. Thus, close association of peninsular Malaysia, Sumatra, Borneo and Java was interpreted in terms of faunal intermingling facilitated by union of these lands on the Sunda shelf during Pleistocene low sea-levels. Sulawesi was placed well separate from Borneo, with the Philippines in an intermediate position, perhaps indicative of greater isolation for the former in the past, interaction being primarily through the latter, perhaps through greater exposure of geological structures between the Minahasa peninsula of Sulawesi, Sangihe and Mindanao. Relationships between the northern and southern Moluccas, New Guinea, the Bismarck Islands and the Solomons also departed from current geography, with the scaling method indicating high stress values between the two-dimensional summary and the raw data, perhaps a measure of the complex geological history of what is now known to be a composite zone of several different structures, even within the island of New Guinea itself, as will be seen later.

Indeed, the history of the archipelago is as much one of fusion and convergence of terranes and other structures such as island arcs as of their fragmentation and divergence (Polhemus, 1996). Hence the focus of the cladistic approach to biogeography, attempting to portray area relationships in the form of a dichotomous tree structure from analysis of biogeographic pattern in plant and animal groups with taxa endemic to those areas needs to be examined carefully. It may thus not be possible to represent the hypotheses of geological evolution of the Indo-Australian archipelago in dichotomous tree form, though attempts have been made (Turner, 1995; Boer, 1995b). Yet this is seen as an important prerequisite for application of cladistic biogeographic methods (Morrone and Carpenter, 1994). Page and Lydeard (1994: their Fig.1) present what are stated to be geological area cladograms for the Caribbean from an earlier paper by Rosen. These lack a time dimension, each perhaps representing a snapshot of geographical juxtaposition of areas of endemism at

five points in geological time from the mid-Cenozoic to the present.

Most recent references to the analysis of Holloway and Jardine (1968) have been in relation to its use of phenetic methodology (cluster analysis of the matrix of faunal dissimilarity coefficients that formed the basis for the non-metric multidimensional scaling just described) to generate just such a tree structure, and this has been compared with results deriving tree structures using the methods of cladistics (*e.g.*, Holloway (1991), using Lepidoptera data for the same area). A point of interest in this comparison relevant to the chapter by Jong (1998 this volume) is that the phenetic analysis of Lepidoptera distributions, reflecting overall faunal similarities, paired the northern and southern Moluccas, whereas the cladistic analyses, reflecting phylogenetic relationships, did not, grouping them independently with New Guinea (Holloway, 1991): this is entirely consistent with the conclusions of Jong.

But the primary purpose of Holloway and Jardine (1968) was to illustrate the complementarity of two approaches to analysis of distributional data, classifying areas in terms of relationships of their biotas (Q-mode), and taxa in terms of their distribution amongst areas (R-mode). This distinction perhaps also encapsulates the divergence between the cladistic and panbiogeographic schools of biogeography, a distinction rarely referred to in the literature, exceptions being Simberloff and Connor (1980) and Page (1989).

It is the purpose of this chapter to return to this complementarity and to suggest it offers an escape from the search for a unique dichotomous tree hypothesis of area relationships that is often the focus of cladistic biogeographic methods. It does not foreclose on the possibility discussed earlier that data to hand may contain several different sets of area relationships that may derive from different periods in geological time, offering a series of biological snapshots of past geography: the dispersive vicariance of Duffels (1983).

In addition, by comparing data from the Lepidoptera (the speciality of the author), offering a wide range of dispersal abilities across the taxa, with those from the cicadas, with a much higher degree of local endemism and very few extremely widespread taxa and therefore generally probably much less dispersive, it is possible to compare pattern in a group where stochastic pattern generation predominates with one where vicariant pattern generation is far more

prevalent, as suggested by Boer (1995b).

Though groups of the second type may prefer pattern that is much more informative in terms of geology, their limited powers of dispersal mean that their diversity in archipelagos will be very much lower than in mainland areas and lower than in other, more mobile groups among the islands, and hence the sample of area cladograms available for analysis of congruence will be relatively small. An extreme example of this is shown by major freshwater fish groups, virtually restricted to continental shelf areas in the Indo-Australian tropics (Darlington, 1957). Thus, the cicadas are represented in the archipelagos east of the Sunda shelf and north of Australia mostly by two major lineages (Boer, 1995b). The Lepidoptera are represented by hundreds, though a number of families, such as the Lasiocampidae, Bombycidae, Eupterotidae and Limacodidae, also exhibit significantly reduced diversity in the more isolated archipelagos. Page and Lydeard (1994) advocated selecting groups with maximal endemism amongst their taxa but, as will be seen in the analyses, groups showing endemism in the remoter archipelagos tend to have taxa that are uninformatively widespread in those adjacent to continental areas, and those with endemism in the latter rarely penetrate the remoter archipelagos.

An R-mode method of pattern analysis

The phylogenetic data for Indo-Australian insect groups, particularly Lepidoptera, that are accumulating do not lend themselves easily to Q-mode cladistic biogeographic analysis. Derivation of a single pattern of area relationships is virtually impossible using Component Analysis (too much sympatry, too many widespread species), and Parsimony Analysis methods yield results that appear to offer little advance over phenetic ones (Holloway, 1991). Morrone and Carpenter (1994) compared these and a further method in relation to a range of data sets and concluded that there still remained considerable problems in their application, and that these derived primarily from the effects of dispersal. There are also major computational problems in the application of such methods. Nelson and Ladiges (1996) have suggested that their protocol for eliminating geographical paralogy (repetition) in cladograms circumvents these problems. Turner (1995: p.103 *et seq.*) encountered similar problems in his analyses of Australasian plant data. The data suggest there may indeed

by a multiplicity of contrasting patterns, possibly of different ages and certainly blurred by dispersal events. In addition, there is no concordance of pattern between montane-restricted and lowland restricted groups (Holloway, 1970, 1986a), though this would be predicted under a purely vicariant model of biological response to geological change.

An R-mode approach sets out to identify distinct groupings of patterns and will therefore offer a better prospect for at least a preliminary biogeographic analysis in the Indo-Australian tropics. Identification of such groupings could provide a prelude to a set of Q-mode area analyses incorporating taxa from each general pattern so identified: the complementarity of methodology advocated by Holloway and Jardine (1968). Trees for these taxa could be assessed for, and 'cleaned' of paralogy using the approach of Nelson and Ladiges (1996), prior to an analysis of congruence in area-relationships. However, this chapter will focus only on the preliminary R-mode analysis, as the sample of cladistic analyses of groups is still relatively small. When more analyses are available, it may prove that some of the R-mode derived groups are distinguished from each other merely by differential paralogy rather than by inherently different structure of area relationships, but this should not be an *a priori* assumption. The development of paralogy itself may be of interest for investigation of aspects of speciation and enrichment of biotas in biodiversity studies (*e.g.*, the widely different species-richness of Australian versus New Guinea genera in the cicada tribe Chlorocystini referred to later).

The initial R-mode method of Holloway and Jardine (applied to further Lepidoptera data by Holloway, 1973, 1974, 1979) classified taxa into faunal elements merely on similarity of presence or absence in the areas incorporated in the study (effectively areas of endemism). The results of such analyses are not dissimilar to the sort of track analyses that have been made by panbiogeographers (*e.g.*, Craw, 1989). An extension of this (Holloway, 1969) grouped higher taxa, mostly genera, in terms not just of presence or absence in each area but also of richness in species – a faunal centre analysis. This approach grouped genera together that shared centres of richness, or massing centres, as well as overall distribution.

A modified method is presented here that incorporates aspects of both these approaches. It classifies higher taxa as in the second method, but their component species are first assigned to

distributional categories (faunal elements or generalised tracks) identified by the first. Representation of species in each higher taxon across these categories is tabulated and converted to a percentage. Pairwise comparisons of the higher taxa give a measure of similarity of representation across the categories for each pair. These similarity coefficients are then submitted to cluster analysis to identify significant groupings of the higher taxa, where similarity of representation of their component species amongst the distributional categories is high.

The single-link cluster analysis method is used. A linkage diagram is also constructed to assess further the structure and cohesion of the single-link clusters. This approach, although somewhat cumbersome, gives better retrieval of the information content of the array of similarity coefficients than do averaging and centroid clustering methods, and is an *ad hoc* and illustrative version of the non-hierarchical clustering method of Jardine and Sibson (1968). A more detailed discussion of the merits of this approach was presented by Holloway (1977, pp. 163-169).

At this stage no information on phylogenetic structure within the higher taxonomic groups is incorporated in the analysis. However, the application of this R-mode method is facilitated by advances in the systematics of the Lepidoptera since the earlier analyses referred to above, and also improved data on their distribution. The arrival of cladistic methodology and the sharpened concept of monophyly associated with it has meant that it is possible to identify and select more reliably groups that are likely to be monophyletic. The same applies to the cicada data.

The data

Lepidoptera

Genera, subgenera or clades (monophyletic groups of species within genera) with five or more species (up to about 30) were selected from recent taxonomic publications. Data for 85 monophyletic groups were located. Phylogenetic hypotheses (cladograms) were available for 38 of these: the rest are from recent revisions where the morphological definition of the groups is unambiguous. However, a number of these are rather large, and the method might most appropriately be applied to groups of a more uniform size range (e.g., 5-15 species), equivalent to the subtrees of Nelson and Ladiges

(1996). All these groups are restricted to the Indo-Australian tropics and subtropics. The data are drawn from the following:

Arctiidae: *Byrsia*, *Neoscaptia* (Holloway, 1984).

Drepanidae: *Macrauzata* (Inoue, 1993a); *Tridrepana* (Watson, 1957).

Geometridae: *Tanaorbinus rafflesii* group (Holloway, 1982); *Crasilogia*, *Nadagarodes*, *Polyacme* (Holloway, 1984); *Astygisa vexillaria* group, *Bracca* (3 clades), *Probitbia* (Holloway, 1991); *Ectropidia*, *Zebeba* (Holloway, 1991, 1993); *Omiza*, *Peratophyga*, *Petelia medardaria* group (Holloway, 1993); *Dindica* (Inoue, 1990); *Dasyboarmia* (Sato, 1987; Holloway, 1993).

Hesperiidae: *Matapa* (Jong, 1983).

Lasiocampidae: *Arguda*, *Lajonquiereia*, *Radhica*, *Syrastrena* (Holloway, 1987a).

Limacodidae: *Susica* (Holloway, 1982, 1986b); *Darna* (Holloway, 1986b; Holloway *et al.*, 1987); *Setora*, *Thosea* (Holloway *et al.*, 1987); *Narosa concinna* group (Holloway, 1991).

Lycaenidae: *Drupadia* (Cowan, 1974); *Curetis* (Eliot, 1990); *Allotinus*, *Logania*, *Miletus* (Eliot, 1986); *Caleta*, *Catochrysops*, *Catopyrops*, *Danis*, *Jamides* (*bochus* and *celeno* groups), *Nacaduba*, *Prosotas*, *Psychonotis*, *Udara* (subgenera *Udara*, *Perivaga*, *Selmanix*) (Hirowatari, 1992); *Callictita* (Parsons, 1986).

Noctuidae: *Lacera* (Holloway, 1979); *Achaea serva* group, *Avitta*, *Ophyx* (Holloway, 1984); *Aegilia*, *Paectes cristatrix* group (Holloway, 1985); *Chasmina* (Holloway, 1989); *Anomis* subgenus *Rusicada* (Holloway and Nielsen, 1998).

Notodontidae: *Besida*, *Cerura kandyia* group, *Phalera* subgenus *Erconholda*, *Phalera grotei* group, *Teleclita strigata* group (Holloway, 1987b).

Nymphalidae: *Euploea* (2 clades), *Ideopsis*, *Parantica* (4 clades) (Ackery and Vane-Wright, 1984); *Tellervo* (Ackery, 1987); *Ptychandra* (Banks *et al.*, 1976); *Chersonesia*, *Cyrestis* (Holloway, 1973); *Idea* (Kitching *et al.*, 1986); *Polyura* (2 clades) (Smiles, 1982).

Papilionidae: *Graphium* (3 clades) (Saigusa *et al.*, 1977).

Pieridae: *Eurema* (2 clades) (Yata, 1990).

Pyrilidae: *Vitessa* (Munroe and Shaffer, 1980).

Saturniidae: *Attacus* + *Coscinocera* (Peigler, 1989).

Thyrididae: *Herdonia* (Inoue, 1993b); *Misalina* (Whalley, 1976).

The distributional categories recognised include endemism to individual islands or tight island groups, together with wider categories (e.g., Sundaland, Melanesian, Coral Sea, Indo-Australian) identified by the faunal element analyses for Lepidoptera by Holloway (1973, 1974, 1979).

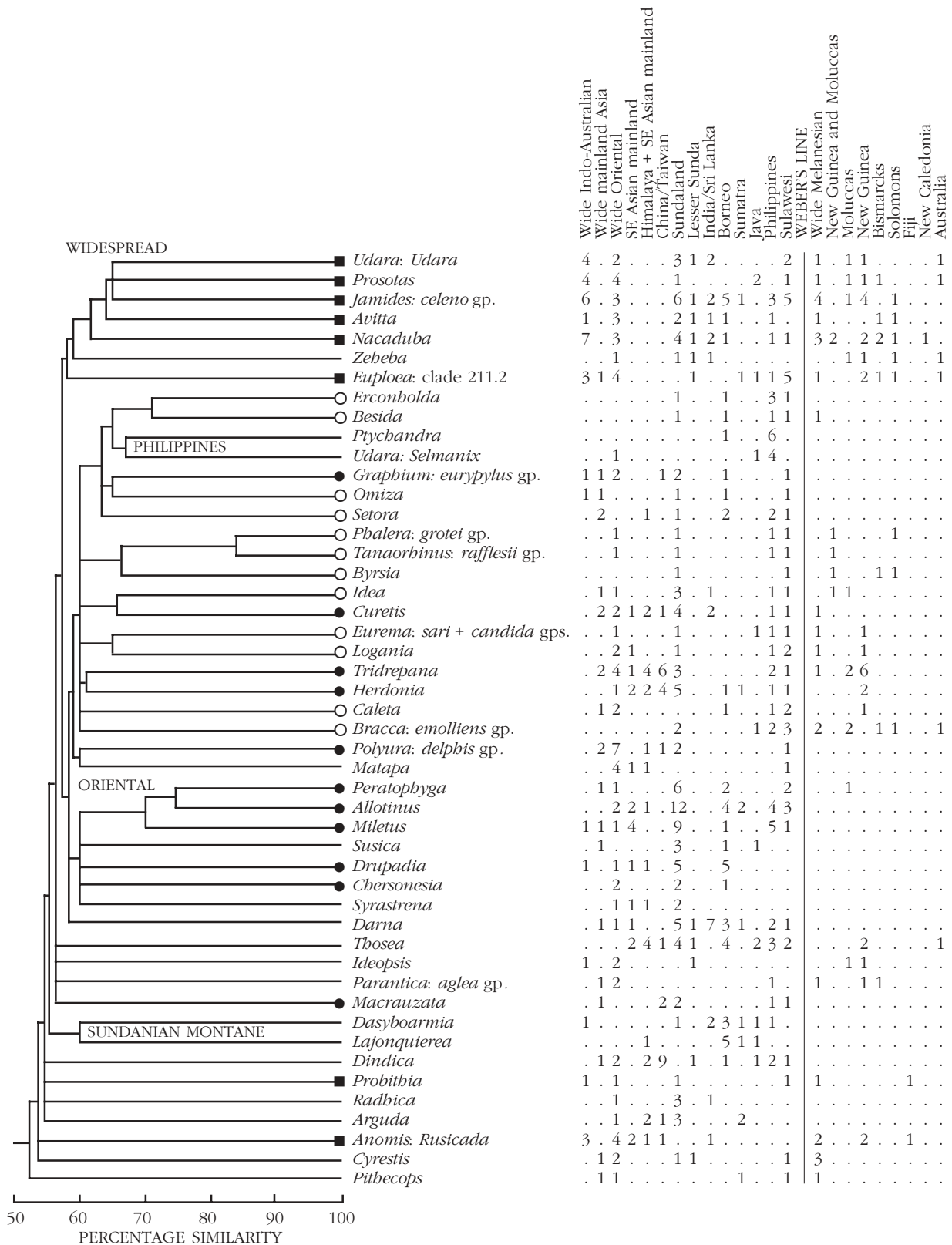


Fig. 1. Single-link dendrogram and raw data for most of the Oriental cluster from the R-mode analysis of Lepidoptera taxa. In the table of raw data the numbers of species of each taxon falling into each distributional category (listed at top) are indicated. Symbols are used to facilitate cross-reference with the clusters recognised on the linkage diagram of Figs. 3 and 4 and discussed in the text. The rest of the dendrogram and data are illustrated in Fig. 2.

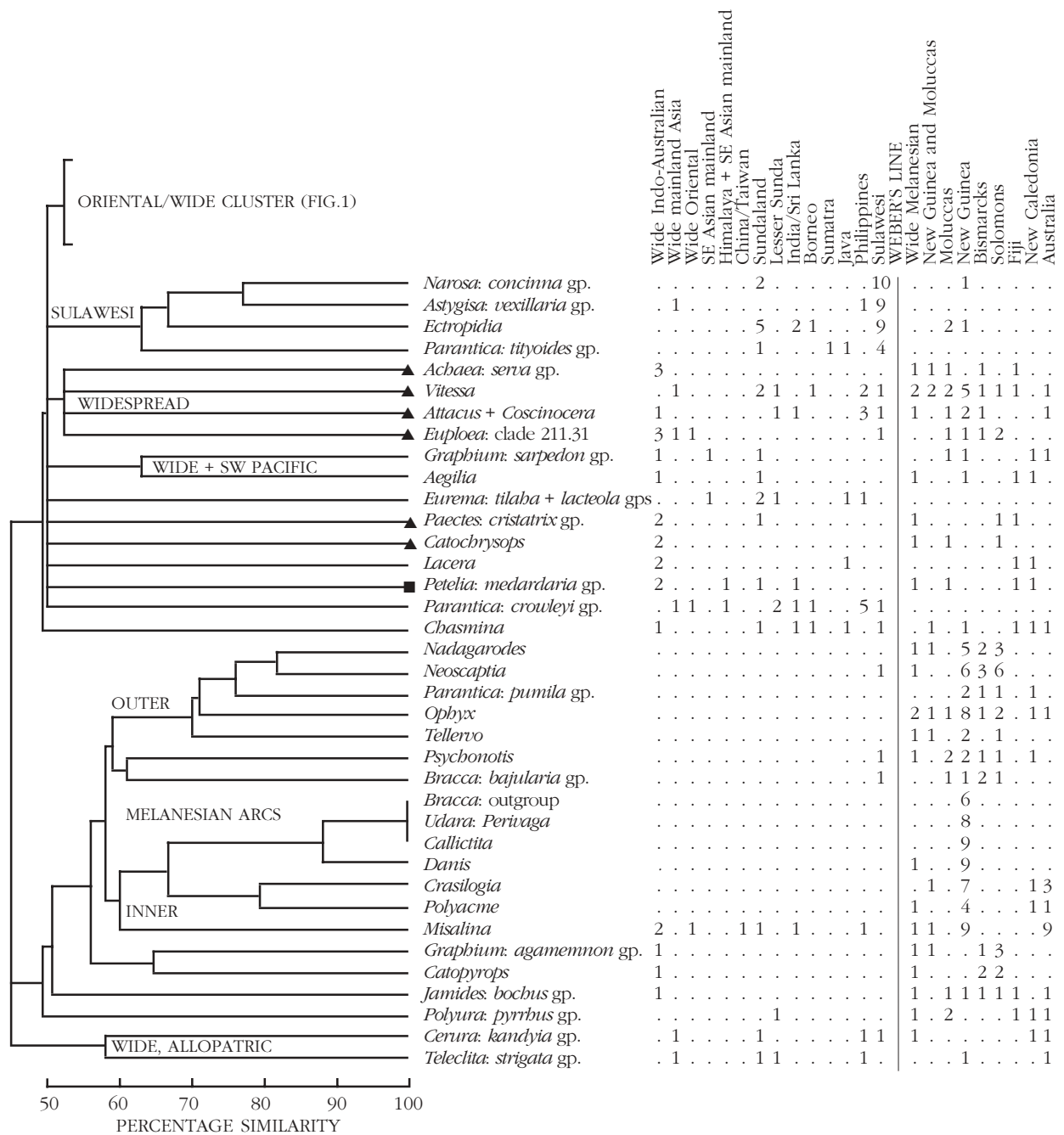


Fig.2. Continuation of the single-link dendrogram shown in Fig.1 from the R-mode analysis of Lepidoptera taxa. In the table of raw data the numbers of species of each taxon falling into each distributional category (listed at top) are indicated. Symbols are used to facilitate cross-reference with the clusters recognised on the linkage diagram of Figs.3 and 4 and discussed in the text.

Cicadas

The majority of the data for the cicadas is published by the group of researchers at the University of Amsterdam who have developed phylogenies for virtually all cicada groups in Sulawesi and from the Moluccas eastwards.

These workers have recently published major biogeographic syntheses of this work (Boer, 1995a, b; Boer and Duffels, 1996a, b), that also give comprehensive reference to the original taxonomic monographs and distributional data. Additional Oriental groups that extend into the archipelago in the genus *Cryptotympana*, revised

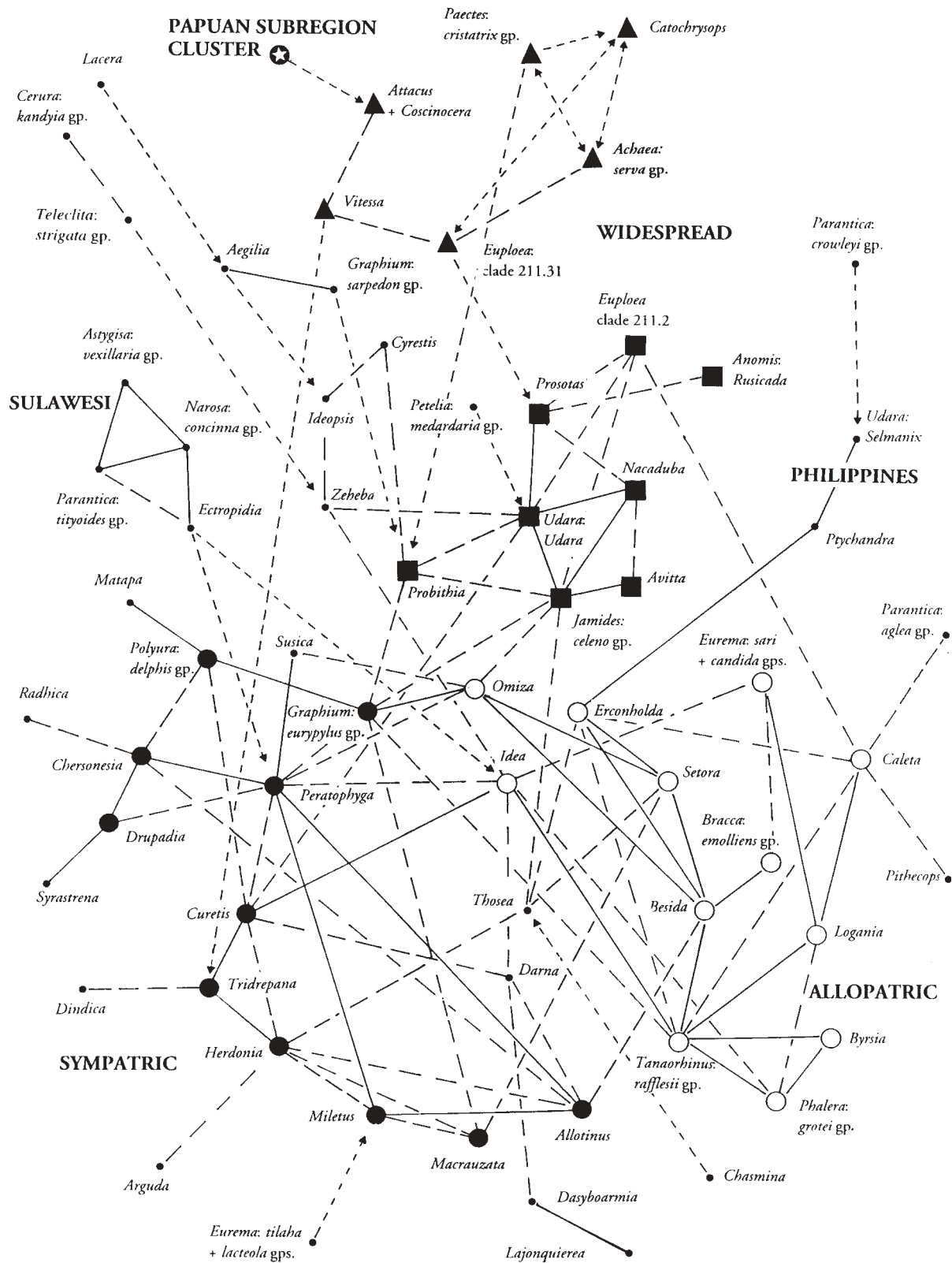


Fig.3. Linkage diagram for the Oriental cluster of Figs.1 and 2. Links of 60-100% similarity are indicated by solid lines and those of 51-59% similarity by long dashed lines. Clustering of taxa at a higher level than this is indicated by short dashed lines with arrows. Large symbols indicate members of the clusters or groupings of taxa mentioned in the text: the same symbols indicate members of these groups in Figs.1 and 2. Outlying taxa that do not fall into these groups are indicated by smaller solid circles. Linkage with the Papuan subregion cluster is indicated by the encircled star.

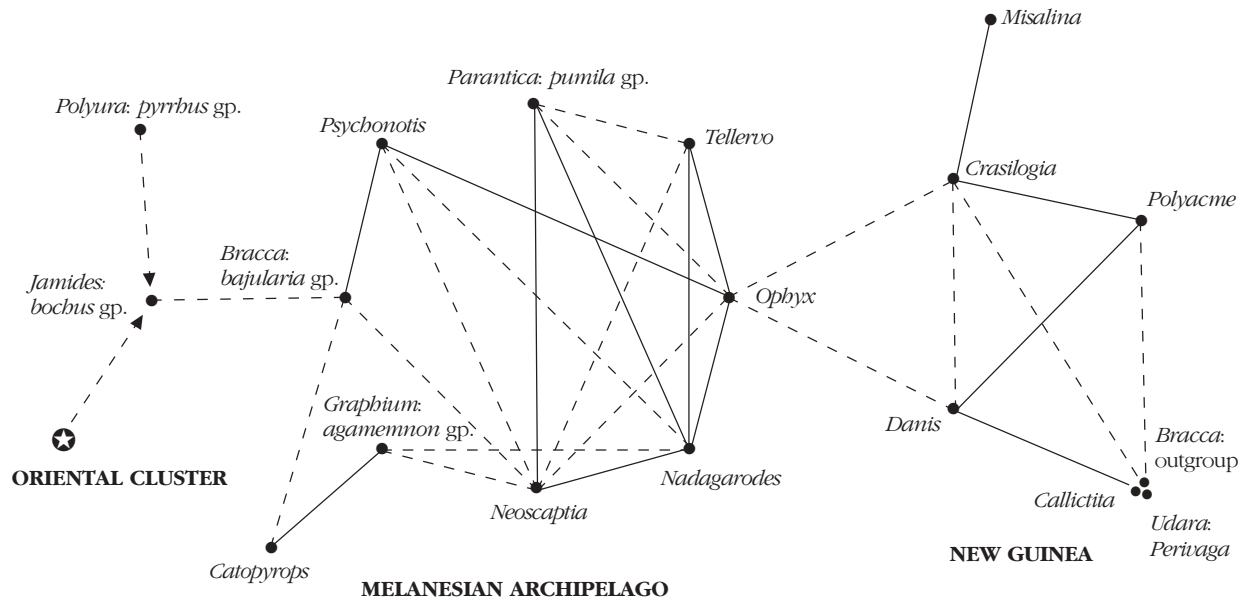


Fig. 4. Linkage diagram for the Papuan cluster of Fig. 2. Conventions are as for Fig. 3.

by Hayashi (1987a, b), *Chremistica* (Bregman, 1985) and *Dundubia* (Bloem and Duffels, 1976) were also included.

These data were initially analysed using the same distributional categories as for the butterflies, but cicada species were virtually unrepresented in the more widespread faunal elements. Within the more easterly archipelagos cicada species are often restricted to one or two islands (including one or two endemic to very small islands, excluded from the analysis), and they are also localised within the island of New Guinea (Duffels and Boer, 1990). Therefore a second analysis was performed on Papuan subregion cicada genera using a much finer-grained set of distributional categories that are virtually those identified in Boer (1995b) and combinations of them. This finer-grained analysis provides an opportunity to test objectively the coincidence of cicada groups as a whole over areas of endemism recognised subjectively by Boer (1995b).

Results: Lepidoptera

The dendrogram resulting from the single-link cluster analysis, and the raw data from which it is derived, are shown in Figs. 1 and 2. The dendrogram indicates a primary segregation of Papuan subregion (Melanesian archipelagos) groups from a combination of Oriental and widespread ones. Many of the Oriental groups

extend into the Papuan subregion (bounded to the west by Weber's Line of Faunal Balance after the findings of Holloway and Jardine, 1968). The widespread groups are represented fairly evenly throughout the whole of the Indo-Australian tropics and make a major contribution to the faunas of Pacific archipelagos.

Linkage diagrams for these two main clusters are shown in Figs. 3 and 4, with links down to 50% similarity being illustrated: clustering in of outlying taxa above that level is also shown. The widespread taxa (solid squares) form a moderately cohesive cluster distinct from a much larger grouping of taxa with much stronger representation (species richness) in the Oriental region. Within this larger grouping there is no definite substructure, but there is some polarization of groups (open and solid circles) across a continuum. There are various small groupings peripheral to these main clusters: a tight quartet of taxa with high endemism in Sulawesi (a comparable situation in the Philippines is much more weakly defined); a loose association of taxa (solid triangles) with some affinity to the widespread cluster, but of a more Melanesian character.

Oriental taxa: sympatric v. allopatric groups

The polarization of Oriental taxa is between taxa (solid circles) that are particularly rich in species

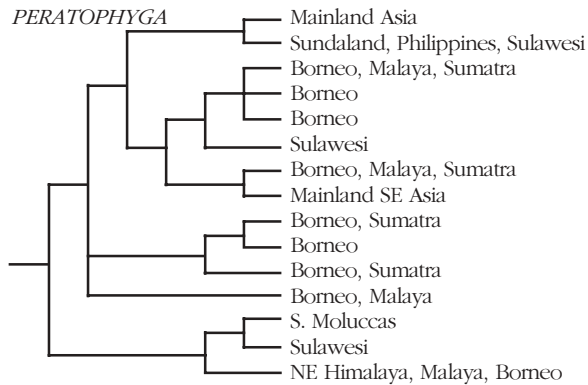


Fig. 5. Cladogram with areas for the ennomine geometrid genus *Peratophyga*, with groupings as justified by Holloway (1993), exemplifying the sympatric Oriental type of genus.

in the mainland Asian and Sundanian distributional categories, and those (open circles) that are less well represented on the Asian mainland but have higher endemism in the Philippines and Sulawesi and are more likely than the other group to be represented in the Melanesian archipelagos. The first group of taxa has some endemism in Borneo, less in the Philippines and Sulawesi, and often shows a high degree of sympatry in mainland or Sundanian areas. Those in the second group have a more even distribution of their species amongst the distributional categories and exhibit greater allopatry, and may therefore offer a better chance of detecting compatibility of area relationships in their cladistic structure. For convenience in the text following, these groups will be referred to as sympatric versus allopatric Oriental groups.

The ennomine genus *Peratophyga* illustrates the sympatric group (Fig. 5). Relationships within the genus are as described by Holloway (1993). The genus is particularly rich in various Sundanian categories, including Bornean endemics: ten out of the fifteen species occur in Borneo, and the clades recognised within the genus are also both sympatric and allopatric in character. In the *eurypylus* group of the swallowtail butterfly genus *Graphium* (Saigusa *et al.* 1977), the component species are generally much more widespread, but again the majority are represented in Borneo.

Within the allopatric group, different degrees of complexity are shown. In *Tanaorhinus*, the *Phalera grotei* group and *Byrsia* there is very little overlap amongst an array of species that fall into distributional categories of intermediate character, *e.g.*, mainland Oriental, Sundanian,

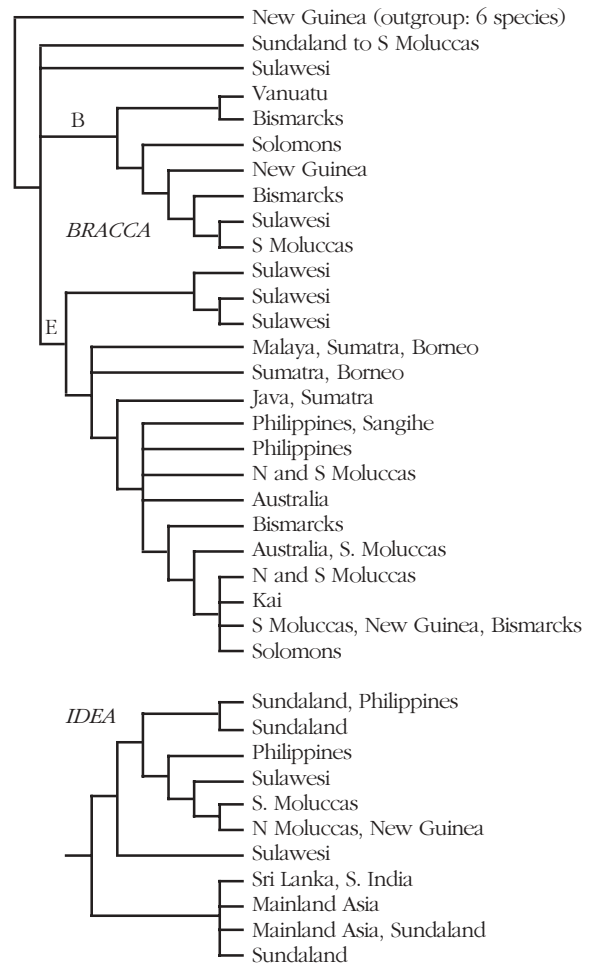


Fig. 6. Cladograms with areas for the ennomine geometrid genus *Bracca* and the danaine butterfly genus *Idea*, from Holloway (1991). The latter and the *emolliens* clade (E) of *Bracca* exemplify the allopatric Oriental type of genus. The *bajularia* clade of *Bracca* (B) exemplifies the Melanesian archipelago type of genus in the Papuan subregion cluster, the *Bracca* outgroup being in the New Guinea subcluster.

Melanesian, as well as island endemics. Holloway (1982, 1987b) grouped these together subjectively with the *Teleclita strigata* and *Cerura kandyia* groups, but these are segregated in the analysis by virtue of representation in Australia and greater allopatry in the western part of their range. Holloway suggested that, as there were no obvious characters to indicate a strongly dichotomous cladistic structure within any of them, and the islands grouped by the more widespread elements largely reflected modern geography, these patterns probably resulted from relatively recent episodes of rapid ancestral dispersal, followed by vicariance over the islands in modern juxtaposition, perhaps in

response to Pleistocene climatic changes.

More complex patterns are exhibited by the *Eurema sari* + *candida* group, *Besida*, *Erconbolda*, the *Bracca emolliens* group and *Idea*, though in none of these is there any strong evidence of commonality of pattern, merely that of trends. In the *Eurema* example a Melanesian sister-pair is sister to an Oriental complex, with one allopatric trio overlapping the composite range of the unresolved remainder extensively. *Besida* is sister to a widespread Melanesian genus (added to the data), but has two Sundanian species and a Philippines-Sulawesi sister-pair. *Erconbolda* also exhibits the Sulawesi-Philippines relationship but its interaction with Sundanian areas is different (Holloway, 1987b).

Phylogenetic hypotheses for the *Bracca* group and *Idea* are shown in Fig.6. In both, there can be seen a sort of progression from west to east within the cladogram, the earliest branches being the more easterly species. However, that for *Idea* 'commences' in India and mainland Asia and 'terminates' in New Guinea, and that for the *emolliens* group of *Bracca* 'commences' in Sundaland and 'terminates' in the Solomons, with earlier branches Melanesian rather than continental Asian. Even within the area of overlap of the two cladograms, that for the *Bracca* group is more species-rich, has a similar outlying taxon in Sulawesi, but lacks corresponding representation of Sulawesi further up the sequence.

Nevertheless, this general west to east progressive pattern of areas is seen also in a Brooks Parsimony Analysis for Lepidoptera where areas lacking a particular clade were coded '?' (uninformative) rather than zero (primitively absent) when data for that clade were tabulated (Holloway, 1991), and in general area cladograms for Hemiptera (Schuh and Stonedahl, 1986) and butterflies (Vane-Wright, 1990), also discussed and illustrated by Holloway (1991). This pattern will be discussed further below.

Groups of widespread taxa

The major widespread cluster contains groups (solid squares) with a high proportion of species in the most widespread category (through the Indo-Australian tropics) and in other widespread categories. Endemism in the Oriental region tends to be low except sometimes in the Philippines and Sulawesi, but the groups include a number of Melanesian archipelago endemics. Several are species-rich genera that, when subjected to cladistic analysis, may subdi-

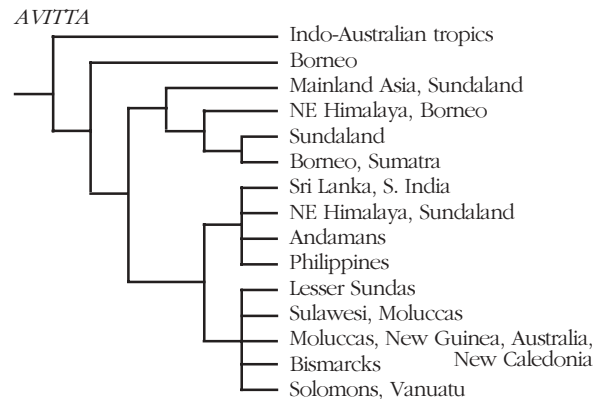


Fig.7. Cladogram with areas for the noctuid genus *Avitta*, exemplifying a widespread Oriental cluster genus. From Holloway (1984).

vide into species groups that fall within some of the other clusters in the analysis. For example, in the noctuid genus *Avitta* (Fig.7), allopatric and sympatric Oriental clades occur as sister-groups.

The looser association of widespread taxa (solid triangles) consists of less species-rich groups where the proportion of Melanesian and Pacific endemics is equal to, or greater than that of widespread taxa, with more allopatry overall. This character is also seen in the *Graphium sarpedon* clade and *Aegilia* pair. Distributions of species of *Paectes* in the 'solid triangle' group and of *Aegilia* were mapped by Holloway (1985).

The widespread groups just discussed are generally considered to be biogeographically uninformative, an assertion that is generally true for much of their distribution through the Indo-Australian archipelago, but the mobility of these groups has also led to them being relatively well represented in remoter Pacific archipelagos where they often show a much higher degree of endemism. There will undoubtedly be a strong stochastic element in any pattern in this endemism but within this, as indicated earlier, some geological signal may be observed. For example, patterns involving New Caledonia, Vanuatu, Rotuma, Samoa and Fiji may reflect changes in the relative positions of these island groups in the past (Holloway 1979: pp. 211-213, 1983; Duffels, 1988).

Sulawesi taxa

The small cluster of taxa with high endemism in Sulawesi consists mostly of those with extensive

radiations of species within Sulawesi, with a few species from these radiations occurring in some cases further east in the Moluccas or New Guinea, and with a sister-relationship to Oriental taxa to the west. These could be considered further examples of west-to-east progressive patterns. An exception within this cluster is the *tityoides* group of *Parantica* where affinities are with the Lesser Sundas and Banda island arcs generally.

Papuan subregion taxa: New Guinea and Melanesian archipelago groups

Groups in the Papuan subregion cluster segregate into New Guinea and Melanesian archipelago components, a segregation supported by the linkage diagram (Fig.4), where the two groups remain separate except for linkage through the noctuid genus *Ophyx*. Members of the New Guinea cluster are virtually restricted to that island. Species in these groups outside New Guinea tend to be in Australia and New Caledonia or in the Moluccas. Any representation further afield in the Melanesian archipelagos is by species in the widespread Melanesian category, presumably relatively dispersive. Examples from the Geometridae, the genera *Polyacme* and *Crasilogia* (including *Papuanticlea*), are shown in Fig.8.

The Melanesian archipelago groups have their species evenly distributed from the Moluccas through New Guinea into the archipelagos to the east. This distribution type is exemplified by the *bajularia* clade of *Bracca* (Fig.6). A phylogenetic hypothesis for *Ophyx*, the genus intermediate between the two groups, is shown in Fig.9. It segregates into two clades, one that would probably fall within the New Guinea cluster if coded separately, and the other an unusual combination of a small Melanesian archipelago group that is sister to an Australia/New Caledonia pair.

Associated with the Melanesian cluster is a pairing of the lycaenid butterfly genus *Catopyrops* with the *agamemnon* group of *Graphium*, where several species endemic to various Melanesian archipelagos are associated with species in more widespread categories. The case of *Graphium* will be revisited later.

These distinct New Guinea and Melanesian patterns are often cited as evidence for the convergence of two distinct geological systems, sometimes termed Inner and Outer Melanesian arcs (Holloway, 1984; Boer, 1995b; references

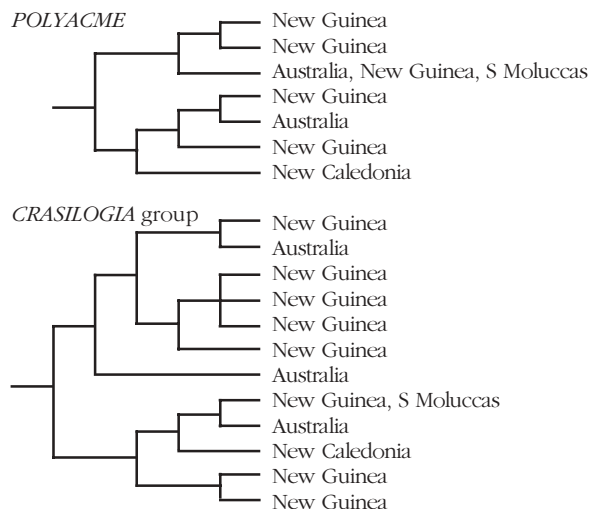


Fig.8. Cladograms with areas for two geometrid genera exemplifying the New Guinea subcluster of the Papuan subregion cluster: *Polyacme* (Ennominae); *Crasilogia* with *Papuanticlea* (upper and lower clades respectively; Larentiinae). From Holloway (1984).

therein), but, given current hypotheses of the geological complexity of the area, this is something of a misnomer (Polhemus, 1996; Polhemus and Polhemus, 1998 this volume), and Inner and Outer Melanesian archipelagos might be preferable terminology. However, the cicada data suggest, along with geological evidence, that the situation is far more complex (Boer, 1995b), and this primary segregation is merely a 'coarse focus' pattern.

There is also the possibility that the apparent segregation of the two groupings has arisen through operation of factors other than Earth history: some genera may have responded to growth of the land area of New Guinea by speciation; others, perhaps more adapted ecologically to archipelagic conditions, including having greater powers of dispersal, may have speciated extensively only in the Melanesian island groups. For example, the geometrid genus *Nadagarodes*, placed in the Melanesian group here, has a cladistic structure (Holloway, 1984) with weak segregation within it of New Guinea and Melanesian clades, but also with indication of much interchange between New Guinea, the Moluccas and the Solomons. The sister-genus was suggested to be *Probitbia*, falling into one of the more widespread categories among the Oriental groupings, extending from India to Fiji (discussed further by Holloway, 1991).

Two factors may strengthen a geological, rather than ecological, interpretation of this di-

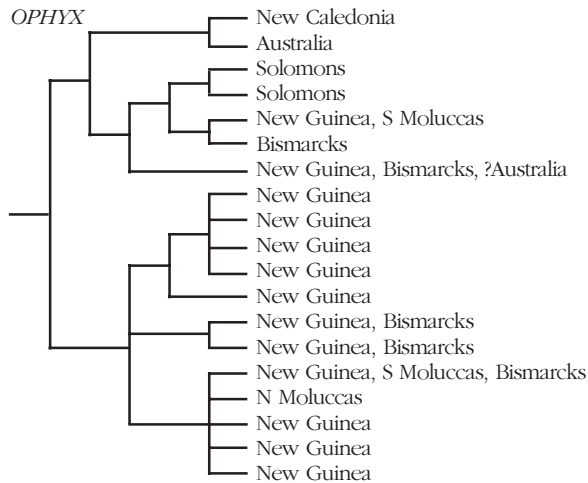


Fig.9. Cladogram with areas for the noctuid genus *Ophyx*, intermediate between the New Guinea and Melanesian archipelago subclusters of the Papuan subregion cluster. From Holloway (1984).

chotomy in pattern. The first is the extent to which putative Melanesian groups still show some restriction to the more recently accreted Melanesian terranes in New Guinea, such as the northern ranges of mountains. The second is the existence of sister-pairs of groups, one of each distribution type. There are few clear-cut examples of this in the Lepidoptera groups in this analysis, the best being the *Danis-Psychonotis* sister-pair in the Lycaenidae, though no phylogenetic analysis of this pairing has been undertaken. The situation in *Ophyx* is another possible example; Holloway (1984) also illustrated possible sister-groups within the arctiid genus *Cyana* where the Melanesian component does also show restriction to northern New Guinea.

Combinations of patterns

Both Melanesian and New Guinea patterns may also be represented amongst a number of closely related lineages, but not in a strict sister-relationship. There are a number of examples amongst the Lepidoptera groups included in the analysis, though sometimes the data were not good enough to permit all lineages to be included. They are drawn from a number of different families.

The swallowtail butterfly genus *Graphium* has already been mentioned, as has the geometrid genus *Bracca*. The analysis of *Graphium* by Saigusa *et al.* (1977) revealed three major lineages. Each of these includes one or more ex-

remely widespread components. One is the largely Melanesian *agamemnon* group referred to above. It is sister to the other pair. One of these, the *eurypylus* group, has already been mentioned as an example of the sympatric Oriental type. The other, the *sarpedon* group, was also mentioned as one of the more widespread group that has a relatively high proportion of more localised species in the eastern part of its range: this is primarily a lineage distributed through the Moluccas, New Guinea, Australia and New Caledonia, a group, therefore, of weak New Guinea cluster character.

In *Bracca* (Fig.6), the Melanesian *bajularia* group is segregated from the *emolliens* group in an unresolved quadrichotomy with two other species, one widespread, one endemic to Sulawesi. The *emolliens* clade itself has already been discussed as illustrating a west to east progressive structure in a sister-relationship to a trio of species endemic to Sulawesi. This whole complex is probably sister to a clade of six species used as an outgroup in the analysis by Holloway (1991). This clade is restricted to New Guinea and falls within the New Guinea group in the analysis.

Holloway (1984) discussed four closely related genera of lithosiine arctiid. Two of these were included in the analysis. One falls into the Melanesian cluster (*Neoscaptia*) and the other, *Byrsia*, has already been noted as an allopatric widespread group of low diversity. The remaining two genera are *Scaptosyle*, probably a sympatric Oriental group, and *Damias*, with over thirty species restricted mostly to New Guinea, but with three species in the southern Moluccas (Seram, Buru). The genus has its greatest richness in the southeastern peninsula of New Guinea and is relatively weakly represented in the northern structures.

In the nymphalid butterfly genus *Parantica*, the *pumila* group is of Melanesian character, but the genus has no New Guinea components, the *pumila* group being sister to the *tityoides* and *crowleyi* groups, the former already mentioned for its high endemism in Sulawesi, and the latter having high endemism in the Philippines as well as a rather widespread Oriental character. This complex is sister to the *aglea* group which has a wide Indo-Australian distribution to as far east as the Solomons (see cladogram in Holloway (1984) from Ackery and Vane-Wright, 1984).

In another powerfully flighted nymphalid genus, *Polyura* (Smiles, 1982), the *pyrrhus* group, weakly associated with the Melanesian cluster in the analysis, is in an unresolved triplet with a

Solomons endemic and the sympatric Oriental *delphis* group. However, this triplet is sister to a single New Caledonian endemic.

Thus, though some gross pattern emerges from the distributions of Lepidoptera groups, that may represent geological signal, the phylogenetic structures within such groups, and between them when they come together in larger groupings, exhibit no strong pattern, indicative of process (e.g., dispersal and speciation) that is probably of a highly stochastic nature. As stated in the introduction, it is rare to find Lepidoptera groups that range from India into the Pacific and yet show the maximal endemicity of their taxa throughout that range advocated by Page and Lydeard (1994) for biogeographical analysis.

Results: cicadas

The analysis of cicadas using the same distributional categories as for the Lepidoptera yielded similar clusters, but with virtually no overlap between Oriental and Papuan subregion groups, the link between the two being at almost zero percentage similarity (Fig.10). Indeed, the range of similarity values registered is considerably more extreme than that for the Lepidoptera.

The Oriental cluster shows more definite internal structure, with a tight trio of groups virtually restricted to Sulawesi and three pairings of groups centred on the Philippines, on Sundaland and mainland Asia, and on the Banda arcs. This is probably a reflection of the much smaller sample of Oriental groups than for the Lepidoptera, for amongst these pairings there is little commonality of area relationships. One of the Philippines groups is associated with Sulawesi and the other with Sundaland. One member of the Banda arc pair has its centre of richness at the western end of the geological structure, in Sumatra, and the other is more diverse at the eastern end, in the Lesser Sundas and around Timor: a further example of a Banda arc pattern is illustrated for a group of *Ptilomera* (water-strider) species by Polhemus (1996).

The Papuan subregion groups are, like those for the Lepidoptera, clearly segregated into New Guinea and Melanesian archipelago clusters, the former relatively tight, the latter less so, with one outlier, *Aceropyga* + *Moana*, that has high endemicity from the Bismarck Islands eastwards, but particularly in Fiji (*Aceropyga*).

As mentioned earlier, these cicada groups fall mainly within two major tribal groupings, the

exception being the *Raiateana* group of genera (Solomons eastwards) that may be related to the Oriental *Cryptotympana* (Duffels, 1988, pp. 80-81) also included in the analysis. Most of the Chlorocystini groups (asterisks in Fig.10) fall within the New Guinea cluster, the exception being one group of the genus *Baeturia*. Two of the four *Cosmopsaltria* groups (daggers) fall within the Melanesian cluster, the others being the outlying *Aceropyga* + *Moana* group and the New Guinea cluster genus *Cosmopsaltria*, which bears a sister-relationship to the other Papuan subregion groups (Duffels, 1983). Both tribes have relatives in Sulawesi, the Chlorocystini being represented by their sister-tribe (Boer, 1995), the Prasiini (double asterisks). The Chlorocystini also have a number of small genera endemic to forests along the eastern seaboard of Australia from Cape York to southern New South Wales, a feature roughly paralleled by some New Guinea groups in the butterfly analysis. The significance of this will be assessed in the final, general discussion.

The areas of endemism recognised for the finer grained analysis of cicada groups are somewhat more numerous than those identified by Boer (1995b), but are generally similar, particularly within New Guinea (Fig.11). Species in each group were either endemic to these or represented in various pairs, triplets or more of them, yielding a total of 50 distributional categories into which all could be assigned. The results of the analysis are shown in Fig.12 both in the form of a dendrogram and a minimum spanning tree.

The dendrogram reveals no strong clustering structure, and similarity levels are generally low, not much exceeding 50%. The spanning tree confirms this, with the groups falling more or less into a chain from groups in New Guinea and the Moluccas through to the Melanesian archipelago groups. The spanning tree does bring together as neighbours the groups in the sub-clusters of the coarse-grained analysis. These groupings do not bear very close relationship to the subjective assignment of whole groups to ancestral areas of endemism by Boer (1995b). He referred *Cosmopsaltria* to central New Guinea, *Baeturia* as a whole, *Guineapsaltria* and *Mirabilopsaltria* to northern New Guinea, *Thaumatopsaltria*, *Papuapsaltria* and *Gymnotympana* to the Papuan peninsula, and *Aedeastria* to the Bird's Head. These assignments need not necessarily be incorrect, but the analysis here does suggest that stochastic processes such as dispersal have tended to blur any clear patterns that

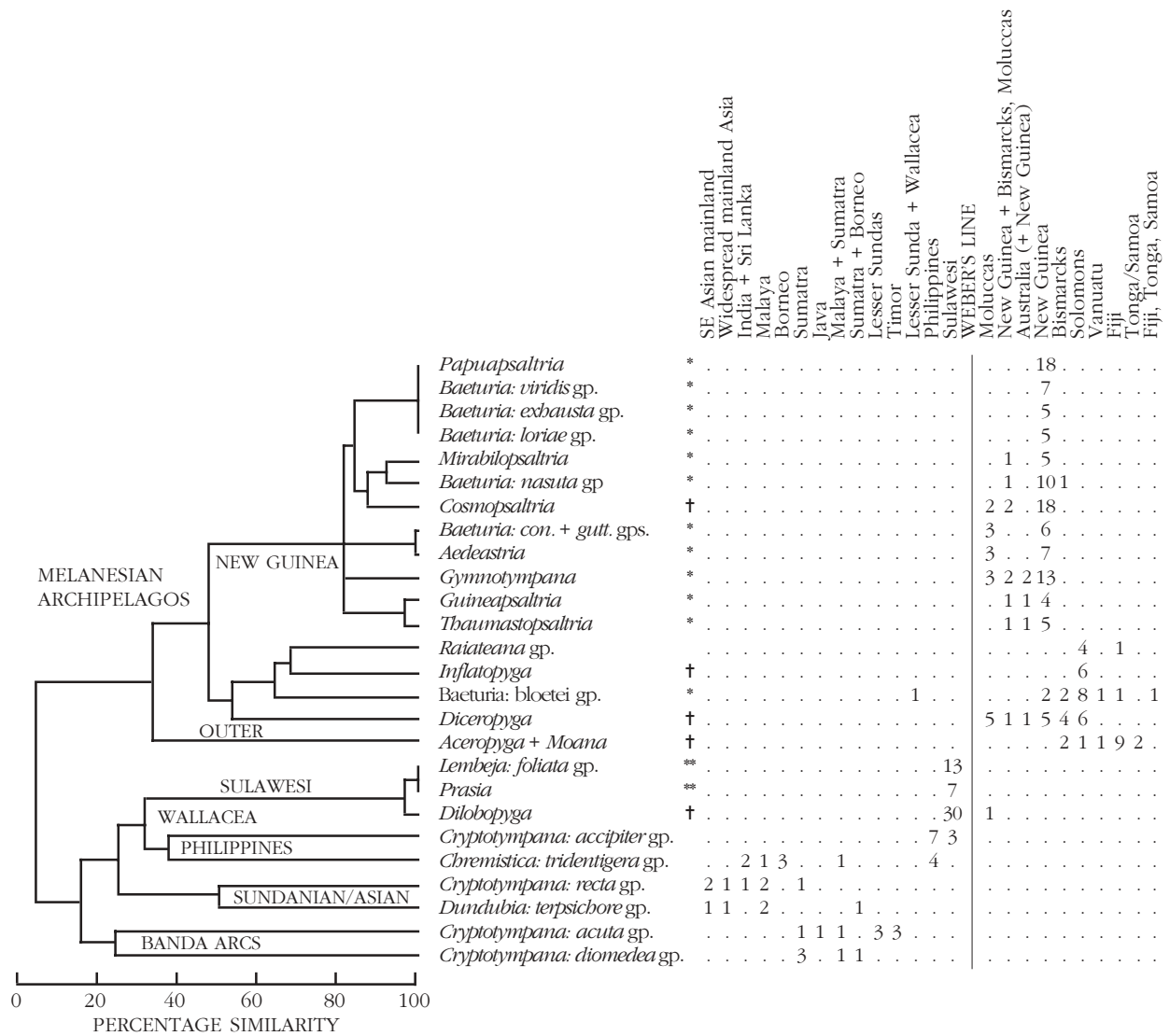


Fig. 10. Single-link dendrogram and data for the R-mode analysis of cicada taxa using the same distributional categories as for the Lepidoptera. Chlorocystini groups are indicated by *, Prasiini groups by ** and Cosmopsaltriaria groups by †.

may have existed, though on a much more localised scale than for the Lepidoptera. This is seen most strongly in *Baeturia* itself where, even if the overall 'weight' of the genus is in northern New Guinea, some groups (*nasuta*, *loriae*) approach *Cosmopsaltria* in their representation in central New Guinea, and another (*bloetei*) has a distribution resembling that of the Melanesian groups of the Cosmopsaltriaria.

The correlation of the analysis with ancestral areas of endemism categories of Boer can be assessed by examining the extent to which taxa in each category have high links primarily with other taxa in that category. Such links are indi-

cated in bold for New Guinea groups in the list following. The list includes the genus or species group, area (or areas in ambiguous cases) of endemism suggested by Boer, followed by the highest few links (percentage similarity in brackets) with other taxa in order of similarity.

Gymnotympana (Papuan peninsula): ***Papuapsaltria*** (51); *Mirabilopsaltria* (56); *Cosmopsaltria* (44); ***Guineapsaltria***, ***Baeturia loriae*** group (43).

Guineapsaltria (Papuan peninsula): *Mirabilopsaltria* (45); ***Gymnotympana*** (43); ***Thaumastopsaltria*** (40).

Thaumastopsaltria (Papuan peninsula):

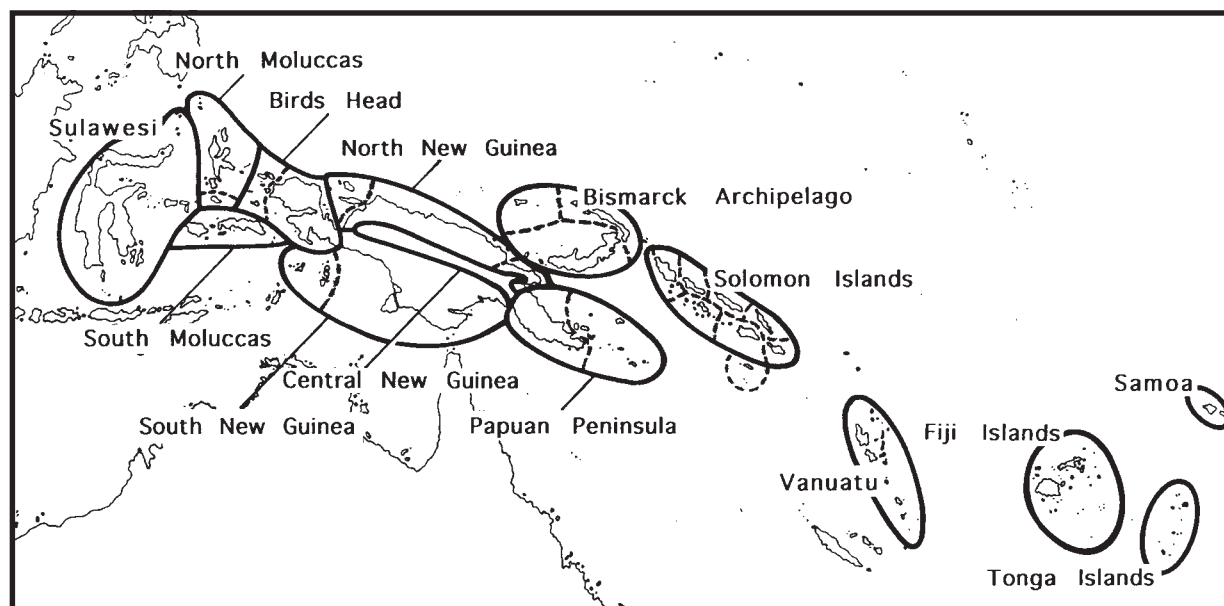


Fig. 11. Areas of endemism recognised for the finer R-mode analysis of cicada patterns, after Boer (1995b). The solid lines delimit the areas of endemism of Boer; broken lines indicate further subdivision of these for this analysis.

Guineapsaltria (40); *Baeturia nasuta* group (38), *Papuapsaltria* (35).

Papuapsaltria (Papuan peninsula): *Baeturia loriae* group (56); *Mirabilopsaltria* (52); *Gymnotympana* (51); *Cosmopsaltria* (47).

Baeturia loriae group (Papuan peninsula, Central New Guinea): *Baeturia nasuta* group (59); *Papuapsaltria* (56); *Gymnotympana* (43); *Cosmopsaltria* (41).

Cosmopsaltria (Central New Guinea): *Mirabilopsaltria* (59); *Papuapsaltria* (47); *Baeturia nasuta* group (46); *Gymnotympana*, *Baeturia exhausta* group (44).

Baeturia nasuta group (Central New Guinea, Northern New Guinea): *Baeturia loriae* group (59); *Cosmopsaltria* (46); *Papuapsaltria* (42).

Mirabilopsaltria (Northern New Guinea): *Baeturia exhausta* group (73); *Cosmopsaltria* (59); *Papuapsaltria* (52); *Gymnotympana*, *Guineapsaltria* (45).

Baeturia exhausta group (Northern New Guinea): *Mirabilopsaltria* (73); *Cosmopsaltria* (44).

Baeturia viridis group (Northern New Guinea): *Mirabilopsaltria*, *Papuapsaltria* (40); *Baeturia nasuta* group (37).

Baeturia conviva + *guttulinervis* group (Maluku, Northern New Guinea): *Aedeastria* (20).

Aedeastria (Bird's Head): *Baeturia exhausta* group, *Mirabilopsaltria* (34); *Cosmopsaltria* (31).

There is some general affinity amongst Papuan peninsula groups on the one hand and Northern New Guinea ones on the other, though *Mirabilopsaltria* of the latter also has links with the former, and *Cosmopsaltria* has its major links with members of both groups.

Discussion

Given this plethora of pattern variation in both insect groups, are there any basic themes within it that might have a geological basis, to which further detail may be added through considering fine-grained pattern in more localised and hopefully more informative groups such as cicadas?

Analyses for both groups do recognise a number of fairly gross areas of endemism within the Indo-Australian archipelago. In the Oriental region there is some segregation of Sundaland, Philippines and Sulawesi groups, with some interaction between Sulawesi and the Philippines, Sulawesi and the Moluccas and New Guinea, and Sulawesi and the Lesser Sundas. The cicada patterns, with finer detail, also include definite Banda arc groups. Some of the smaller subgroups of *Lembeja*, not included in the analysis, also feature Sulawesi and the Lesser Sundas (Jong, 1985, 1986, 1987). This variety of associations between Sulawesi and neighbouring areas

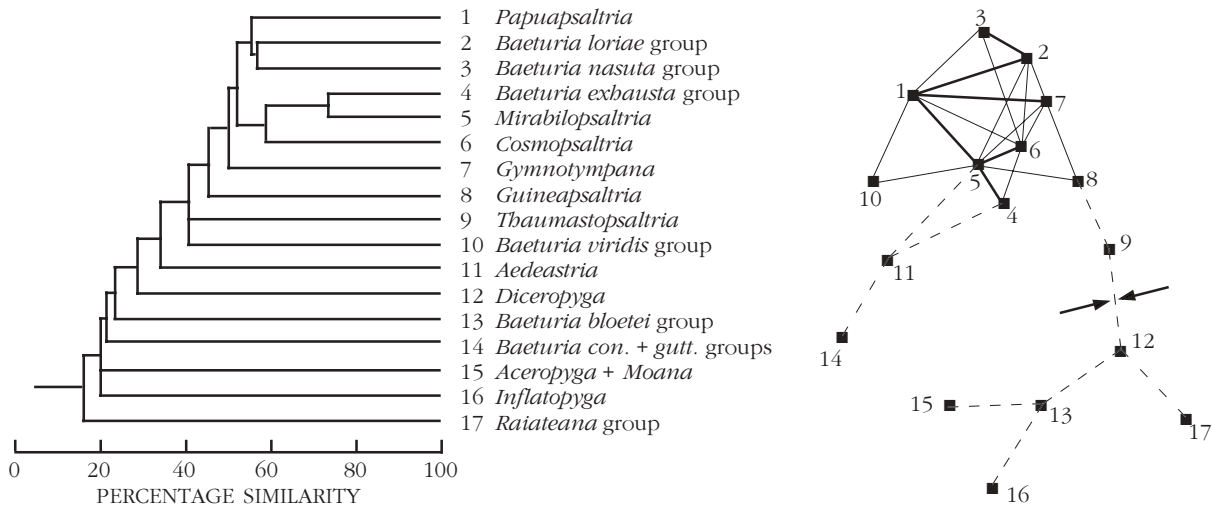


Fig. 12. Single-link dendrogram (left) for the finer R-mode analysis of cicada patterns, with the linkage diagram to which it is related (right). In the linkage diagram heavy solid lines indicate links at 50% and above, light lines those at 40-49%. Broken lines indicate taxa clustering in (minimum spanning tree) at a lower level of similarity. Heavy arrows indicate the division between the New Guinea and Outer Melanesian Archipelago groups of Fig.10.

is of interest, and may suggest a composite origin for the current island, discussed briefly below. In the Papuan region there are two much clearer patterns: the New Guinea groups and Melanesian archipelago groups, the former often with Australian associations. Cicada groups sharing these patterns have very much more species richness than do Lepidoptera groups, but there are fewer of them. When this species richness occurs in larger islands, such as New Guinea and Sulawesi, the cicada taxa concerned are often localised within the island, and may reveal something of any geologically divergent histories among the components. In the Lepidoptera, such internal localisation, if it ever occurred, has usually been blurred by subsequent movements of the species, leading to a high degree of sympatry (Holloway, 1991).

Boer (1995b) focused mainly on the similarities between the biogeography of the Prasiini + Chlorocystini and the *Cosmopsaltria* cicada groups, but the differences, particularly in relation to Sulawesi and the composite nature of the Papuan subregion, may be as interesting. It is worth considering these groups in a little more detail (Fig.13), though the reader is recommended also to consult Boer (1995b), and Boer and Duffels (1996a, b).

As mentioned earlier, the Papuan subregion *Cosmopsaltria* groups, with the exception of

Cosmopsaltria itself, are distributed mainly amongst the Melanesian archipelagos. Duffels (1990) proposed a possible phylogeny for the *Cosmopsaltria* group within Sulawesi, and reviewed the localisation of the species within the island. The group is represented by sister-genera, *Dilobopyga* and *Brachylobopyga*. *Dilobopyga* has three major species groups. Most of the species are localised within the island, and some subgroups within the major groups are concentrated in one or other of the geographical components. The genus is largely restricted to the north, centre and eastern peninsulas. Apart from an island-wide species, only two species are localised in southwest Sulawesi, a sister-pair, one on the island of Saleyer. There is one species in the southern Moluccas. *Brachylobopyga* has only a pair of species, one central and another in the southwest. So, as for the *Lembeja foliata* group of the Prasiini, discussed below, the greatest diversity is in the north and east of the island, though with richness also in the centre. Within both groups there are indications of vicariance between western and eastern groups of species.

The tribe Prasiini is strongly centred on Sulawesi. Its sister-group, the tribe Chlorocystini, occurs from the Sula Islands east to Samoa and northeastern Australia as discussed earlier. The sister relationship of the two together is thought

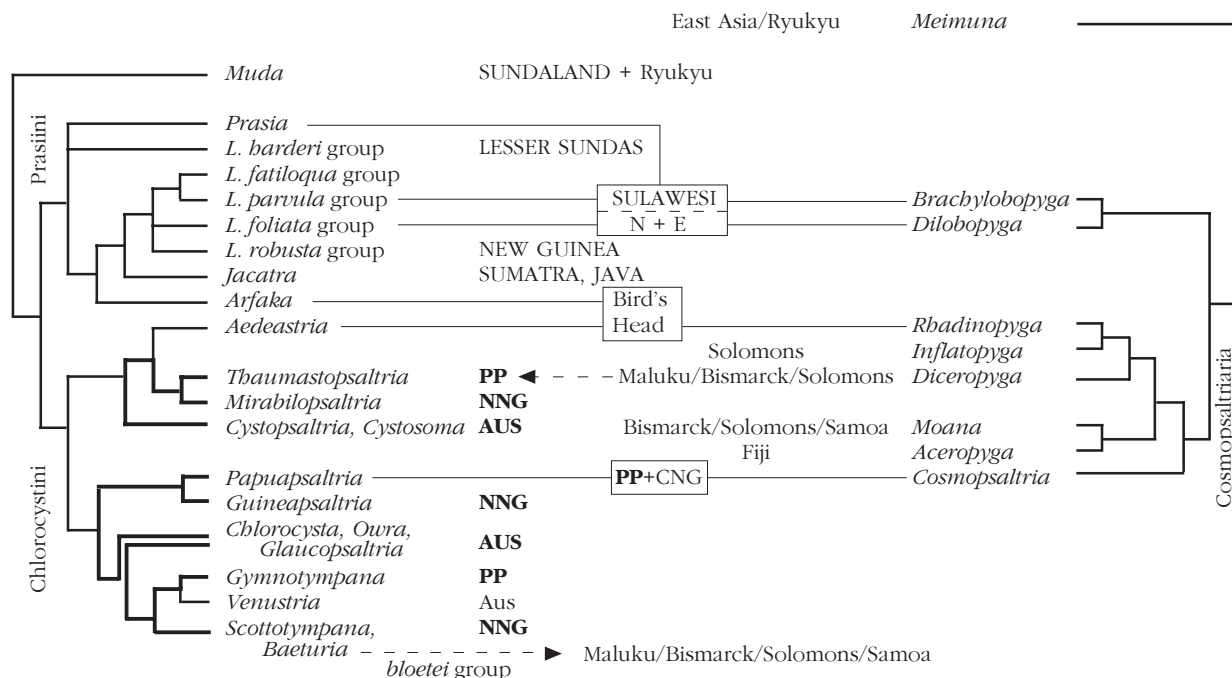


Fig. 13. Diagrams of phylogenetic hypotheses for the Prasiini and Chlorocystini cicadas (left) and the Cosmopsaltriaria (right) from Boer (1995b), indicating major instances of overlap in their distributions. Areas listed to the left and right are possible Inner and Outer Melanesian archipelago ancestral ranges for each group. Central blocked areas indicate areas of overlap that are ambiguous, possibly indicating early dispersal between the two systems or colonisation of intermediately situated areas. Broken lines with arrows suggest instances where more recent dispersal may have occurred. The foci of endemism within the Chlorocystini follow those recognised by Boer (1995b). The repeated (paralogous) three-area pattern involving Australia is indicated by heavier lines and bold type: the double line to *Chlorocysta*, *Owra* and *Glaucopsaltria* represents a single branch on the cladogram, as the last genus is sister to the first two. From Holloway (1997).

to be the Sundanian genus *Muda* (Fig. 13). Among the Prasiini, the genus *Prasia* itself is endemic to Sulawesi, with seven species (Jong, 1985). The genus *Arfaka* is found in the Bird's Head (Vogelkop) area of New Guinea, and a group of taxa currently in *Lembeja* is restricted to the Lesser Sunda Islands.

The Prasiini are completed by sister-genera, *Jacatra*, found in Java and Sumatra and thus the only exclusively Sundanian member of the group, and *Lembeja sensu stricto* that also contains groups endemic to Sulawesi, but ranges widely from northern Borneo and Mindanao to the Lesser Sundas, New Guinea and northern Queensland. This extensive range is exhibited by one group, the *fatiloqua* group (Jong, 1987; Boer, 1995b) that is found in northern Borneo, Mindanao, Sulawesi, Sumba, Sumbawa, south New Guinea and north Queensland. The connection with northern Borneo appears to have been via Mindanao rather than direct from Sulawesi – a distribution also shown by *Ayesha*

spatulata (Duffels, 1990) – an extended Philippines-Sulawesi-Lesser Sunda pattern. Other groups of *Lembeja* include one in New Guinea, Obi and Queensland that is sister to a major group endemic to Sulawesi. Whilst the species of *Prasia* form an allopatric array distributed throughout the main island, those of the *Lembeja foliata* group are concentrated in the north and east of the island, also Sangihe Island (Jong, 1987), whereas those of the *fatiloqua* and *parvula* groups are found in the extreme north and the extreme southwest (Jong, 1986). There are two sister-pairs that span these extremes. The Lesser Sunda species appear to form an interrelated group, some still undescribed. Twenty species of *Lembeja* occur in Sulawesi (Duffels, 1990).

Phylogenetic and biogeographic analyses of the Chlorocystini by Boer (1995a, b) indicate a thrice repeated pattern involving Australia as sister area to a pair of areas of endemism in New Guinea: the southeast Papuan peninsula and the

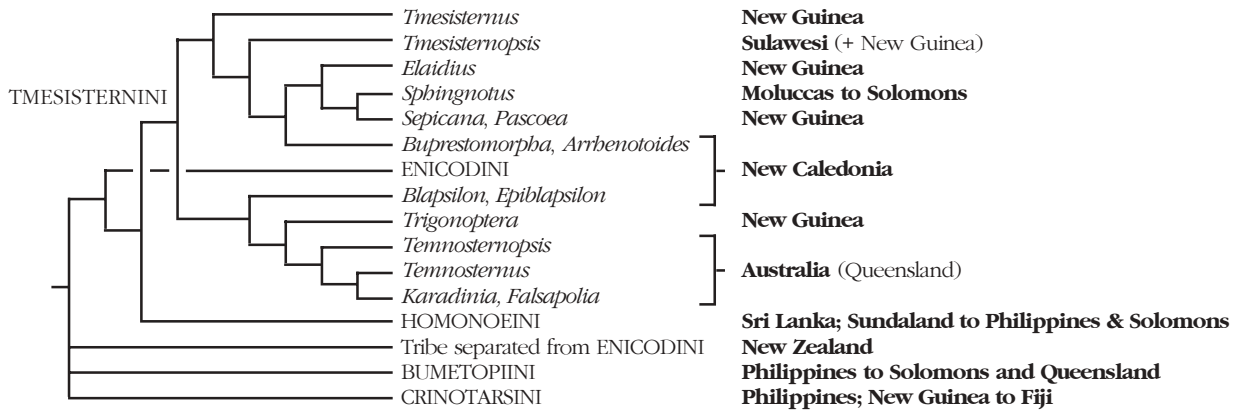


Fig. 14. Relationships within the Tmesisternini tribal complex of the cerambycid beetles suggested by Gressitt (1984), with distributions also included.

central northern part of New Guinea. This pattern is indicated by thick lines in Fig. 13. In contrast to the *Cosmopsaltria*, only one of three of the northern New Guinea components shows a wide extension into neighbouring archipelagos, the genus *Baeturia* with a species group that ranges from the Moluccas to Samoa. Its Papuan peninsula sister-group also shows some extension, to the northern Moluccas and again to Australia. In one of the other trios there is unique representation of the New Guinea Bird's Head.

Thus, whilst the Chlorocystini have their main representation in Australia – at a generic level only, as species richness is an order of magnitude lower than in New Guinea: the relevance of this when considering area relationships is debatable (Nelson and Ladiges, 1996) – and south-eastern and northern New Guinea, the *Cosmopsaltria* have their main representation in archipelagos from the Bismarck Islands to Fiji and Samoa in a sister-relationship to a grouping in the central and southeastern mountains of New Guinea (Fig. 13). The archipelagic group overlaps principally with the Chlorocystini in the Bird's Head and Papuan peninsula, and is also represented in the Moluccas. The sister-group to this complex is in Sulawesi, discussed above, and the sister genus to the whole subtribe is suggested to be *Meimuna*, an east Asian genus extending no further south than the Ryukyu Islands. Thus the main feature in common between these two tribal groupings is rich representation in Sulawesi. Otherwise they appear to have developed roughly in parallel, the Chlorocystini + Prasiini along a more southerly axis than the *Cosmopsaltria*, alone of the two involving Sundaland and the Lesser Sundas.

Hence, despite considerable disparity in the geography of these two tribal groupings outside Sulawesi, they show at least partial convergence in their geography within the island. The higher taxonomic diversity of the Prasiini is as much in the Banda arcs (Sumatra to Lesser Sundas) as in Sulawesi, and also extends to the eastern and southern periphery of New Guinea, so the component of convergence with the *Cosmopsaltria* may postdate the initial development and radiation of ancestral lineages of the tribe. There is a further overlap of *Cosmopsaltria*, Prasiini and Chlorocystini in the New Guinea Bird's Head, with each contributing a genus endemic to, or centred on, that area: *Rhadinopyga*, *Arfaka* and *Aedeastria* respectively (Fig. 13). There may also be an early north-south separation of the biota of Sulawesi, with the weak east-west one mentioned above developing later (see also Holloway, 1997).

Similar northern versus southern patterns can be seen in a number of weevil and longhorn beetle groups (Gressitt, 1956, 1982). The Pachyrhynchini weevils are a northern group. Both northern and southern groups are seen in the longhorn (Cerambycidae) Tmesisternini tribal complex. The northern groups are rarely represented on Sulawesi, if at all. But, unlike the *Cosmopsaltria*, all are represented in the Philippines, the weevil tribe being extremely diverse there. Another good example of a northern group ranging from the Philippines to Fiji excluding Sulawesi is the frog genus *Platymantis* (Allison, 1996). Morley (1998, this volume) suggests the flora of the eastern archipelagos could have been derived from floras in the Philippines and Sulawesi, an observation

that is not inconsistent with such northern and southern patterns. The two lineages of *Aporosa* discussed by Schot (1998, this volume) also show parallels.

Gressitt (1984) had begun to investigate the Tmesisternini complex in detail just before his untimely death. In this work he gave an outline of a phylogenetic hypothesis for the complex. This is summarised in Fig.14. The northern groups referred to above are the Bumetopiini and Crinotarsini. The Tmesisternini are an essentially southern group, with a natural group of four genera in Queensland, a genus in Sulawesi and three distinct groups in New Guinea. One of these also includes a genus, *Sphingnotus*, that, like the *Baeturia bloetei* group in the Chlorocystini cicadas, is found in the outer Melanesian archipelagos, but consists of only three rather widespread species.

A novel feature of the beetle group relative to the Chlorocystini is the inclusion of New Caledonia in both lineages of the Tmesisternini. The sister-group of the Tmesisternini, the Homonoieini, ranges widely through the Indo-Australian tropics, but the Tmesisternini + Homonoieini pairing is itself sister to the Enicodini, a tribe endemic to New Caledonia. The outgroups include a tribe endemic to New Zealand as well as the two northern archipelagic distribution tribes mentioned above. A partial explanation of these differences might be that the ancient history of the beetle group is Australasian/Gondwanan, whereas that of the cicadas is Oriental, but this does not necessarily explain why New Caledonia features within the southern Queensland-New Guinea-Sulawesi (+ Melanesian archipelagos) patterns in the beetles but not in that for the Chlorocystini + Prasiini. The New Caledonian cicada fauna is entirely Australian in affinity (Holloway, 1979, pp. 234-235). A more exclusively Australian, New Caledonian and New Guinea pattern is seen in the plant genus *Arytera* (Sapindaceae; Turner, 1995).

The equation of gross pattern even between such biogeographically informative groups as the longhorn beetles and cicadas is thus not without problems: the development of these patterns may also involve stochastic processes, and this is not necessarily unexpected in complex archipelagic situations where emergence and convergence of geological structures, and change of relative positions, have been much more frequent than the sort of sundering and divergence that could lead to clear, repeated vicariant patterns. Objective comparison of bio-

geographic pattern with hypotheses of changes in geography due to plate tectonic processes thus is difficult: the paper by Boer (1995b) represents the most significant attempt to date. We still need a methodology for pattern analysis that does not introduce the sort of constraints that the past focus on a hypothetical unique set of area relationships has threatened to do. A complementary combination of R-mode and Q-mode approaches as first advocated by Holloway and Jardine (1968) may be one way forward.

Michaux (1991, 1994, 1998 this volume) has already made preliminary observations on the relationship of panbiogeographic, R-mode types of pattern to the geology of the region. The northern and southern types of distribution discussed above perhaps correlate with his (1994) Outer Melanesian track (the former) and a combination of his Inner Melanesian track with continental Australia and his Inner Banda track, excluding Borneo (the latter).

But there is a prime need for many more modern phylogenetic treatments of taxa from the region to add to our pattern sample and to enable us to explore further the complementarity of cladistic (Q-mode) and panbiogeographic (R-mode) approaches to analysis of biogeographic pattern in relation to Earth history. We also need a better understanding of biological process (dispersal, speciation, response to climatic factors) to facilitate interpretation of the patterns derived. Sneath (1982) and Page and Lydeard (1994) noted that the sort of geographically progressive cladistic pattern described earlier, shown by so many Indo-Australian biological groups, could equally well arise through dispersal processes as vicariant ones: gradual biological dispersal through the archipelago from west to east or progressive vicariance of land areas through introduction of sea barriers in the same direction.

Even if there is evidence of correlation between biological and geological data in the structure of area relationships, geologists frequently ask whether it is possible to date divergence in biological lineages so as to permit direct comparison with geological dates. This is a topic where there is still much disagreement. Holloway and Nielsen (1998), reviewing cladistic biogeographic analyses of the Mediterranean, noted that area relationships established to be common to a number of biological groups and related to the post-Oligocene history of the area by some authors were also manifest in a phylogenetic hypothesis based on molecular data for another group that suggested the events

concerned were much more recent.

Dating of speciation events that relies on assumption of a molecular clock and uses distance data has been strongly criticized by cladistic biogeographers (*e.g.*, Morrone and Carpenter, 1994), but should not be rejected entirely. As Page and Lydeard (1994) indicated, the distance measures must be ultrametric for them to be clock-like (discussed also by Jardine *et al.*, 1969), and care must be taken with the analyses. If these conditions are satisfied, such analyses could well provide useful additional information to test concordance between biogeographic pattern and geological hypotheses (Page and Lydeard, 1994; Hedges *et al.*, 1994).

The complexity of the Indo-Australian tropics will undoubtedly require the sort of pragmatic approach adopted by Funk and Wagner (1995) in interpreting pattern in various plant and animal groups that have speciated in the Hawaiian archipelago. They developed a series of hypothetical patterns that might be expected under different process assumptions (rate of evolution relative to dispersal, mode and time of colonisation, direction of dispersals, etc.) in relation to current knowledge of the geological evolution of the Hawaiian island chain, and compared them with actual patterns. The most frequent pattern was of the progression type, with dispersal from older to younger islands, this progression being in the form of clades or grades in relation to the islands, dependent on the relative frequency of speciation relative to dispersal. This last distinction might equally be applicable to the differences observed within similar gross patterns in Lepidoptera and cicadas, leading to much greater species-richness within each pattern element of the latter, the paralogies of Nelson and Ladiges (1996).

Is it possible, therefore, to represent the patterns discussed in this chapter in some sort of sequence that might have some bearing on the geological history of the area? The basal groupings in many of the more complex patterns in the Lepidoptera or cicadas are: Oriental-Sundanian; tropical Australia with New Guinea or New Guinea alone, possibly with a focus on the Papuan peninsula and the Central and Sepik structures of the latter; outer Melanesian archipelagos, possibly also including some components now seen as northern structures within New Guinea; Sulawesi, possibly a component of the current island that was relatively isolated from both Oriental and Papuan land areas at that time. Establishment of these patterns is therefore likely to have been relatively early.

Intermediate patterns include development of an area of endemism in the Philippines that would appear to have had some interaction with a component of Sulawesi, such as its northern peninsula, development of patterns in the Banda arcs that also included interaction with a component of Sulawesi, probably the southwestern peninsula, and progressive breakdown of the segregation of the New Guinea areas of endemism from those of the Melanesian archipelagos. The development of the *Cosmopsaltria* pattern endemic to the New Guinea areas could have preceded considerably the expansion of the Chlorocystini into the outer archipelagos in the form of the *Baeturia bloetei* group, and also the extension of *Diceropyga* of the *Cosmopsaltria* into the Papuan peninsula. This interpretation departs somewhat from that of Boer (1995b), though he also considered differential timing of development of the various patterns. The interaction of structures between Sulawesi and New Guinea with the major foci of endemism is still not clear. Cicada patterns involving the Bird's Head of New Guinea are complex, with interaction seen with Sulawesi, New Guinea and Melanesian archipelago (Solomons) groups (Fig. 13). None of the islands comprising the current Moluccas appears to have acted as a strong centre of endemism, their faunas bearing a general relationship to neighbouring areas, though more so with areas to the east than to the west (see also Jong, 1998 this volume).

Patterns that are probably progressively more recent are the allopatric and widespread categories among Oriental taxa. The former, where progressive, do not appear to discriminate separate areas of endemism, or composites in Sulawesi or New Guinea. The species of the latter, more often than not, transcend the older areas of endemism and, through stochastic interchanges between islands, enable a strong signal from modern geography to be recaptured in scaling analyses such as in Holloway and Jardine (1968). Whilst tending to obscure signals from the past, these groups may well be establishing the foundations of signals that will be detected in the distant future.

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