Patterns of distribution of Malesian vascular plants

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Abstract

A miscellaneous selection of Malesian plant distributions is presented, including examples from the Palmae, Gramineae, Euphorbiaceae, Elaeocarpaceae, and various fern genera. Hypotheses of the tectonic evolution of the area may be required to explain many of the observed patterns that are described. Two major distribution types are identified repeatedly, the first displaying a strongly Sundan bias and the second focusing on E Malesia. Patterns involving New Guinea are complex as they tend to include a variable combination of other islands such as Sulawesi, Maluku, the Bismarck archipelago and the islands of the W Pacific. A number of striking disjunctions exist, some of which have relatively narrow overall ranges, such as those of the palm genera Crypsostachys and Riboflaoxylon which occur across Malesia excluding central parts of the region. In other examples, however, the separation is more profound including disjunctions between parts of Malesia and Madagascar in Oenopia (Palmae) and NExitus (Gramineae), and between Fiji, Vanuatu and Palawan in Vettechla (Palmae). At this stage, the significance of these distributions for the understanding of the geological history of SE Asia remains unclear. It is noted that distributions of species from the genus Antidesma (Euphorbiaceae) are more easily explained in terms of dispersal and environmental factors. Formal cladistic biogeographic analyses of these and other groups should aid interpretation of the region’s history.

Introduction

Over the last four decades, there has been a radical change in the methods used by systematists to classify organisms. This change has had a concurrent effect on biogeographical methods. Ball (1975) describes three phases in biogeographical studies which he calls the descriptive or empirical phase, the narrative phase and the analytical phase. Biogeographical work concerned with the analytical phase has appeared increasingly in the systematic literature and it is here that modern methods are most evident. Previously, most classifications have been based on intuition and overall similarity which, though they may stand the test of time, are nevertheless subjective. Despite the introduction of statistical techniques which aimed to make similarity-based or phenoetic classifications more testable, theoretical objections have led to the decline of phenetics in favour of cladistic methods. Cladistics uses character patterns of extant organisms to construct a hypothesis of their evolutionary or phylogenetic relationships. These patterns are generally visualised in the form of branching diagrams or cladograms which can be interpreted appropriately.

This paper is concerned mainly with the necessary precursors to the analytical phase, the descriptive and narrative phases of biogeography. In selecting taxa for discussion we have chosen only those which we believe will prove to be sound when subjected to the rigours of cladistics. The only groups which are acceptable in the clastid’s eyes are those described as monophyletic. A monophyletic (natural) group contains all the descendants of a common ancestor and is defined by shared characters, or synapomorphies, that support a specific node on a cladogram. A group which contains some, but not all descendants of a common ancestor may appear to be coherent, but cannot be defined in the same way and, indeed, it can be argued that it cannot be defined at all. These
paraphyletic groups are a partial and arbitrary expression of the product of common ancestry and make no sense in an evolutionary context. The inclusion of non-monophyletic groups in biogeographical studies is flawed for these reasons. For basic introductions to cladistic theory, general overviews may be found in Patterson (1982), Wiley et al. (1991) and Scotland (1992).

There is a substantial literature describing plant distributions in Malesia which we do not summarise here. Instead we present distributions from a miscellany of vascular plant families. Firstly, two monocotyledonous families are discussed; from the palm family, generic distributions within the three subfamilies Nypoideae, Calamoideae and Arecoideae, and from the grass family, distributions within the two bamboo genera, Dimoclea and Nastus. Secondly, in the dicotyledons, the genera Antidesma (Euphorbiaceae) and Elaeocarpus (Elaeocarpaceae) are considered. The fern genus Christensenia (Marattiaceae) and a variety of other fern and angiosperm examples from the diverse flora of New Guinea complete the assortment. The term Malesia is used in this paper to identify the area bounded to the north by the Thai-Malaysian border and to the south by the Torres Straits (Steenis, 1950; Johns, 1995). It includes the following political entities: Brunei Darussalam, Indonesia, Malaysia, Papua New Guinea, Philippines and Singapore. It is an area of exceptional biological diversity.

**Palmae**

The Palmae (Arecales) are a diverse, largely tropical and subtropical family of about 200 genera and 2700 species. In the latest classification of the family (Uhl and Dransfield, 1987) six subfamilies are recognised. The delimitation of these subfamilies is currently under rigorous phylogenetic analysis, and preliminary evidence suggests that four of the six (Goryphoideae, Calamoideae, Nypoideae and Phytelephantoideae) are monophyletic whereas two, Ceroxylonoidae and Arecoideae, may be paraphyletic (Uhl et al., 1995). However, the relationships of many of the tribes, subtribes and genera within the subfamilies need further study.

The Malesian and W Pacific region represents one of the richest areas of palm diversity in the world. An estimated 1000 species in 95 genera are found in the area from Indochina to Australia and the W Pacific islands of Fiji and New Caledonia. All subfamilies mentioned above are represented in the region except for the Phytelephantoidae.

Palm distributions in the region have been discussed previously in an anecdotal fashion (Dransfield, 1981, 1987; Uhl and Dransfield, 1987) but these discussions lack a firm cladistic basis. However, with the explicit analytical framework that we are developing, we have been able to select a number of genera or groups of genera that we believe to be monophyletic and display distribution patterns of considerable biogeographic interest.

We present examples from three subfamilies: Nypoideae, Calamoideae and Arecoideae. As mentioned above, the last subfamily is probably paraphyletic but the examples we have chosen from within it are, we believe, monophyletic.

**Nypoideae**

This is the only subfamily in the Palmae represented by a single extant species. *Nypa fruticans* is distinguished from all other palms by a number of unique features including the prostrate dichotomously branched stem, the erect inflorescence bearing a terminal head of pistillate flowers, the lateral spikes of staminate flowers and unusual features of the flowers themselves (Uhl and Dransfield, 1987). Furthermore, the spiny zonosulcate pollen grains are highly distinctive. With the exception of similar but much smaller and incompletely zonosulcate pollen produced by many species of the genus *Salacca* (Calamoideae), such pollen grains are not encountered elsewhere in the family, and are unknown outside the Palmae. The pollen grains are notably uniform in their morphology throughout the geographic range of the genus. In a recent phylogenetic study of the whole family, *Nypa* is resolved as sister taxon to all other palms (Uhl et al., 1995).

*Nypa fruticans* is a mangrove palm, often growing in vast natural stands in a variety of estuarine conditions. Its present day distribution extends throughout Malesia and also includes Sri Lanka, the Ganges delta, Indochina, NW Australia, the Solomon Islands and Ryukyu Islands (Uhl and Dransfield, 1987). It has also been introduced to W Africa and to Panama where it is now well established.

Unlike its modern counterpart, fossil *Nypa* pollen, *Spinizonocolpites* (Muller, 1968), has been shown to possess a range of spine lengths and spine distributions. This variation has been demonstrated by a number of authors to be very
Fig. 1. Distribution maps for *Spirotzonoclyptites* generated using Atlas palaeomapping program (Cambridge Paleomap Services, 1992), incorporated into Plant Fossil Record 2.2 (Lhotak and Boulter, 1995).
localised, often occurring in quite small matrix samples (e.g., Harley et al., 1991). The distribution of *Spintzonocolpites* in the fossil record is remarkable (Fig.1). It is known from the Upper Cretaceous (Senonian) of Borneo (Muller, 1968) although there is some doubt about the age of this record (Morley, 1998 this volume). Upper Cretaceous records are widespread throughout the palaeotropics, including Meso and northern S America, W and N Africa, the Middle East and India. From the Paleocene, northern palaeolatitude records extend to c.65°N, and include examples from northern USA, Europe and Pakistan (Frederiksen, 1994). In the southern hemisphere, there are records of *Spintzonocolpites* in S Australia (Stover and Evans, 1973) and N Island, New Zealand (McIntyre, 1965). Eocene records are more frequent and by the Eocene the widespread pantropical distribution was stable (Fig.1C). There are additional records from NW Australia (Hekel, 1972) and the Lower Eocene of Tasmania, which is the most southerly occurrence of *Spintzonocolpites* at palaeolatitude 65°S (Cookson and Eisenack, 1967; Pole and McPhail, 1996). For the Miocene (Fig.1B), records are substantially reduced. There are records from Africa, India and Malaysia, including numerous and varied *Spintzonocolpites* grains from offshore cores in the West Java Sea (R. J. Morley, pers. comm., 1997). By the end of the Miocene (Fig.1A), the distribution did not extend far outside the area now occupied by *Nypa fruticans*. There are few African records, one or two unsubstantiated records in Europe, and there is a Pliocene record from New Zealand (Couper, 1953). Records for India, Papua New Guinea and SE Asia indicate a similar distribution to the early Miocene.

### Calamoideae

This large subfamily with 22 genera and 650 species is pantropic. Three highly distinctive genera with palmate leaves are confined to northern S America. Currently, they are regarded as comprising a separate tribe, Lepidocaryeae, but continuing studies have proposed stronger links with genera within the other tribe, Calameae, than had been suspected.

In Africa, there are three endemic genera of climbing palms (rattans). A fourth rattan genus, *Calamus*, is represented in Africa by a single species, but is extraordinarily diverse in Asia. The massive tree palm genus *Raphia* is very diverse in Africa. One species extends to S
America and another to Madagascar, but both these distributions are thought to be man-made.

All other calamoid genera are restricted to the Asian and W Pacific region where they display varied distribution patterns (Figs. 2 and 3). However varied these patterns may be, there is one conspicuous trend. The greatest diversity in terms of species and genera is overwhelmingly Sundaic rather than Papuasian. The largest genus *Calamus*, distributed from the W Ghats and China to Fiji and Australia and in Africa (1 species) and with a total of 370 species, is almost certainly paraphyletic (Kramadibrata, 1992, Baker unpublished), but even when the distributions of individual, potentially monophyletic groupings within the genus are examined, there is a similar bias of diversity in Sundaland. The genera *Korthalsia* with 26 species of climbing palms and *Daemonorops* with about 115 species are two other examples of genera with major diversity in Sundaland and with a decrease in number of species eastwards. The distribution of these genera strongly suggests a south-eastwards invasion from Sundaland to Papuasia that could have occurred after the Miocene juxtaposition of the two ends of Malesia (but see also Morley, 1998 this volume).

A further type of distribution can be found in certain genera which are almost exclusively Sundaic, but with local variations. For example, *Ceratolobus* (6 species) is found in Sumatra, Java, Malay peninsula and Borneo. *Salacca* (c.20 species) is more widely distributed reaching China in the north and Palawan and Mindanao in the east. *Plectocomiopsis* (6 species) is found in Sumatra, the Malay peninsula (including S Thailand) and Borneo, while closely related *Myrialepis* (1 species) occurs in Indochina southwards to the Malay peninsula and Sumatra, but not Borneo or Java. *Eleiopanax* (1 species) is restricted to peat-swamp forest in the Malay peninsula (including S Thailand); Sumatra and Borneo (see also *Cyrtostachys* below). *Pogonotum* (3 species) is confined to peninsular Malaysia and Borneo, while *Calospatha* (1 species) is endemic to peninsular Malaysia and *Retispata* (1 species) to Borneo. These local distribution patterns within Sundaland emphasise the close relationship of the floras of these land masses. Differences may be explicable in terms of vegetation changes in relation to climatic fluctuations and chance dispersal and extinction events.

*Eugeissona* (6 species), distinguished by a large range of unique characters but still clearly a member of the subfamily, is distributed in the
Malay peninsula and Borneo. Two fossil poly-
nomorphs of lower and middle Miocene age in
Borneo have been referred to *Eugesisoma* sug-
gesting the presence of the genus in Borneo
from at least the early Miocene. Fossil pollen,
*Quilonipollenites*, of Lower to Middle Miocene
(21-14 Ma) age from India (Muller, 1972, 1979;
Morley, 1977; Phadate and Kulkhari, 1984) has
also been referred to *Eugesisoma* (see also Morley,
1998 this volume).

There are two highly distinctive genera which
do not display the Sundiac bias. *Metroxylon*, the
sago palm, with five species, is found in the
Caroline Islands, Fiji, Vanuatu, the Solomon Is-
lands, the Bismarck archipelago and New
Guinea. *M. saga*, now widely dispersed by man
across Malesia as a starch-producing crop, is
thought to be native to New Guinea. The other
genus, *Pigafetta*, with two species of massive
pioneer tree palms, is represented in Sulawesi
by *P. elata* and in Maluku and W New Guinea
by *P. filarii*. Both species of *Pigafetta*, possessing
relatively very small seeds, produced in
large quantities, are apparently efficient colonis-
ers of open habitats within their range so it
seems surprising that the genus is not more
widespread than it is. That these two genera are
so distinct from other Asian calamoids both in
their morphology and their distribution is clearly
suggestive of a very different biogeographic his-
tory from the other calamoid genera.

Current molecular and morphological work is
providing exciting new insights into the generic
relationships within the Calamoideae (Baker et
al., 1998; Baker and Dransfield, unpublished
work). A robust phylogeny of the Calamoideae
will be a powerful tool in biogeographic studies
of SE Asia.

**Arecoideae**

As stated above, this very large subfamily may
prove to be paraphyletic. We have chosen four
unusual examples from tribe Areceae, a tribe
which, while being pantropic, is most diverse in
the W Pacific. In marked contrast to the
Calamoideae, the tribe displays greatest diver-
sity at the Papuan end of the Malesian region,
with only a few genera (e.g., *Pinauga, Nenga*
and *Iguanura*) displaying a Sundiac bias.

*Orania* with about twenty species is the sole
member of subtribe Oraniinae. There are three
species in Madagascar, one in the western part
of Sundaland, three or four in the Philippines,
one in Maluku, one in Aru Islands and nine in
New Guinea (Fig.4A). This remarkable genus
deserves a modern phylogenetic study.

*Veitchia* with about eighteen species belongs
to subtribe Psychospermatinae. This subtribe is
defined by a suite of presumed apomorphies
unusual within the Areceae. Intergeneric rela-
tionships are currently being reassessed by Scott
Zona at Fairchild Botanic Garden; while the lim-
its of *Veitchia* may be uncertain, there seems no
doubt that the subtribe itself represents a mono-
phyletic group. *Veitchia* is present in Fiji (10
species) and Vanuatu (5 species). A single spe-
cies (*V. merrillii*) is restricted to karst limestone
in Palawan and neighbouring islands (Fig.4A).
This is an extraordinary disjunction. Even if the
limits of *Veitchia* are changed, the presence of
this species in Palawan is still remarkable, as the
rest of the members of the subtribe are found
only in Maluku, New Guinea, Australia and W
Pacific islands.

*Rhapaloblaste* (subtribe Iguanurinae), a mor-
phologically remarkably uniform genus that we
regard as being natural, also displays unusual
disjunction. One species is present in the
Nicobar Islands and one in peninsular Malaysia
while the other four species are found in
Maluku, New Guinea and the Solomon Islands
(Fig.4B).

*Cyrtostachys* (sole genus of subtribe Cyrtos-
tachydrinae) has a single species, *C. reida*,
widespread in peat-swamp forest in Sumatra,
Malay peninsula and Borneo, while the seven
remaining species are restricted to New Guinea,
the Bismarck archipelago and the Solomon Is-
lands (Fig.4C). Pollen referred to *Cyrtostachys*
occurs in Upper Miocene deposits in Borneo
(Muller, 1972).

**Gramineae**

The genera *Dinocloa* and *Nastus* are members of
the tribe Bambuseae, the woody bamboos
(subfamily Bambusoideae, family Gramineae).
Phylogenetic relationships within the tribe are
not yet understood and are currently being in-
vestigated, but at present it is divided into 8-9
subtribes (Soderstrom and Ellis, 1987, Dransfield
and Widjaja, 1995). These two genera have been
chosen to illustrate the widely differing distribu-
tions that occur within the Bambuseae.

*Dinocloa* is a natural, well-defined genus of
23-39 species, each with a limited distribution. It
is placed in the Bambusinae, a subtribe with a
largely tropical Asian distribution which is most
diverse in tropical mainland Asia. The genus it-
Fig. 4. Distributions of genera in subfamily Arecoideae (Palmac). A: Orania and Veitchia, B: Rhopaloblaste, C: Cyrtostachys.
The genus *Nastus* is included in subtribe Nastinae, which contains genera distributed in the southern hemisphere of the Old World tropics. The genus comprises about 19 species, distributed from Reunion and Madagascar to Java, Sumba through New Guinea and Solomon Islands, and possibly in Sumatra (Fig. 5). This disjunct distribution is remarkable and parallels to some degree that of the palm genus *Orania*. However, *Nastus* remains a poorly known genus.

**Antidesma (Euphorbiaceae-Phyllanthoideae)**

*Antidesma*, a genus of dioecious shrubs and trees, is commonly found in the understorey of the tropical rain forest. It is distributed throughout the palaeotropics from W Africa to the Pacific Islands and from the Himalayas to N Australia. The highest diversity, both in species number and character variation, exists in Malesia, where about 90 of the 150 currently recognised species occur, c.70 of which are endemic to the region (Fig. 6A). Despite the large number of species, no subgenera or sections can be recognised within *Antidesma*, and the great variability in some species complexes suggests that speciation is actively taking place.

The genus *Antidesma* belongs to the subtribe Antidesminae, the most notable character of which is the enlarged, U-shaped connective of the anthers that is found nowhere else in the family. The unilocular fruits and highly reduced flowers of *Antidesma* suggest that the genus is monophyletic. Furthermore, the genus is the only representative of the subtribe in Asia. Its closest relative *Hyeronima* occurs in S America and the Caribbean, while the genus with the largest number of ancestral character states in the subtribe, *Thecacoris*, is distributed in Africa and Madagascar. This strongly suggests that the subtribe and the genus *Antidesma* have originated in Gondwana, although no confirmatory fossil evidence has yet been presented.

The distribution data presented below have

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*Fig. 5. Distributions of genera in subfamily Bambusoideae (Gramineae), *Dinobloa* and *Nastus*.**
been taken from a forthcoming revision of the
genus in western and central Malesia
(Hoffmann, unpublished work).

**W and S Malesian elements**

The majority of species fall into this category.
Examples of species endemic to one island in-
clude *A. brachyboitys* (E Sarawak and Brunei
Darussalam), *A. montis-silam* (Sabah), *A. ortho-
gyne* (Malay peninsula) and *A. pleuricum* (Phil-
ippines). Other species are common to more
than one island, e.g., *A. tetradrum* (Sumatra,
Java and Bali), *A. pendulum* (Sumatra, Borneo
and Malay peninsula) and *A. leucopodum* (Su-
matra, Borneo, Malay peninsula and Mindanao:
Fig.6B). The Philippines show the highest de-
gree of endemism, followed by Borneo and the
Malay peninsula.

In *Antidesma* there is no sharp boundary
between the W and the S Malesian province of
Steenis (1950). *A. tetradrum* for example oc-
curs in Sumatra, Java and Bali, while its pre-
sumed sister species *A. venenosum* is common
throughout Borneo. *A. minus*, a species com-
mon to the submontane regions of Java and
Sumatra, illustrates Steenis’ statement about the
similarity of the mountain flora of Java and that
of most of Sumatra. Furthermore, the two spe-
cies extending across the Makassar Straits, *A.
stipulare* and *A. tomentosum* (see below), occur
in W Malesia and Java but not in the Lesser
Sunda Islands.

**E Malesian elements**

In his account of the Euphorbiaceae of New
Guinea, Airy Shaw (1980) recognised 32 species
on the island, 27 of which he reported to be
endemic. As most of them are poorly known at
the moment, these figures might change with a
critical revision. *A. excavatum* (syn. *A. molucca-
num*) is the only E Malesian species with a wide
distribution. It is common to N Sulawesi,
Maluku, New Guinea, the Admiralty and Sol-
omon Islands (Fig.6B).

**Species extending across Makassar Straits**

The distribution of *A. stipulare* bridges the phyto-
geographic demarcation line of the Makassar
Straits (Steenis, 1950), including comparably dry
Maluku and S Sulawesi (Fig.6B). *A. tomentosum*
has a similar but slightly more northwestern dis-
tribution (Malay peninsula, Sumatra, W Java,
Borneo, Philippines and N Sulawesi) with more
humid conditions.

**Species extending across the Isthmus of Kra**

Several species do not respect the demarcation
line between Malaysia and SE Asia slightly north
of the Thai-Malay border (Steenis, 1950), e.g., *A.
puncticulatum* (Fig.6C) and *A. velutinosum*
(Burma, Thailand, Malay peninsula, Anambaris
and Natuna Islands, Sumatra, Java). *A. japoni-
cum* (peninsular Malaysia, Thailand, Burma,
Indochina, SE China, S Japan, Taiwan, Luzon) is
an example of the similarity of the upland flora
of N Luzon and E Asia (Steenis, 1950).

**Monsoon forest elements**

*A. acidum* (syn. *A. diandrum*) is the only spe-
cies in the genus with a disjunct distribution
(Fig.6D). This disjunction is known from many
other taxa including the teak tree, *Tectona
grandis* (Verbenaceae). *A. acidum* is found in
the teak forests of Java and listed among the
drought indicating plants (Steenis and Schippers-Lammertse, 1965). The species is also
somewhat isolated morphologically.

The taxa sharing this distribution pattern re-
quire a two-seasonal climate with an annual
drought period. They are present in the
monsoon forests of Burma, Thailand and
Indochina, avoid the everwet central part of W
Malesia from the Isthmus of Kra southwards, but
reappear in Java, parts of the Philippines,
Sulawesi and the Lesser Sunda Islands. Because
of the high number and the composition of taxa
concerned, this cannot be explained by anthropo-
genic dispersal only. Instead, it dates back to
the extension of areas with periodical drought
during the Pleistocene, which then disappeared
again in the post-glacial period leaving many
taxa with disjunct distribution areas. This has
been discussed in detail by Steenis (Meeuwen et
al., 1960).

**Widespread species with a broad ecological
spectrum**

The three most widespread Asian species hardly
show any ecological preferences. This applies
particularly to the very common *A. montanum*,

Fig 6. Distributions in the genus Antidesma (Euphorbiaceae). A: worldwide distribution of Antidesma (numbers indicate the number of species in the outlined areas); B: A. stipulare and A. excavatum, A. leucopodium; C: A. puncticulatum; D: A. acidum.
which occurs in most habitats from India (excluding Sri Lanka) to S Japan, Indochina, the Philippines, W Malasia, Java and Sulawesi. *A. ghaesembilla* is found throughout the region including India, S China, New Guinea and N Australia. It is the only species in the genus that prefers open vegetation such as secondary scrub and savannah. *A. buntius* is widely cultivated as a fruit tree, which makes it impossible to establish its original distribution. The species is known from Nepal and Sri Lanka to the Philippines and Maluku, although no collections from the Malay peninsula have been seen.

It has been shown for many plant taxa that the ecological amplitude and geographic distribution of polyploids may exceed that of related diploid taxa (Briggs, and Walters, 1984, Skalinska, 1946). According to the chromosome numbers compiled by Hans (1970, 1973), three African species and the two Asian species *A. ghaesembilla* and *A. acidum* are diploid with \( n = 13 \), which is the base number in most Phyllanthoideae. On the other hand, *A. acuminatum* (*A. montanum*-complex) and *A. buntius* have been found to be polyploid. In the former species both diploid (\( n = 13 \)) and hexaploid (\( n = 39 \)) races have been observed, whereas *A. buntius* has been shown to be 18-ploid (\( n = 117 \)). All polyploid records are based on collections from India, where the genus reaches its northern limit, and both taxa are among the most widespread, variable and ecologically tolerant taxa.

A possible evolutionary scenario based on the facts presented here would suggest the origin of the genus in wet tropical eastern Gondwana, followed by migration to and extensive radiation in tropical Asia. Climatic changes during the Pleistocene affected the disjunct distribution of *A. acidum* (see above). Unfortunately, we have no means yet to date any of the other events. The most promising systematic approach to render this outline more precise would involve an extensive survey of chromosome numbers in the genus and analysis of molecular data.

**Elaeocarpaceae**

The Elaeocarpaceae are a mostly tropical family of some 500 species, the majority of which are rainforest trees. Six of the family’s nine genera (*Aceratium*, *Aristotelia*, *Dubouzetia*, *Elaeocarpus*, *Peripentadenia* and *Sloanea*) occur in Australia which therefore has more genera of Elaeocarpaceae than any other land mass. Furthermore, several species of *Elaeocarpus* in Australia do not fit into the otherwise effective classification within the genus. Preliminary analysis (Goode, 1987) supports the suggestion that the family has undergone a major radiation in the Australian region, certainly in Gondwana although, of course, the number of taxa in an area does not necessarily indicate that the group has evolved there. Furthermore, the family “is represented in the Tertiary fossil record in Australia by pollen, leaves and fruit” while fruits identifiable as belonging to *Elaeocarpus* have “been recognised as a ubiquitous element of the Tertiary flora of Australia” (quotes from Rozefelds and Christophel, 1996). Rozefelds and Christophel also quote references reporting fossil wood from the Tertiary in India and the Paleocene in Patagonia.

*Elaeocarpus* is a genus of some 360 species distributed widely in the Old World tropics, but not in Africa. It is currently known from the area bounded by Madagascar, eastern India including Ceylon, the warmer parts of China and Japan, New Caledonia, eastern Australia, New Zealand, the western Pacific and Hawaii. The majority of the species occur in SE Asia, Malaysia, the Philippines, Indonesia and New Guinea. Many species appear to be successional while others are restricted to the forest depths. They occur from sea-level to 3000 m or more.

Although formal analysis is lacking, several groupings within the genus *Elaeocarpus* are almost certainly monophyletic. The distribution patterns of four of these groupings are presented. Unfortunately, the large and widespread groups (currently known as section *Coilepeta* and section *Monocera*) cannot be discussed as it is doubtful that they are monophyletic.

Section *Elaeocarpus* is most speciose in the western part of its range, tailing off eastwards after Borneo (Fig.7A). There is evidence of further speciation in New Guinea, with two small groups of species, one endemic, the other not found west of Sulawesi, in addition to the widespread *E. solomonensis*. In Fig.7B the *Polystachys* group presents a different pattern. Also included in Fig.7B are the hypothesised nearest relatives to the *Polystachys* group, which are in Sulawesi and Australia (Goode, 1997).

The *Acronodia* group has a rather similar pattern of current distribution (Fig.7C) but apparently its closest links are with China and Madagascar (Goode, 1996). Section *Oreocarpus* includes a single species (*Elaeocarpus culminicola*) found in various forms from the Philippines, Sulawesi, Maluku, New Guinea and the Bismarck archipelago, Aru Island, Melville Island
Fig. 7. Distributions in the genus *Elaeocarpus* (*Elaeocarpaceae*). A: section *Elaeocarpus*; B: the *Polystachyus* group and its hypothetical nearest relatives; C: section *Acronodia* and *E. culminicola*.
and NE Queensland (Fig. 7C). The six remaining species of the section are all found in Australia alone.

**Curious plant distributions in Pauasia**

Some curious distributions of ferns and angiosperms have been selected as evidence for relationships between certain land masses and parts of Pauasia. Such evidence carries a caveat that the plant collection density for New Guinea is particularly low (Johms, 1995).

*Christensenia*, a fern genus in the Marattiaceae, comprises a single species, *C. aesculifolia*, distributed from India and SE Yunnan to Malesia and the Solomon Islands (Camus, 1990). With the exception of a single collection from the Vogelkop peninsula in Irian Jaya, this species has not been recorded from the mainland of New Guinea. Within Pauasia the genus occurs at several sites on New Ireland and in the Solomon Islands.

The Vogelkop peninsula includes several other floristic elements which it shares with central and western Malesia, but not with the remainder of New Guinea. The dipetecarp *Hopea inexpecta* (*Hopea* Section *Dryobalanoides*), the only representative of this section east of Wallace’s Line, is restricted to the Kebar Valley in the Vogelkop where it is locally frequent in lowland rain forest. The rubiaceous ant plant genus *Myrmephytum* is represented in the Philippines, Sulawesi, Maluku and by five species in the Vogelkop peninsula.

Distribution patterns also suggest a relationship between western and central Malesia, the Bismarck archipelago and the Solomon Islands, excluding New Guinea. Several other distributions support this suggestion. The genus *Sararanga* (Pandanaeae) occurs in the Philippines (*S. philippinensis*), and is represented by a second species (*S. sinuosa*) along the island arc to the north of New Guinea. It is found also on Manus Island and New Ireland in the Bismarck archipelago and throughout the Solomon Islands with three small localised populations known from the north coast of New Guinea on Napan Island, near Jayapura and Vanimo. A similar pattern is also shown by the ferns *Pneumatopteris rodgersiana* and *Christella barveyi*.

Some species which reflect this pattern of distribution also occur on the New Guinea mainland in SE Papua, suggesting an additional relationship between the Solomon Islands and the Papuan peninsula. For example, the fern *Cephalomnes boryanum* occurs on Manus, New Ireland, the Solomon Islands, Woodlark Island, the Louisiade archipelago and on the mainland of SE Papua.

**Discussion**

At this stage, it would be inappropriate to speculate on the geological significance of the data presented here. Any one explanation of these very preliminary data could easily be replaced by another interpretation while formal analysis is lacking. A few generalisations can be made. Firstly, we believe that the distributions that we have discussed probably require a tectonic explanation. This seems to be particularly true for the curious disjunctions that have been discussed, such as those found in *Orania* and *Nastus* between Malesia and Madagascar, and in *Rhopaloblaste* and *Gyrostachys* between E Malesia and W Malesia. However, it is important to be aware of the potential impact of extinction in generating apparently disjunct distributions which at one time may have been continuous. Furthermore, we find it far easier to explain W Malesian plant distributions than those of E Malesia as the geological evolution of the former region is better understood. We anxiously await the elucidation of the geological evolution of E Malesia, especially of the Pauasian region.

Although dispersal events are of no interest to vicariance biogeographers, they are a biological reality. It is important to take dispersal into account when one is considering biogeographical patterns of a single group in isolation from other groups so as to avoid mistaking ecological noise for biogeographical signal. One of our examples, the distribution of *Antidesma*, is thought to be heavily influenced by long distance dispersal, as the small bright red or black fruits are attractive to birds. Therefore, it is likely that the distribution of many *Antidesma* species is a reflection of their climatic, altitudinal and edaphic preferences rather than of tectonic movements.

The efficiency of birds in long-distance plant dispersal is difficult to assess, as a number of factors must be taken into account, such as the retention time of the seed in the digestive system and the viability of the transported seed after defecation or regurgitation. Both depend on the characteristics of the seed (*e.g.*, attractiveness and nutrient content of the fruit pulp or aril, seed size and robustness) as well as the bird (*e.g.*, size, presence of grit in the muscular gizzard, flight speed, territorial behaviour). For ex-
ample, some birds may avoid open spaces to avoid potential attacks by predators, thereby failing to deposit seeds in these habitats, while other birds may cross open areas flying at high altitude and act as effective dispersal agents for seed. The major difficulty lies in the fact that most studies necessarily concentrate on only one aspect of this complex process, usually either the behavioural patterns and physiology of a particular bird taxon or the dispersal type of the plants found in a certain ecosystem.

A recent project on forest regeneration on Krakatau investigates the re-colonisation of the once sterilised islands by bird-dispersed plants (Whittaker and Jones, 1994). Three or four species of Anitesma have arrived on Krakatau so far. A. montanum, the most common and most widely distributed species of the genus, has become the dominant element of the forest understorey (Whittaker and Schmitt, pers. comm., 1997). However, as Krakatau is only 40 km away from the nearest mainland, the dispersal of seeds across greater distances may follow different rules.

Robust biogeographic hypotheses could be constructed from the data presented in this paper if the examples used were taken further into the analytical phase, historical biogeography. Historical biogeography can be practised on different levels. A simple approach is to discuss the biogeographical implications of a single group, with reference to a phylogeny. However, this is, in a sense, still narrative biogeography as it lacks independent support. The alternative, cladistic biogeography in the strict sense, uses phylogenetic hypotheses derived from any number of organisms relevant to a region to assess relationships between areas of endemicism within that region. Under the assumption that the Earth and its biota share a common history, it uses biological data to identify area relationships that occur repeatedly and that are congruent with each other, and then relates them to Earth history, principally geological events. Despite the reality of influences such as climate, dispersal and pollination, it is very probable that a geological theme underpins all current plant distribution patterns. The methods of cladistic biogeography aim to reveal the theme by using phylogenetic hypotheses of phylogenetic relationship to identify the repeating signal and dismiss the ecological noise. The theory and techniques used in cladistic biogeography are well summarised in Humphries and Parenti (1986), Humphries et al. (1988) and Humphries (1992), and some excellent examples of these techniques being applied in Malesian plant groups may be found in Linder and Crisp (1995), Turner (1995) and Ridder-Norman (1996).

SE Asia contains a diverse flora which undoubtedly reflects its complex geological history. When rigorous systematic methods are applied to the members of this flora, further patterns may be revealed and related to tectonic evolution. Preliminary discussions such as ours are necessary to assess the potential value of groups in biogeographical studies.

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