



Historical biogeography of *Rhododendron* section *Vireya* and the Malesian Archipelago

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ABSTRACT

Aim *Vireya* rhododendrons are distinctive and easily recognizable by their general form; however, they are virtually circumscribed geographically, predominantly distributed throughout the biogeographically intriguing Malesian Archipelago. Hypotheses of the evolutionary relationships of the group have been proposed but the biogeography of vireyas has not been analysed based on molecular phylogeny. Recently, the first detailed molecular phylogenetic investigation of section *Vireya* was completed based on cp- and nrDNA sequence data, therefore making this cladistic biogeographic study of vireya rhododendrons possible.

Location Malesia, Australia, Solomon Islands, Taiwan, Himalayas, north Vietnam and south China.

Methods Based on distribution maps, areas of endemism were determined for the biogeographic region of Malesia. Area relationships were analysed based on a recent molecular phylogeny of species in section *Vireya*. The method of paralogy-free subtree analysis was applied.

Results Individual distribution maps were produced for 74 species of *Rhododendron* section *Vireya*. Species clades with bootstrap support proved to be biogeographically informative. Major clades correspond to three regions: eastern Malesia, western/middle Malesia and Taiwan/north Vietnam/south China. Within eastern Malesia, Australia, New Guinea, the Bismarck Archipelago and Solomon Islands are related. In western Malesia, northern Philippines, Borneo, southern Moluccas and north and west Sulawesi are related. These areas are more distantly related to Sumatra, the Malay peninsula, Java, Bali, Palawan, Lesser Sunda islands and the southern Philippines. The position of the Himalayas is equivocal and part of a basal polytomy in the summary area cladogram.

Main conclusions Two alternative hypotheses are proposed for the evolution of vireya rhododendrons based on the pattern of area relationships. The first hypothesis is that the vireyas are an old group, with ancestors present on Gondwana, rifting north in the Cretaceous. The second alternative hypothesis is that vireyas are a young group that has dispersed eastwards from India to Australia and the Solomon Islands since the current Malesian islands formed.

Keywords

Cladistic biogeography, distribution maps, Malesia, paralogy-free subtree analysis, *Rhododendron* section *Vireya*, Southeast Asia.

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INTRODUCTION

The Malesian Archipelago has been of interest to naturalists and scientists alike since 1869, when Alfred Russel Wallace

recognized a biotic discontinuity between the Indo-Malay and Australian bird and mammal faunas (Michaux, 1991). What became to be known as Wallace's line separates the islands of Bali and Lombok, and Borneo and Sulawesi, and runs to the

south-east of the Philippines (George, 1981). Subsequent to Wallace, in the late 1800s and early 1900s, Huxley, Lydekker and Weber proposed other lines to separate the Australian and Asian faunas (George, 1981). All of these lines fall in the middle of the Malesian Archipelago in the region bounded by the Sunda and Sahul continental shelves: the Lesser Sunda Islands, Moluccas, Sulawesi, and Philippines. This region was aptly named 'Wallacea' by Dickerson in 1928 (Cox, 2001).

The Malesian Archipelago continues to be of the great interest to biogeographers today, with a large number of studies based on floral and faunal taxa endemic to Malesia and its neighbouring regions (e.g. Whitmore, 1987; Ladiges *et al.*, 1991; Hall & Holloway, 1998; Evans *et al.*, 2003; Heads, 2003; Ladiges *et al.*, 2003). Most studies have concentrated only on taxa that are distributed in either the east or the west of Malesia and that do not span the entire archipelago, as in fact do many taxa, including rhododendrons.

Vireya biogeography

Rhododendron L. is a species-rich genus of flowering plants (family Ericaceae Juss.), comprising over 1000 species. It is currently divided into eight subgenera, which include various sections and subsections (Sleumer, 1980; Chamberlain *et al.*, 1996). *Rhododendron* subg. *Rhododendron* is the lepidote (scaly) group, based on the presence of scales on leaves and other organs. Section *Vireya* (Blume) Copel. f. is the largest of three sections within this subgenus, characterized traditionally by seeds with tailed appendages at both ends, capsule valves that twist on opening, placentas that separate as thread-like structures and by their predominantly Malesian distribution. The last revision of section *Vireya* was by Sleumer (1966).

An analysis of the biogeography of vireyas based on molecular phylogeny has yet to be performed. Several authors have proposed tentative explanations for the origin and evolution of species in particular areas of Malesia. Copeland (1929) noted that taxa in the Philippines appear to be related to species on neighbouring islands, including Borneo and New Guinea, and speculated about their possible origins. van Balgooy (1987) made similar observations for the flora of Sulawesi, concluding that taxa came from northern, southern and eastern routes, rather than from the west, despite being geographically close to Borneo. Stevens (1982) suggested that diversification of Ericaceae in New Guinea has occurred since the late Miocene (c. 10 Ma) at the earliest, and was dependent on the arrival of only a few ancestors from West Malesia. Based on interspecies promiscuity among vireyas, Williams & Rouse (1997) also considered the section to be of a relatively young age.

Specht (1988) considered *Rhododendron* to be an old genus. He hypothesized that rhododendrons were on Gondwana before its break-up, and that the lepidote group (subg. *Rhododendron*), including sect. *Vireya*, dispersed northwards from Australia into the archipelago, while the elepidote rhododendrons (all other subgenera) moved north with India and dispersed outwards from there. Irving & Hebda (1993)

proposed that, in their early history, rhododendrons extended more or less continuously from North America to Europe and Greenland, and into China and north-east Asia, with their present-day, more restricted distribution a result of climatic deterioration over time. They hypothesized that the vireyas are relatively young, evolving in the last few million years, because 'they are concentrated in one essentially continuous region', and the terranes where they are found are of recent origin. Irving & Hebda (1993) acknowledged that their assumptions and hypotheses were speculative as they had no specialized knowledge of rhododendrons, and instead based their ideas solely on geology, climate and the ecology of present-day species.

The recent panbiogeographic study of Heads (2003) is the only biogeographic study of the vireyas that takes the taxonomy of the section into account, although it is not based explicitly on phylogenetic relationships because no cladistic analysis was available until now. Heads (2003) used the *Flora Malesiana* classification (Sleumer, 1966) and all subsequent taxonomic revisions to map generalized distributions of 276 species of vireya in their subsections and series. He related centres of endemism to tectonic history. Heads (2003) indicated that this approach related 'the characters underlying the taxa, rather than the taxa *per se*'.

The first detailed phylogenetic investigation of section *Vireya* was only recently completed, and was based on DNA sequence data (Brown *et al.*, 2006, in press). Because biogeographic studies should be based on sound systematics (Humphries & Parenti, 1999), it is understandable that no detailed cladistic biogeographic investigations have been completed for the section.

In our study we have prepared distribution maps for species of *Vireya*, including all those represented in the recent molecular phylogenetic analyses (Brown *et al.*, 2006, in press). We use these distribution maps to delineate areas of endemism, superimposing the areas on the molecular taxon cladogram. The cladogram summarizes all clades (nodes) that were resolved with support, based on chloroplast DNA (*psbA-trnH* and *trnT-trnL*) regions. The method of paralogy-free subtree analysis (Nelson & Ladiges, 1996) is applied to analyse the relationships of the geographic areas of endemism in the region of Malesia and to infer the evolutionary history of *Rhododendron* section *Vireya*.

METHODS

Molecular phylogeny

A summary molecular phylogeny based on cpDNA sequences was produced based on parsimony and Bayesian analyses in Brown *et al.* (2006). A total of 65 species were sequenced for this summary phylogeny (Fig. 2); 58 of these species were sequenced for both the *trnT-trnL* and the *psbA-trnH* intergenic spacer regions, while the other 7 species (marked with an asterisk in Fig. 2) were only sequenced for the *trnT-trnL* intergenic spacer due to amplification difficulties (Brown

et al., 2006). Bootstrap values (> 50%) indicating support for nodes are shown.

Species maps

Distribution maps were available in the literature for only about 20 species of *Vireya* (see references in Heads, 2003). Maps of all species in the summary molecular phylogeny were produced using the ANH map program (version 2.0, 13 November 1997, Canberra, Australia). The species included in the summary phylogeny from outside the section *Vireya* were not mapped; instead, their distributions for the cladistic biogeographic analyses were taken from the literature (Chamberlain *et al.*, 1996).

To cover the total known distribution of each species, locality information was obtained from herbarium specimens, and supplemented with locality information from the literature (data available on request; Sleumer, 1958, 1973; Argent & Madulid, 1995, 1998; Takeuchi, 2000). Specimens from several herbaria were examined for locality information: Arnold Arboretum, Harvard University (A), Australian National Herbarium (CANB), Royal Botanic Garden Edinburgh (E), Nationaal Herbarium Nederland, Leiden, University branch (L), and the New York Botanical Garden (NY). Where the latitudes and longitudes were not recorded on the specimen label, geocodes of these localities were estimated for the closest known location from a number of sources: PNG (Papua New Guinea) localities list (1991–present, Australian National Herbarium, unpubl. data); the Australian National Herbarium Specimen Information Register (ANHSIR) data base; IBIS (Indonesia Biodiversity Information System) Herbarium Bogoriense, Indonesia; Microsoft® Encarta® Interactive World Atlas, 2001; Orchids of Sarawak (Beaman *et al.*, 2001); Global Gazetteer (<http://www.calle.com/world>); NIMA Geographic Names Database (GNDB; <http://gnpswww.nima.mil/geonames/GNS/index.jsp>); Taiwan mountain localities (<http://www.indexmundi.com/taiwan>).

Areas of endemism

Recognizing areas appropriate for the level of study can be problematic (Platnick, 1991) and a number of ways to best define areas have been proposed (e.g. Humphries & Parenti, 1986; Axelius, 1991; Harold & Mooi, 1994; Morrone & Carpenter, 1994). We recognized areas based on geological information (Hall, 2002), previous biogeographic studies of the region (de Boer & Duffels, 1996; Ridder-Numan, 1998; Heads, 2001), and the distributions of the species included in these analyses.

Twenty biogeographic areas, A–T, were found throughout the Malesian Archipelago and neighbouring regions (Fig. 1): Bismarck Archipelago and the Solomon Islands (A), Papuan Peninsular (B), north-eastern Australia (C), New Guinea craton (D), central New Guinea (E), northern New Guinea (F), Vogelkop Peninsula (G), south Moluccas (H), Lesser Sunda Islands (I) (restricted to the islands to the west of Flores

because no species in this study extends further east into this island arc), north and west Sulawesi (J), southern Philippines (K), northern Philippines (L), Palawan (M), north and south Borneo (N), Java and Bali (O), north and south Sumatra (P), Malay Peninsula (Q), Taiwan (R), north Vietnam and south China (S), and the Himalayas (T).

Paralogy-free subtree analysis

The method of paralogy-free subtree analysis removes paralogous (redundant) nodes and utilizes only the data relevant to cladistic biogeography (Nelson & Ladiges, 1996). Geographic paralogy is revealed by geographic distributions that are duplicated or found to be overlapping among related taxa; it is analogous to paralogy of molecular systematics (Nelson & Ladiges, 1996; Ladiges, 1998; Humphries & Parenti, 1999; Crisci, 2001). Different causes, such as dispersal, sympatric speciation and imprecise characterization of geographic areas, can result in geographically paralogous nodes (Nelson & Ladiges, 1996). Humphries & Parenti (1999) considered that paralogy-free subtrees 'should lead to straightforward ways of expressing area interrelationships', and Crisp *et al.* (1999) commented that the method 'has the considerable advantage of simplicity in concept and application'.

Each terminal taxon of the molecular phylogeny was replaced by a list of the geographic areas in which it occurs. Paralogy-free subtrees (with no area duplication) were found by inspection and coded as characters for a parsimony analysis. Characters were binary coded, with missing areas coded as question marks. Multiple parsimonious trees are recovered because of the number of question marks in the data matrix, which result in resolved nodes that are unsupported by data. Rather than compute a strict consensus tree, the shortest tree with the least resolution (the minimal tree) was found (Nelson & Ladiges, 1996). The program Hennig86 (Farris, 1988), with option 'dos equis', was used for the parsimony analysis and search for the minimal tree. The minimal tree summarizes the relationships of the areas to one another (area cladogram).

RESULTS

Species maps

The distributions of 74 species were mapped (Appendix S1 in Supplementary Material), and are summarized below.

Borneo

Nine of the mapped species are endemic to the island of Borneo (Appendix S1a, b, d, i, o, p, y, ll & tt): *R. abietifolium* Sleumer, *R. acuminatum* Hook.f., *R. alborugosum* Argent & J.Dransf., *R. burttii* P.Woods, *R. edanoi* ssp. *pneumonantherum* (Sleumer) Argent, *R. ericoides* Low ex. Hook.f., *R. intranervatum* Sleumer, *R. lowii* Hook.f. and *R. polyanthemum* Sleumer. Four of these taxa are restricted to the Gunung (Mount) Kinabalu area, which is located in the Malaysian state of Sabah:

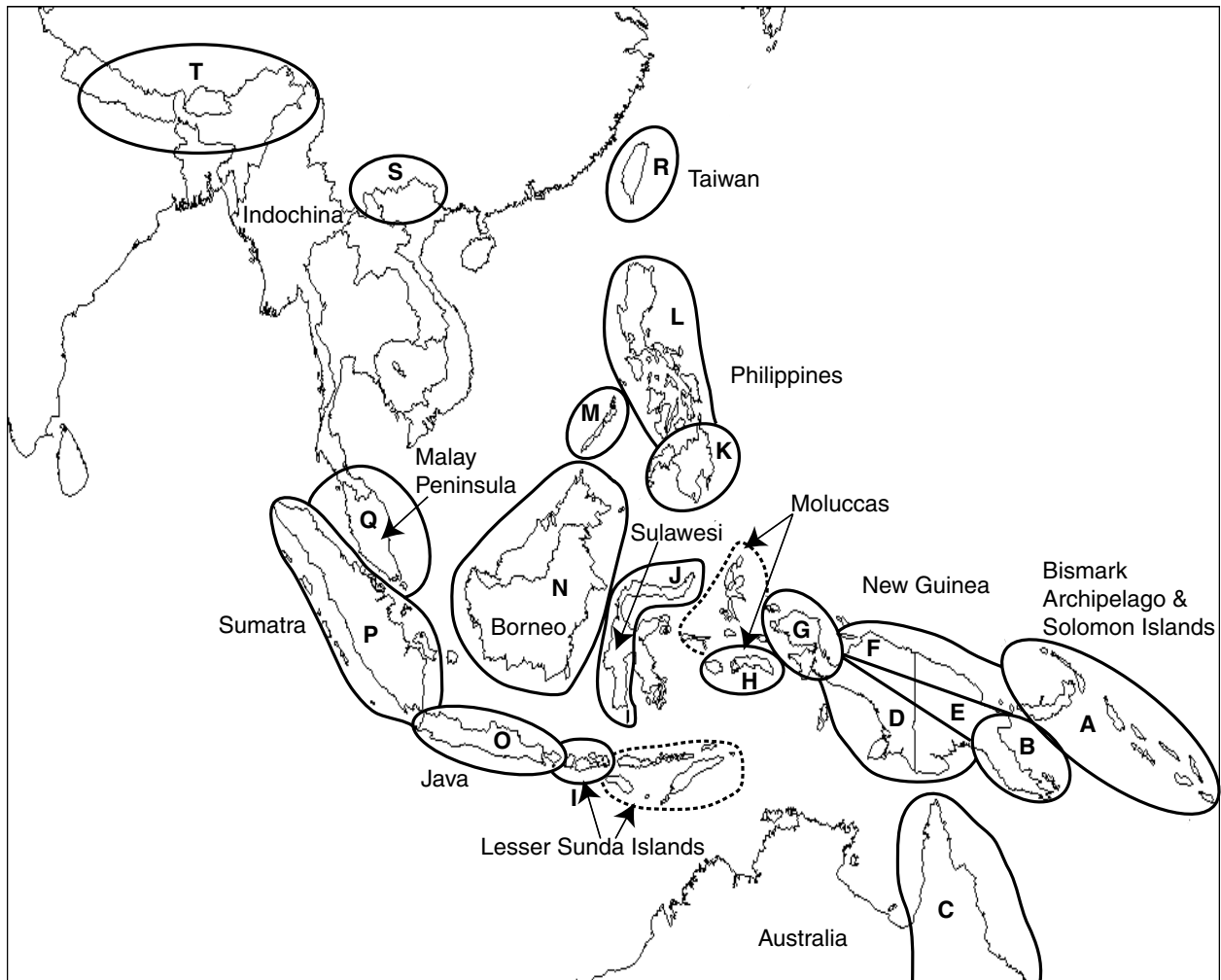


Figure 1 Map of Malesia and surrounding region. Islands and 20 areas of endemism are outlined and labelled. The political division on the island of New Guinea is indicated; the west Irian Jaya (Indonesia) and the east PNG (Papua New Guinea). The 20 areas of endemism used in the paralogy-free subtree analysis are: Bismarck Archipelago and the Solomon Islands (A), Papuan Peninsular (B), north-eastern Australia (C), New Guinea craton (D), central New Guinea (E), northern New Guinea (F), Vogelkop Peninsula (G), south Moluccas (H), Lesser Sunda Islands (I), north and west Sulawesi (J), southern Philippines (K), northern Philippines (L), Palawan (M), Borneo (N), Java and Bali (O), Sumatra (P), Malay Peninsula (Q), Taiwan (R), north Vietnam and south China (S) and the Himalayas (T). Two areas outlined with a stippled line are defined based on geological information and previous biogeographic studies; no species of vireya in this study are found in defined areas, hence the areas are excluded.

R. abietifolium, *R. acuminatum*, *R. lowii* and *R. polyanthemum* (Appendix S1a, b, ll & tt). *Rhododendron ericoides* has also been recorded from G. Kinabalu, although it is not endemic there, and is also recorded from the G. Mulu National Park in Sarawak (Malaysia; Appendix S1p). *Rhododendron burttii* has been collected from both Sabah and Sarawak, the two Malaysian states on the island of Borneo (Appendix S1i). The other three endemic Bornean species are distributed in Sarawak and the Indonesian province of Kalimantan (Appendix S1d, o & y): *R. alborugosum*, *R. edanoi* ssp. *pneumonanthum* and *R. intranervatum*.

Rhododendron javanicum (Blume) Benn. and *R. malayanum* Jack (Appendix S1bb & oo), while not endemic to Borneo, have been collected from numerous locations on this island.

Java

Only one endemic species of vireya is mapped for the island of Java (Appendix S1e): *R. album* Blume. Several of the widespread species, however, are also recorded from Java (Appendix S1l, bb, oo, aaa & vvv): *R. citrinum* (Hassk.)Hassk., *R. javanicum*, *R. malayanum*, *R. retusum* (Blume) Benn. and *R. zollingeri* J.J.Sm.

Lesser Sunda Islands

None of the mapped species is endemic to the Lesser Sunda Islands. Several of the widespread taxa — *R. citrinum*, *R. javanicum* and *R. zollingeri* (Appendix S1l, bb & vvv) — are found

on the island of Bali, while one of these species has also been collected further east on the islands of Flores and Lombok (Appendix S1vvv): *R. zollingeri*. One possible explanation for the wide distribution of *R. zollingeri* in the Lesser Sunda Islands is dispersal, although further study of populations across the Lesser Sunda Island is required to test dispersal and vicariance hypotheses.

Malay Peninsula

Only one mapped species is endemic to the Malay Peninsula: *R. robinsonii* Ridl. It is found throughout the western and central states of Selangor, Pahang and Perak (Appendix S1ccc). *Rhododendron jasminiflorum* var. *heusseri* (J.J.Sm.) Sleumer, *R. javanicum* and *R. malayanum* (Appendix S1aa, bb & oo), while not endemic to the Malay Peninsula, have also been collected there.

Moluccas

Rhododendron meliphagidum J.J.Sm. and *R. ruttenii* J.J.Sm. are endemic to the Moluccas; both found only in the Manusela National Park on the island of Ceram (Appendix S1pp & fff). *Rhododendron malayanum*, which is widespread across the archipelago, has also been recorded from Ceram (Appendix S1oo).

New Guinea

Twenty-nine species endemic to the island of New Guinea, which includes both the republic of Papua New Guinea (PNG) and the Indonesian province of Irian Jaya, have been mapped (Appendix S1h, j, k, m, n, s, t, u, v, w, x, z, ee, ff, hh, ii, nn, qq, ss, zz, eee, hhh, iii, jjj, lll, nnn, rrr, ttt & uuu): *R. baenitzianum* Lauterb., *R. carringtoniae* F.Muell., *R. christi* F.Först., *R. comonae* F.Först., *R. culminicola* F.Muell., *R. gardenia* Schltr., *R. goodenoughii* Sleumer, *R. gracilentum* F.Muell., *R. herzogii* Warb., *R. hyacinthosmum* Sleumer, *R. inconspicuum* J.J.Sm., *R. inundatum* Sleumer, *R. konori* Becc., *R. laetum* J.J.Sm., *R. leptanthum* F.Muell., *R. leucogigas* Sleumer, *R. maius* (J.J.Sm.) Sleumer, *R. multinervium* Sleumer, *R. phaeochitum* F.Muell., *R. rarum* Schltr., *R. rubineiflorum* Craven, *R. saxifragoides* J.J.Sm., *R. solitarium* Sleumer, *R. spondylophyllum* F.Muell., *R. superbum* Sleumer, *R. tuba* Sleumer, *R. vitis-idaea* Sleumer, *R. womersleyi* Sleumer and *R. zoelleri* Warb.

Of these species, 17 have been found only in the east (PNG) (Appendix S1h, j, k, m, t, u, w, hh, qq, ss, zz, eee, iii, jjj, lll, nnn & ttt), predominantly distributed throughout the central mountain ranges, but also on the Huon Peninsula, in the northern Torricelli Mountains, and on the islands of New Britain, New Ireland and Goodenough Island. In contrast, only three species have distributions that are restricted to the west of the island (Irian Jaya): one in the central region, one in the Cyclops Mountains to the north and the other on the Vogelkop Peninsula (Appendix S1z, ff & ii). The bias between east and west distribution is possibly

a collecting artefact, with Irian Jaya not as well explored as PNG. Nine of the endemic species are distributed across the whole island, extending from the Morobe Peninsula, through the central PNG mountain range and central Irian Jaya, to the Vogelkop Peninsula (Appendix S1n, s, v, x, ee, nn, hhh, rrr & uuu).

Rhododendron loranthiflorum Sleumer and *R. luraluense* Sleumer are also found in New Guinea, but are not endemics, their distribution extending eastwards to the Solomon Islands (Appendix S1kk & mm).

Philippines

Six of the mapped species are endemic to the islands of the Philippines (Appendix S1g, dd, ww, ddd, mmm & sss): *R. apoanum* Stein, *R. kochii* Stein, *R. quadrasinaum* var. *rosmarinifolium* (Vidal) Copel.f., *R. rousei* Argent & Madulid, *R. taxifolium* Merr. and *R. williamsii* Merr. *Rhododendron apoanum* is restricted to the southern island of Mindanao (Appendix S1g), while four species, *R. quadrasinaum* var. *rosmarinifolium*, *R. rousei*, *R. taxifolium* and *R. williamsii*, are found only on the islands in the north: Luzon, Mindoro, Biliran and Sibuyan (Appendix S1ww, ddd, mmm & sss). *Rhododendron kochii* is distributed throughout the northern and southern Philippines, being found on the islands of Luzon, Mindanao, Mindoro and Negros (Appendix S1dd).

Two other species are mapped, although they are not restricted to the Philippines (Appendix S1bb & vvv): *R. javanicum* and *R. zollingeri*. In the Philippines, both species are found on the island of Luzon, while *R. javanicum* has also been recorded from the islands of Mindanao and Palawan.

Sulawesi

Eight of the mapped species are endemic to the island of Sulawesi (Appendix S1f, r, gg, rr, vv, xx, bbb & ppp): *R. alternans* Sleumer, *R. eymae* Sleumer, *R. laguncularpum* J.J.Sm., *R. nanophyton* Sleumer, *R. pudorinum* Sleumer, *R. radians* J.J.Sm., *R. rhodopus* Sleumer and *R. vanvuurenii* J.J.Sm. Two of these — *R. eymae* and *R. nanophyton* (Appendix S1r & rr) — are restricted to G. Rantemario in the south, the highest mountain on the island, reaching c. 3400 m a.s.l. *Rhododendron alternans*, *R. laguncularpum* and *R. pudorinum* are also restricted to the south of the island (Appendix S1f, gg & vv), while *R. rhodopus* and *R. vanvuurenii* occur in both southern and central Sulawesi (Appendix S1bbb & ppp). *Rhododendron radians*, the other Sulawesi endemic, is more widespread, and is found in the southern, central and northern parts of the island (Appendix S1xx).

Rhododendron javanicum, *R. malayanum* and *R. zollingeri* (Appendix S1bb, oo & vvv) have also been collected in south and central Sulawesi, although they are not endemic to the island.

Sumatra

Four species endemic to the island of Sumatra are mapped (Appendix S1c, uu, yy & kkk): *R. aequabile* J.J.Sm., *R. pubigermen* J.J.Sm., *R. rarilepidotum* J.J.Sm. and *R. sumatranum* Merr. *Rhododendron rarilepidotum* and *R. sumatranum* are restricted to the northern part of the island (Appendix S1yy & kkk), while *R. pubigermen* occurs in the north and south, on the west coast (Appendix S1uu). The other species endemic to Sumatra, *R. aequabile* (Appendix S1c), has been recorded only from the mid-west coast to the southern tip of the island.

While not endemic to the island, *R. citrinum*, *R. jasminiflorum* var. *heusseri*, *R. javanicum*, *R. malayanum* and *R. retusum* (Appendix S1l, aa, bb, oo & aaa) have also been collected from Sumatra.

Locations outside Malesia

Two species are known from northern Queensland, Australia, and both were mapped (Appendix S1jj & qqj): *R. lochia* F. Muell. and *R. viriosum* Craven. The distributions of these two species do not overlap, with *R. viriosum* (Appendix S1qqj) distributed in the Cook district, and *R. lochia* (Appendix S1jj) found further south on Mount Bartle Frère, Bell Peak North and the Bellenden Ker Range.

Two vireyas from the Himalaya region are mapped: *Rhododendron santapaui* Sastry et al. (Appendix S1ggg) restricted to Assam (India), and *R. vaccinioides* Hook.f. (Appendix S1ooo), widespread across Bhutan, Burma, eastern Tibet, India and Nepal.

The other two species mapped and located outside Malesia are: *R. kawakamii* Hayata (Appendix S1cc) from Taiwan and *R. euonymifolium* H.Lév (Appendix S1q) from north Vietnam and southern China (Guizhou and Guangxi provinces).

Area analysis

Figure 2 is the summary cladogram for sampled taxa within *Rhododendron* subg. *Rhododendron* (node 0) based on DNA sequence data (Brown *et al.*, 2006). Two species (*R. maddenii* and *R. lindleyi*, node 4) classified in section *Rhododendron* were included in the molecular analyses, and in some trees nested within section *Vireya*, although the consensus tree placed them at the basal polytomous node. All other species in the cladogram are from section *Vireya*. The clades at nodes 2 and 3 are subsect. *Pseudovireya* and the clade at node 1 is termed informally 'Euvireya'. The Euvireya group consists of two main clades of geographic significance: node 5 includes eastern Malesian species and node 6 western and middle Malesian species. In each of these main clades, there are species endemic to particular areas, with repeated patterns indicating geographic paralogy.

Paralogy-free subtree analysis based on Fig. 2 produced 13 area subtrees (Fig. 3). The nodes of these subtrees were coded as 23 characters in a data matrix (Table 1) with an all-zero outgroup, which, when analysed in Hennig86 with exhaustive

branch swapping (mb*, bb*), produced an overflow of trees (7108+) of length 23, CI = 1.00 and RI = 1.00. Of these equally parsimonious trees, the one with the minimal number of resolved nodes (the 'minimal tree') is shown in Fig. 4. The position of some areas is unresolved (due to widespread taxa or lack of endemics). Hence, areas I, M, O, Q, R, S and T – Lesser Sunda Islands, Palawan, Malay Peninsula, Taiwan, north Vietnam/south China and the Himalayas – were deleted from the data matrix shown in Table 1, resulting in a new, reduced matrix of 20 characters for the fourteen remaining areas and an all-zero outgroup (Table 2).

The analysis of this reduced data matrix with implicit enumeration (ie*) resulted in 124 most parsimonious trees of length 20, CI = 1.00 and RI = 1.00. The strict consensus tree (length 20) shows the same area relationships as the minimal tree for the first analysis (Fig. 4) that included all areas.

Node 1 of the area cladogram (Fig. 4) is a polytomy, including the Himalayas (T) and branches leading to three nodes. Node 2 relates Taiwan (R) to the area of north Vietnam/south China (S). The position of these areas in the polytomy is minimal; however, they can be moved up the tree without altering its length (indicated by the dashed line, Fig. 4). This is possible because of a lack of informative characters relating the areas of Taiwan and north Vietnam/south China to the rest; the only subtree to contain information regarding the relationships of these areas is subtree 13 (Fig. 3).

Node 3 relates the eastern areas, including Bismarck Archipelago and Solomon Islands (A), north-eastern Australia (C) and all five New Guinea areas (B, D, E, F, G). North-eastern Australia (C) and the New Guinea craton (D) are differentiated from the Papuan Peninsular (B), Central New Guinea (E), northern New Guinea (F), the Vogelkop Peninsula (G) and the Bismarck Archipelago and Solomon Islands (A), which form a group at node 4 (Fig. 4). These relationships are shown by subtrees 1 to 6 (Fig. 3).

Node 5 relates the western and middle Malesian areas of southern Moluccas, Lesser Sunda Islands, north and West Sulawesi, southern Philippines, northern Philippines, Palawan, Borneo, Java and Bali, Sumatra, and the Malay Peninsula (areas H to Q). Subtrees 7 to 13 (Fig. 3) show the relationships within this group (Fig. 4). The position of the Lesser Sunda Islands (I), Palawan (M), Java and Bali (O) and the Malay Peninsula (Q) is minimal; however, this group of areas can move up the tree without affecting tree length because area relationships are based solely on widespread taxa in the case of Lesser Sunda Islands (I) and Palawan (M), or in the case of the Malay Peninsula (Q) there is insufficient information to resolve the area's position. The subtrees include information regarding the relationship of Java and Bali (O) to other western Malesian areas, with Java and Bali (O) more closely related to Sumatra (P) than to the areas of eastern Malesia (A–G; subtree 11, Fig. 3). However, the position of area O in the minimal tree remains uncertain (shown as the dashed line in Fig. 4) because its relationships to the other areas at node 5 are not determined.

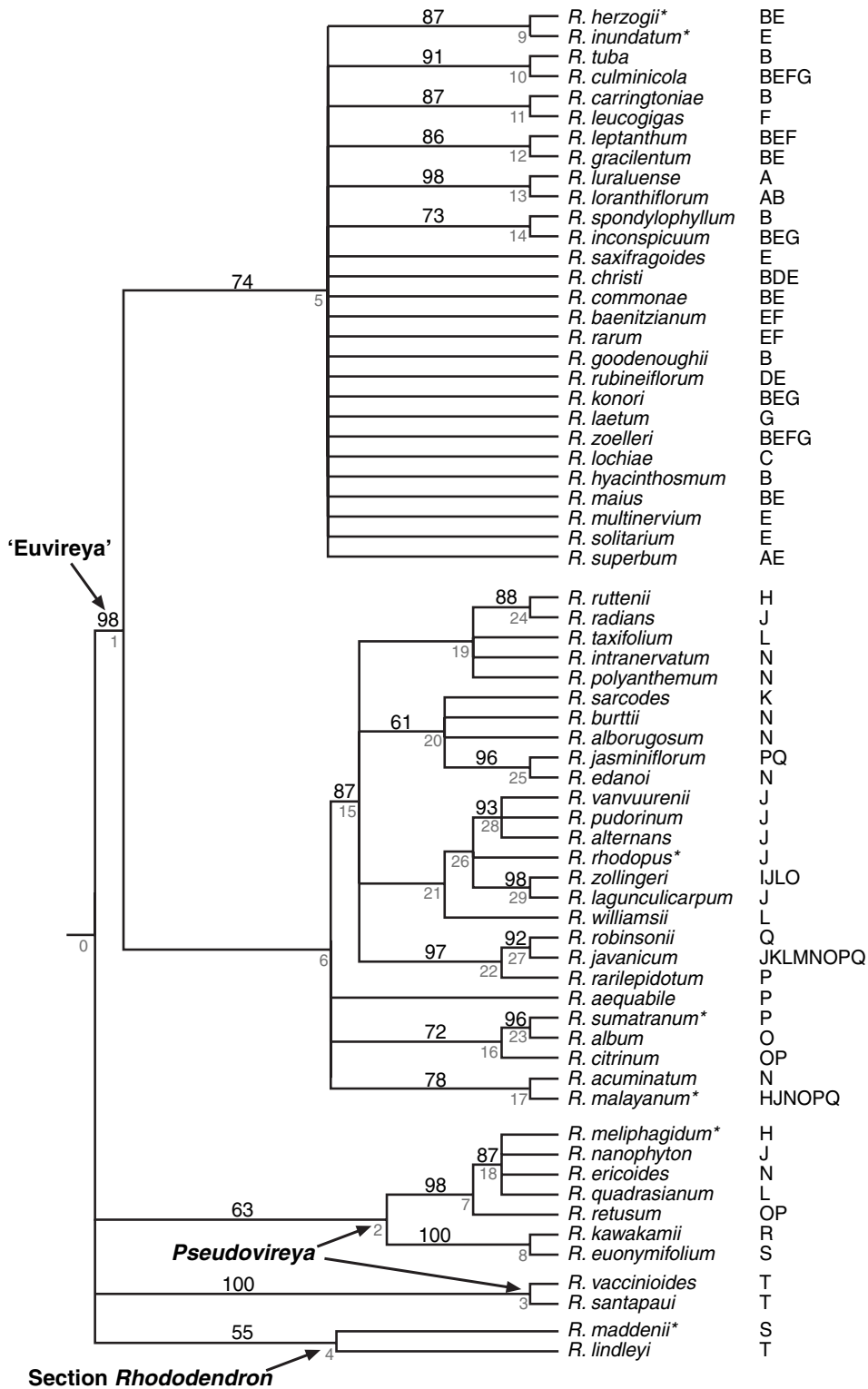


Figure 2 Taxon area cladogram. The summary phylogeny used for the paralogy-free subtree analysis is shown. Bootstrap values > 50% are shown above the node they support. Node numbers are shown beneath the node. * indicates that a species was only sequenced for the *trnT-trnL* intergenic spacer region due to amplification difficulties for the *psbA-trnH* spacer. Letters to the right of the species name correspond to the areas of endemism in Fig. 1. Areas: Bismarck Archipelago and the Solomon Islands (A), Papuan Peninsular (B), north-eastern Australia (C), New Guinea craton (D), central New Guinea (E), northern New Guinea (F), Vogelkop Peninsula (G), south Moluccas (H), Lesser Sunda Islands (I), north and west Sulawesi (J), southern Philippines (K), northern Philippines (L), Palawan (M), Borneo (N), Java and Bali (O), Sumatra (P), Malay Peninsula (Q), Taiwan (R), north Vietnam and south China (S), and the Himalayas (T).

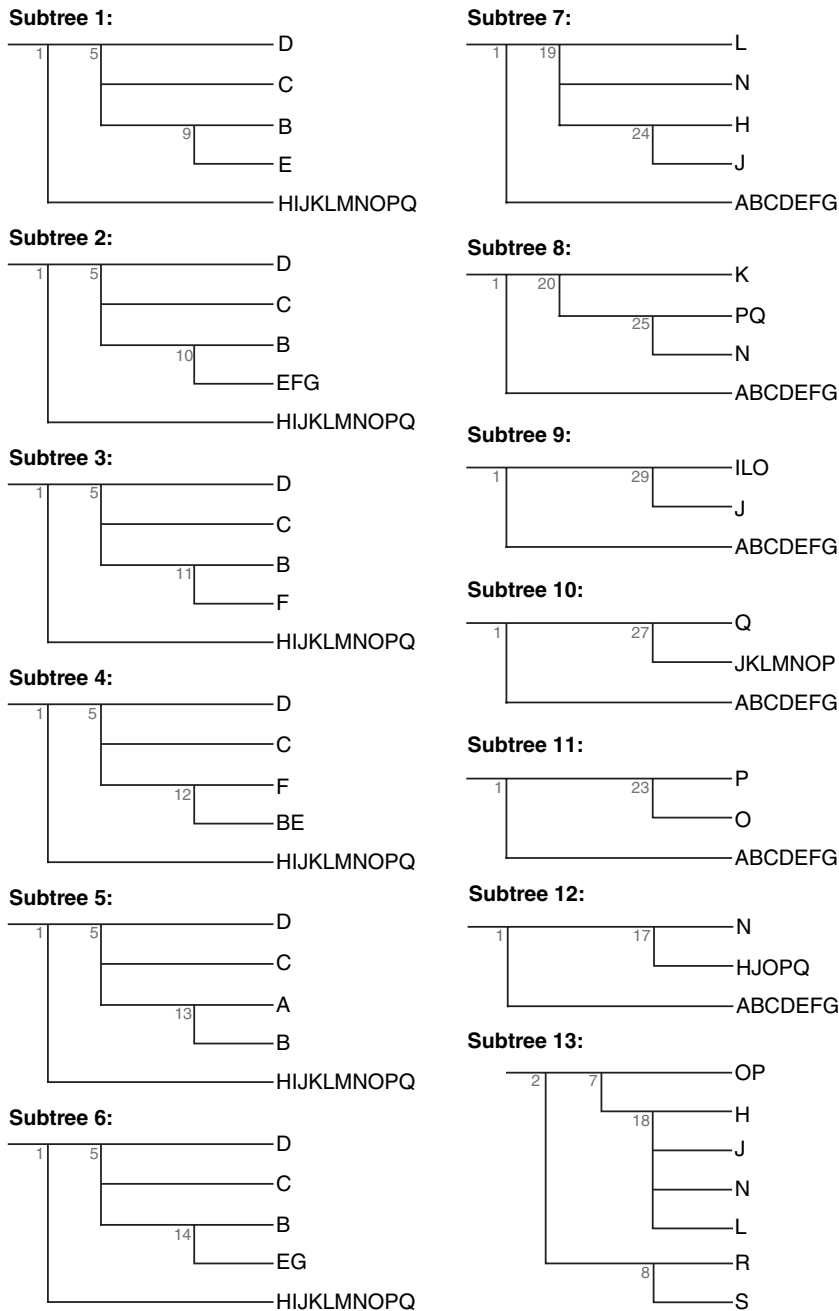


Figure 3 Area subtrees. Thirteen area subtrees identified by the paralogy-free subtree analysis are shown. The node numbers (indicated below the node) relate to the nodes of the taxon area cladogram (Fig. 2). Areas: Bismarck Archipelago and the Solomon Islands (A), Papuan Peninsular (B), north-eastern Australia (C), New Guinea craton (D), central New Guinea (E), northern New Guinea (F), Vogelkop (G), south Moluccas (H), Lesser Sunda Islands (I), north and west Sulawesi (J), southern Philippines (K), northern Philippines (L), Palawan (M), Borneo (N), Java and Bali (O), Sumatra (P), Malay Peninsula (Q), Taiwan (R), north Vietnam and south China (S) and the Himalayas (T).

The relationships and order of differentiation of areas within the clade at node 5, which can be discussed with confidence, are as follows (Fig. 5). The earliest geographic segregation within node 5 relates the southern Philippines (K) to the rest of the western and middle Malesian areas (areas H, J, L, N, P, Q; Fig. 5c). The area of Sumatra (P) is the next area to be differentiated in the western Malesian region (Fig. 5d). The relationship between the northern Philippines (L) and Borneo (N) is unresolved (node 7) in relation to the southern Moluccas (H) and north and west Sulawesi (J; node 8, Fig. 4), the latter two (H & J) inferred to be sister areas.

DISCUSSION

Cladistic biogeography endeavours to understand the relationships of geographic areas based on the biotic patterns presented in phylogenetic trees (Humphries & Parenti, 1999). It assumes that the phylogenies of taxa, and the nodes within it, contain information regarding the history of the areas that they inhabit (Ladiges, 1998; Ebach & Edgecombe, 2001). The history of areas elucidated via cladistic biogeography can be the result of vicariant or dispersal events. Nevertheless, evidence from other sources such as geological or climatological studies is required to infer which type of event has occurred.

Table 1 Nodes of area subtrees coded as a character matrix. Areas not represented in a subtree are coded by a question mark. The tree is rooted by an all zero outgroup

Area	Characters																						
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Bismarck Archipelago and Solomon Islands (A)	?	?	?	?	?	?	?	?	1	1	?	?	0	0	0	0	0	0	0	?	?	?	
Papuan Peninsular (B)	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	?	?	?	
North-eastern Australia (C)	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	?	?	?	
New Guinea craton (D)	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	?	?	?	
Central New Guinea (E)	1	1	1	1	?	?	1	1	?	?	1	1	0	0	0	0	0	0	0	?	?	?	
Northern New Guinea (F)	?	?	1	1	1	1	1	1	?	?	?	?	0	0	0	0	0	0	0	?	?	?	
Vogelkop Peninsula (G)	?	?	1	1	?	?	?	?	?	?	1	1	0	0	0	0	0	0	0	?	?	?	
Southern Moluccas (H)	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	?	?	?	?	1	1	1	0
Lesser Sunda Islands (I)	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	?	?	?	?	?	?
North and West Sulawesi (J)	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	?	1	1	?	1	1	1	0
Southern Philippines (K)	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	0	?	1	?	?	?	?	?
Northern Philippines (L)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	?	1	1	?	?	1	1	0
Palawan (M)	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	1	?	?	?	?	?
Borneo (N)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	?	1	?	1	1	1	0
Java and Bali (O)	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	1	1	1	1	1	0	0
Sumatra (P)	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	1	?	1	1	1	1	0	0
Malay Peninsula (Q)	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	1	?	1	?	1	?	?	?
Taiwan (R)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1
North Vietnam/south China (S)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1
Himalayas (T)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Geological history of Malesia

The geological history of Malesia is complex, and somewhat controversial, and has been discussed in considerable detail in the literature (e.g. Audley-Charles, 1987; Michaux, 1991; de Boer & Duffels, 1996; Hall, 2001; Metcalfe, 2001; Morley, 2001; Hall, 2002). A detailed plate tectonic reconstruction of south-east Asia and the south west Pacific in the Cenozoic (last 60 Myr) was presented most recently by Hall (2002). It includes a comprehensive outline of the geological history of Malesia, based on present and past plate motions, seismic and volcanic activity, and palaeomagnetic and isotopic data.

The Malesian Archipelago is bounded by three major plates: the Pacific to the east, the Indo-Australian to the west and south, and the Indo-China to the north (Michaux, 1991). The archipelago formed as a result of Australia and India rifting away from Gondwana, moving northward and colliding with the Asian plate. India rifted from Australia and Antarctica *c.* 130 Ma, and collided with the Asian continent *c.* 50 Ma (McLoughlin, 2001; Hall, 2002). Australia later rifted from eastern Antarctica (rifting initiated at *c.* 96 Ma but was not complete until *c.* 35 Ma; McLoughlin, 2001), and moved northwards into the Tethys Ocean colliding with the Asian margin later than India (Audley-Charles, 1981). Both Australia and India continue to move northwards today (Hall, 2002).

As Australia moved north, slivers of continental crust were occasionally sliced off as microcontinents; these also moved north ahead of the main continental margin. The Bird's Head of New Guinea is one such microcontinent, although the

location from where it was sliced remains in dispute; Hall (2002) infers that it is of north-western Australian origin, while Pigram & Panggabean (1984 in de Boer & Duffels, 1996) believe it to be of east Queensland or central New Guinea origin. Several of the islands, or island groups — Moluccas, New Guinea, Philippines and Sulawesi — are considered to be of composite origin (Audley-Charles, 1981; Hall, 2002). In addition to microcontinents, areas comprise also of components that are remnants of volcanic island arcs — central Philippines; north, central and south-eastern New Guinea; and the Bismarck Archipelago (de Boer & Duffels, 1996) — or are part of the continental shelf, e.g. Borneo, Java, Malay Peninsula, southern New Guinea, Palawan and Sumatra (Hall, 2002). The western Malesian islands of the Sunda shelf are also known as Sundaland.

Environmental changes, including changes in sea-level, degree of seasonality of precipitation or temperature, all influence biogeographic patterns. Climatic conditions can also be affected by geological events; for example, Hall (2002) suggests that orogeny in northern New Guinea during the Pliocene–Pleistocene, is likely to have contributed to increased aridity in Australia and increased rainfall in New Guinea. Some studies have investigated the past climate of the Malay Archipelago, with many focusing on Quaternary changes (e.g. Whitmore, 1981a; Morley, 1982; Morley & Flenley, 1987; Newsome & Flenley, 1988; van der Kaars, 1991; Urushibara-Yoshino & Yoshino, 1997).

Morley & Flenley (1987) investigated Neogene and Quaternary environmental changes in the Malesian Archipelago

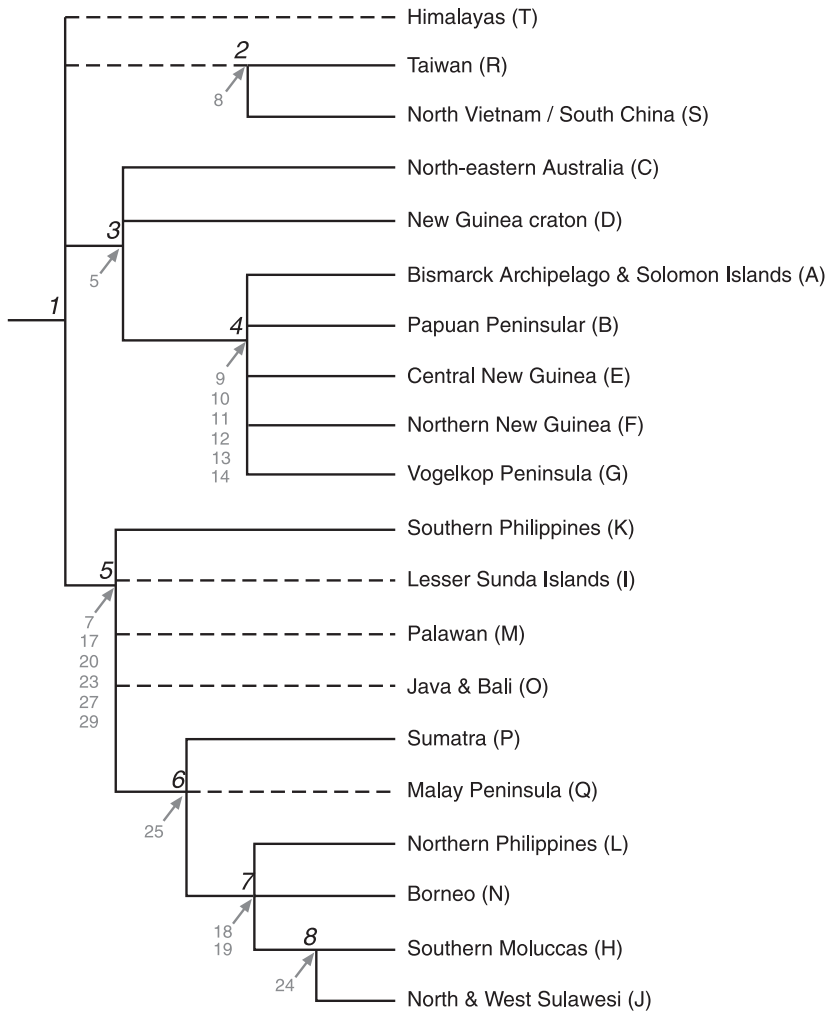


Figure 4 Minimal Tree. Biogeographic area relationships as shown in the minimally resolved most parsimonious tree (length 23, CI = 1.00, RI = 1.00). Dashed lines indicate areas that are in their minimal position but have the ability to move up the tree without altering the length of the tree. Analysis of the data excluding these areas resulted in a strict consensus tree (length 20, CI = 1.00, RI = 1.00) showing the same relationships (solid lines). Node numbers (italics) are shown above the node they relate to, while numbers below the node (grey) indicate the nodes from the taxon area cladogram (Fig. 2) that support each biogeographic node. Areas: Bismarck Archipelago and the Solomon Islands (A), Papuan Peninsular (B), north-eastern Australia (C), New Guinea craton (D), central New Guinea (E), northern New Guinea (F), Vogelkop Peninsula (G), south Moluccas (H), Lesser Sunda Islands (I), north and west Sulawesi (J), southern Philippines (K), northern Philippines (L), Palawan (M), Borneo (N), Java and Bali (O), Sumatra (P), Malay Peninsula (Q), Taiwan (R), north Vietnam and south China (S) and the Himalayas (T).

Table 2 Nodes of area subtrees coded as a character matrix with equivocal areas deleted. Areas not represented in a subtree are coded by a question mark. The tree is rooted by an all zero outgroup

Areas	Characters																	
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bismarck Archipelago and Solomon Islands (A)	?	?	?	?	?	?	?	?	1	1	?	?	0	0	0	0	0	?
Papuan Peninsular (B)	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	?
North-eastern Australia (C)	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	?
New Guinea craton (D)	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	?
Central New Guinea (E)	1	1	1	1	?	?	1	1	?	?	1	1	0	0	0	0	0	?
Northern New Guinea (F)	?	?	1	1	1	1	1	1	?	?	?	?	0	0	0	0	0	?
Vogelkop Peninsula (G)	?	?	1	1	?	?	?	?	?	?	1	1	0	0	0	0	0	?
Southern Moluccas (H)	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	?	?	1
North and West Sulawesi (J)	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	?	1	1
Southern Philippines (K)	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	0	?	?
Northern Philippines (L)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	?	1	1
Borneo (N)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	?	1
Sumatra (P)	0	0	0	0	0	0	0	0	0	0	0	0	?	?	1	1	?	1

and found that glacial periods were prominent during the Pleistocene, and therefore land connections between mainland Asia and Sundaland are probable throughout the last 2 Myr.

Geological data confirm this, although Hall (2002) suggests that the region between the Malay Peninsula and western Borneo has been elevated throughout the Cenozoic. These

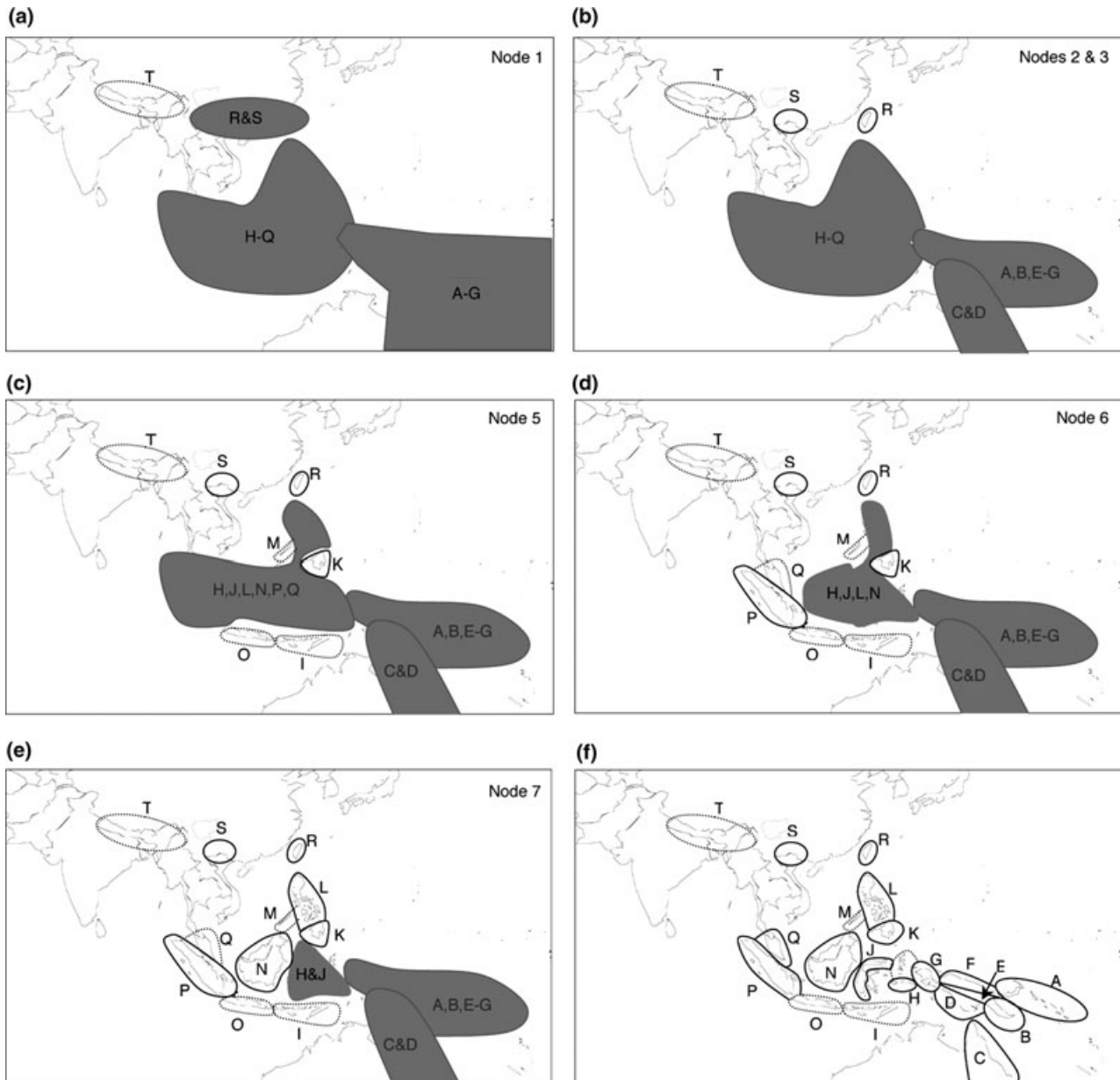


Figure 5 Relative timing of the differentiation of biogeographic areas. The order of differentiation is based on the nodes of the minimally resolved tree (Fig. 4); grey areas are those areas that are differentiating at the same time. After an area has been distinguished it is shown as an open black symbol; stippled lines show those areas that are differentiated but can move position in the minimal tree without altering the tree length. Letters corresponding to the areas of endemism (Fig. 1) are indicated. Areas: Bismarck Archipelago and Solomon Islands (A), Papuan Peninsular (B), north-eastern Australia (C), New Guinea craton (D), Central New Guinea (E), northern New Guinea (F), Vogelkop Peninsula (G), south Moluccas (H), Lesser Sunda Islands (I), north and West Sulawesi (J), southern Philippines (K), northern Philippines (L), Palawan (M), Borneo (N), Java and Bali (O), Sumatra (P), Malay Peninsula (Q), Taiwan (R), north Vietnam and south China (S) and the Himalayas (T). (a) The four clades of the polytomy (node 1) – Himalayas (T), Taiwan and Vietnam and south China (R&S), western and middle Malesia (H–Q), and eastern Malesia (A–G) – differentiated from each other. (b) Taiwan (R) and Vietnam and south China (S) differentiate from each other, as do the areas A, B, E–G from areas C and D in eastern Malesia (nodes 2 and 3). (c) Southern Philippines (K) differentiates first from the other western and middle Malesian areas; areas I, M and O (Lesser Sunda Islands, Palawan and Java & Bali) are indicated as differentiating at the same time as K, although timing of their differentiation may be later (node 5). (d) Sumatra (P) completes differentiation from the main western Malesian area; the Malay Peninsula is also indicated to differentiate at this time, although timing of its differentiation may be later (node 6). The areas Moluccas (H), Sulawesi (J), Borneo (N) and northern Philippines (L) are not yet differentiated from each other. (e) Borneo (N) and northern Philippines (L) differentiate (node 7); Sulawesi (J) and Moluccas (H), and all the eastern areas (A–G) are yet to differentiate; the timing and order of these remaining events are unknown. (f) All areas of endemism have completed differentiation (nodes 4 and 8), as defined in Fig. 1.

glacial periods resulted in fluctuations between wet and dry conditions. During the last glacial period conditions in the Malesian region and northern Australia were thought to have been about 2 °C cooler and drier than the present (Whitmore, 1981a; Morley, 1982; van der Kaars, 1991). Such conditions would have allowed the montane forests, such as those inhabited by species of *Rhododendron*, to occupy a greater area than they do today, with the present-day atypical conditions increasing both sea level and the forest limits (Whitmore, 1981a).

More recently, the vegetation in the region has been influenced by human activities, with forest clearing evident over the last 8000 to 7000 years to the present-day (Morley, 1982; Newsome & Flenley, 1988; Haberle *et al.*, 1991).

Interpreting the *Vireya* area pattern

The most striking result from the *Vireya* analysis is the identification of major clades corresponding to eastern Malesia and western/middle Malesia. The close relationship found between Australia and New Guinea for *Vireya* is repeated for many other groups, such as cicadas, butterflies, tea trees, eucalypts and genera of Proteaceae (Holloway, 1987; Crisp *et al.*, 1995; de Boer & Duffels, 1996; Brown *et al.*, 2001; Ladiges *et al.*, 2003).

In contrast to this striking overall result, relationships between areas within the two major regions are unclear. Area relationships within New Guinea remain unresolved based on the vireyas, there being no consensus among other studies (de Boer & Duffels, 1996; van Welzen *et al.*, 2001), particularly regarding the relationship of the Vogelkop Peninsula. The relationships between the areas in western and middle Malesia are also inconsistent across a variety of organisms, with almost every combination of sister areas being reported (Schuh & Stonedahl, 1986; Holloway, 1987; van Welzen, 1992; Ruedi, 1996; Repetur *et al.*, 1997; Ridder-Numan, 1998). The results presented here do little to resolve the problem (Fig. 4).

The relationships of sister areas Taiwan and north Vietnam/south China is uncertain, being placed in the polytomy at node 1 of the area cladogram (Fig. 4), although they may be related to the Himalayas (Croizat, 1968; Ridder-Numan, 1998; Denduangboripant *et al.*, 2001; A.L. Denton & B.D. Hall, unpubl. data). Croizat (1968) suggested that a classic biogeographic role of Formosa (Taiwan) is as an 'appendage to the Sino-Himalayan Domain', and that it is part of the track: Nepal–north Burma and Thailand/south China–Formosa–Luzon.

Determining the age of the clades and the underlying processes that have led to the evolution of section *Vireya* is difficult. Nodes of the phylogeny are not dated using molecular dating algorithms because of a lack of precise calibration points for these data and evidence of variable DNA substitution rates. Based on cpDNA Milne (2004) attempted to estimate the divergence age of *Rhododendron* subsection *Pontica*, 'a group with a tertiary relict distribution'. He found that only his synonymous *matK* mutation data set met the

assumption of a molecular clock, with other regions violating assumptions.

Geological data, biogeographic patterns and fossils are used to argue two contrasting hypotheses.

Hypothesis 1: Vireyas are a Gondwanan group

Section *Vireya* is an old group, with ancestors present on Gondwana before India rifted north in the Cretaceous (130 Ma). As the islands of Malesia formed and moved into their present position, vireya rhododendrons dispersed further into Malesia; hence today both areas (Himalayas and Australia) are related to Malesia. Ancestral taxa that rifted north on India were probably similar to section *Rhododendron* or were *Pseudovireya*-like, while the 'Euvireya'-like vireyas were most likely of Australian rain forest ancestry.

Based on geological evidence, node 6 (Figs 4 & 5d) — Sumatra, Malay Peninsula, northern Philippines, Borneo, south Moluccas and north and west Sulawesi — may be at least 60 Ma because the region between the Malay Peninsula and western Borneo has been hypothesized to have been elevated throughout the Cenozoic (Hall, 2002). Therefore, nodes 1, 3 and 5 would be at least that age, but arguably older.

Similar scenarios have been suggested for the establishment of 'primitive' angiosperms in tropical Asia–Australasia (Morley, 2001) and for several other plant groups, including genera of Proteaceae (Whitmore, 1981b), *Nastus* Juss. (Whitmore, 1981b), and a number of palms (Dransfield, 1981). Specht (1988) hypothesized that ancestral *Rhododendron* taxa were present on Gondwana before its break up. He supposed that the ancestor of the lepidote rhododendrons (subgenus *Rhododendron*) remained on the Australian plate and expanded from the northern part into Malesia and then mainland Asia *c.* 15 Ma, after the Australia plate made contact with Sundaland. Specht also considered that the ancestor of the elepidote rhododendrons (all subgenera except subgenus *Rhododendron*) was on the Indian plate as it rifted northwards, and then spread to the north and east, after India collided with the Asian mainland, where it diversified and reached its present-day distribution.

What does the fossil record tell us of the minimum age of rhododendrons? The oldest macrofossil assigned to the genus *Rhododendron* dates from the Paleocene (65–55 Ma) with fossil leaves and seeds found in north-west Greenland and at Ash Quarry in Newbury, England (Collinson & Crane, 1978). The oldest fossil flower assigned to the Ericales dates from the Turonian (*c.* 90 Ma), in the mid-Cretaceous (Nixon & Crepet, 1993). Rhododendrons were more abundant throughout the Eocene and Miocene, with more, widespread records of *Rhododendron* fossils recorded for this period: pollen found in Germany, and leaves in Alaska, Austria (Köflach, Stoob and Hausruck), USA (Vermont), Japan and eastern China (Zhejiang; Collinson & Crane, 1978; Zetter & Hesse, 1996).

No fossils of *Rhododendron* have been reported in Australia, although rain forest habitat, including those areas of north-eastern Australia where the two Australian species

Rhododendron lochiaie and *R. viriosum* occur today, was originally established in the Cretaceous, and are thought to have remained largely unaltered in terms of genera present since then (Barlow & Hyland, 1988; Specht, 1988). Relictual angiosperms have survived to the present day in these rain forests because of a combination of processes: these areas were not exposed to aridity as much of the continent was, and as a result of Australia drifting northwards, rain forest patches were generally not affected by the cooling of the climate throughout the Neogene (Morley, 2001). Tropical rain forests were also present on India as it drifted northwards in the early Eocene (Morley, 2001) with environments suitable for *Rhododendron*.

These ancestral tropical rain forests of north-eastern Australia most likely extended north to New Guinea, on the Australian craton, as argued for the sister relationship of *Eucalyptopsis* C.T. White and *Stockwellia* D.J. Carr, S.G.M. Carr & B. Hyland in the eucalypt group (Ladiges *et al.*, 2003). Similar patterns — Atherton related to New Guinea — have also been found in other Myrtaceae genera (e.g. *Thaleropia* Peter G. Wilson, Wilson, 1993) and in the Proteaceae (*Telopea* Sol. ex Baill. and *Alloxylon* P.H. Weston and Crisp, Crisp *et al.*, 1995). Barlow & Hyland (1988) also hypothesized that 'Tertiary New Guinea' was part of the Australian refugial area.

An old Gondwanic element in tropical floras has been supported by various authors. Barlow & Hyland (1988) considered that strong taxonomic links existed between the tropical floras of Africa, Asia and Australia, and Croizat (1968) considered that the Pacific 'massings' of taxa, such as the *Columba* L. pigeons and *Ficus drupacea* Thunb., were old (at least early Cretaceous in age) and stemmed from ancestors originally bound with the Indian Ocean, India, Australia and Africa, therefore suggesting Gondwana. Heads (2003) presents a detailed argument for Mesozoic and Cenozoic events shaping the biogeographic differentiation of vireyas and other taxa in Malesia. Heads asserts that the simplest explanation for highly speciose groups such as the rhododendrons, is that 'there is no point centre of origin and the groups have developed by vicariance in immobilism of an already global ancestral complex' (p. 435, Heads, 2003).

Hypothesis 2: Vireyas are young

Section *Vireya* is a young group, which dispersed eastwards from India to Australia and the Solomon Islands since the islands of Malesia were in, or close to, their present-day positions. Two main radiation-dispersal events into Malesia are likely to have occurred, representing the two lineages resolved in the phylogeny, *Pseudovireya* and 'Euvireya' (Brown *et al.*, 2006, in press). There was only one eastward radiation, into New Guinea, Australia and the Solomon Islands, followed by mass speciation leading to the present-day diversification, possibly related to recent orogenic events in New Guinea, opening up a myriad of new niches and habitats for the vireyas to exploit. Although vireyas are morphologically diverse, there is little variation in the DNA regions between related taxa,

particularly those within the eastern Malesian clade whose relationships are not well resolved. Weak breeding barriers exist between many *Vireya* taxa and most subsections of section *Vireya* (Williams & Rouse, 1997). This promiscuity was taken by Williams Rouse to be an indicator of a young group.

Based on an estimated age of Ericaceae on a calibrated Angiosperm phylogeny and fossil data (Magallón *et al.*, 1999; Wikström *et al.*, 2001), Milne (2004) concludes that the subgenus *Rhododendron* (represented by only one species in his analysis) is 46–32 Ma. That result infers that section *Vireya* is younger, although note our earlier reservations of this analysis.

If hypothesis 2 is correct, then based on geological evidence node 5 (Fig. 4) could be at least 60 Ma, but node 3 (Fig. 4) would only be *c.* 10 Ma, when the islands were close enough for vireyas to island-hop to their present distribution (Hall, 2002). Vireyas would have had to have dispersed over many hundreds of kilometres of unsuitable habitat unless continuous, or almost continuous, corridors existed. Barlow & Hyland (1988) argued that throughout the late Quaternary during climate and vegetation fluctuations, pockets of rain forest were close enough to allow exchange of flora between the forests of New Guinea and Australia. The small, light weight seeds of *Vireya* could be dispersed by wind, but the distances that they can travel and remain viable are yet to be determined.

A similar hypothesis has been put forward for genera of the Dipterocarpaceae (Whitmore, 1981b), and even though some of these genera, such as *Vatica* L. and *Hopea* Roxb., extend to New Guinea, none extends into Australia or the Solomons, as do vireya rhododendrons.

CONCLUSIONS

The molecular phylogenetic analysis of the vireya rhododendrons has revealed a major clade divergence that correlates with a distinct biogeographic pattern: one major clade restricted to the east of Wallace's line and another to the west. Based on geographic pattern, presence of taxa in relictual rain forests that include ancient angiosperms (e.g. north-east Australia), and fossil minimal ages, it can be argued that the vireyas are an old Gondwanan group. The alternative hypothesis that the group is young relies on accepting that low molecular distances between taxa within clades reflects a young age, which in turn requires long-distance dispersal to explain distribution patterns. It may be that deep divergences within the vireyas have an old history but diversification within clades is more recent.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article from <http://www.Blackwell-Synergy.com>:

Appendix S1 Individual species distribution maps (5° intervals).

BIOSKETCHES

Gillian Brown recently completed her PhD at CSIRO Plant Industry and The University of Melbourne, where she worked on the phylogeny and biogeography of *Rhododendron* section *Vireya*. Her research to date has focused on phylogeny and biogeography of large genera within three plant families: Myrtaceae (*Melaleuca* and *Callistemon*), Ericaceae (*Rhododendron*) and the *Leguminosae* (*Acacia* and genera of the tribe Ingeae).

Gareth Nelson is an Honorary Professorial Fellow at the School of Botany in Melbourne, after retiring from the Ichthyology Department, Natural History Museum, New York. He is well known for his contributions to the development of cladistics and vicariance biogeography.

Pauline Ladiges FAA is Head of the School of Botany at The University of Melbourne. Her research interests are phylogenetic systematics and historical biogeography of Australian plants, and she is best known for her work on the eucalypts. With Gareth Nelson, she has developed the biogeographical method of subtree analysis.

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