

## MALESIAN VIREYA RHODODENDRONS—TOWARDS AN UNDERSTANDING OF THEIR EVOLUTION

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**ABSTRACT.** The variation between Malesian species of *Rhododendron* sect. *Vireya* is primarily in floral, indumentum, and vegetative features. Great diversity in these characters is underlain by considerable uniformity in characters of vegetative anatomy, fruit, seed, and apparently chromosomes. Most of the subsections and series currently delimited within the group are unsatisfactory for phylogenetic studies, and this constrains discussion on the evolution of the group. The changes of flower colour and flower type with altitude in Papuasias which also occur, although less markedly, throughout Malesia, are outlined. The four main pollinators of *Rhododendron* in Papuasias seem to be birds, moths, butterflies, and bats. The preponderance of deeply lobed corolla types, notable infraspecific variation in flower colour, and almost complete absence of two of the most striking Papuanian flower types, are the main characteristics of floral variation in West Malesian species. Preliminary geographic analyses emphasise the richness of the Papuanian *Rhododendron* flora, and also that of the Celebes, when compared to that of the rest of Malesia. Distribution and diversification are discussed in the light of present geography and quaternary climatic changes in the area; both these factors would seem to have had a different effect in the two halves of Malesia.

### INTRODUCTION

*Rhododendron* subgen. *Rhododendron* sect. *Vireya* is a fascinating group of plants. It is largely geographically separated from the rest of the genus, having only a few species growing on the southeast Asia mainland, yet showing very great diversification in montane and subalpine habitats in tropical Malesia.† In Malesia there are only six species belonging to other subgenera, whereas 287 of the c.297 species of sect. *Vireya* occur in that region (Table 1), growing from sea-level to over 4000m. All taxa have scales, but lack other multicellular hairs (Sleumer, 1966), the corolla lacks zygomorphic markings (Stevens, 1976), the seeds have long tails at either end (or they are at least pointed there), the epidermis/hypodermis complex is mucilaginous and multilayered (Breitfeld, 1888; Hayes, Keenan & Cowan, 1951: details of its structure are not well understood), and the smaller vascular bundles are embedded in the mesophyll. Corolla pigments in the group may also be distinctive (Spethmann, 1980). Despite the great diversity in floral and vegetative features that I shall discuss, genetic barriers to interspecific hybridization are not well developed. Thus diversity of some characters within the group stands out against the similarity of other characters.

After a brief discussion of the characters used to subdivide the section and delimit its species, I shall summarize observations on the diversity and possible ecological significance of flower types in the section. I shall

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†In this paper, Malesia includes the area from the Malay Peninsula to the Philippines, New Guinea, and the Solomon Islands; West Malesia, the area from Malaya to the Lesser Sunda Islands, Borneo, and the Philippines; and Papuasias includes New Guinea and the islands to the east, including the Solomon Islands. The Celebes-Moluccas area is discussed separately.

TABLE I  
Distribution of *Rhododendron* sect. *Vireya* in Malesia

Subsection	West Malesia	Celebes-Moluccas	Papuasias	SE Asian mainland	Australia	Total	Notes
<i>Pseudovireya</i>	11	4	14	6		32	<i>R. lindaueanum</i> Papuasias/ Celebes <i>R. quadrasianum</i> Celebes/ West Malesia
<i>Siphonovireya</i>			7			7	
<i>Phaeovireya</i>		2	39			41	
<i>Malayovireya</i>	15	1				15	<i>R. malayanum</i> Celebes/ West Malesia
<i>Albovireya</i>	5	4	6			14	<i>R. zollingeri</i> Celebes/ West Malesia
<i>Solenovireya</i>	8	4	26			38	
<i>Euvireya</i> series							
<i>Linnaeoidea</i>			12			12	
<i>Saxifragoidea</i>			1			1	
<i>Taxifolia</i>	1					1	
<i>Stenophylla</i>	1		3			4	
<i>Citrina</i>	1					1	
<i>Buxifolia</i>	16	4	23			43	
<i>Javanica</i>	40	15	32	2	1	87	<i>R. zoelleri</i> Papuasias/ Moluccas <i>R. javanicum</i> West Malesia/ Celebes
Total	98	34	163	8	1	296	

\*Nomenclature follows Sleumer (1966); for comments, see text.

then discuss the distribution of species throughout Malesia, emphasizing areas of especially high diversity, and considering distributions and diversity against recent geological and vegetational changes in montane Malesia. This allows some evolutionary problems to be highlighted, although in the end what stands out is our ignorance of the evolution of the group.

#### TAXONOMIC BACKGROUND

In order to discuss the evolution of a group satisfactorily, one should have an hypothesis of its phylogeny, with the various lineages ideally recognized by their possession of unique, derived characters. With such an hypothesis, one can then begin to understand the relationship of the taxa. However, within sect. *Vireya*, we are far from such an understanding; its classification was not designed with a view to understanding evolution. I shall look briefly at the characters that have been used to subdivide sect. *Vireya*, and some that have not, both to give an idea of the taxonomically important variation within the group, and also to convey the uncertainty about phylogenetic relationships within the group. My subsequent caution in discussing evolution (cladistic and patristic changes) is partly due to this underlying uncertainty at all taxonomic levels in the section.

The three sets of characters used by Sleumer to delimit subsections and series were scale type, corolla type, and leaf size and shape; basically, single character differences separate these taxa, yet there are problems with all these characters. It can be difficult to separate entire from slightly incised scales (Sleumer, 1966, 1973; Stevens, 1978), and one then has to decide if specimens belong to subsects *Pseudovireya* or *Siphonovireya* or not on the size of the central portion. Kores & van Royan (1982) recently reduced *R. saruwagedicum* (*Pseudovireya*) to *R. yelliottii* (atypical *Albovireya*). However, subsect. *Malayovireya*, with its dense, dark scales of two sizes, subsect. *Albovireya* (excluding *R. yelliottii* and *R. laguncularpum*), with its dense covering of scales, and subsect. *Phaeovireya* (including *R. leucogigas*; but excluding *R. hooglandii*—fide Kores), with its deeply incised scales, borne on a little podium, all seem coherent and largely monophyletic subsections, that is, including all and only known descendants of an ancestral species.

Corolla shape, size, colour, and associated characters show great variation in the *Vireya* rhododendrons, as will be discussed below, and furnish very useful taxonomic characters. However, although the long, narrowly tubular flower type that distinguishes subsects *Solenovireya* and *Siphonovireya* is distinctive, so are other flower types, and it is unclear whether the former subsection in particular is monophyletic.

Leaf size and shape is a key character used for dividing up the variation, rather than a character that necessarily brings related species together. Variation in leaf size and shape is considerable—petioles may be absent, or very long, the lamina may be orbicular to linear, the margins flat to strongly recurved, and the length 5 to 150mm. Although there is much in the leaf to help in discriminating species, when used at higher levels it usually functions simply as a key character, and may even be doubtfully useful at that, as in the separation of ser. *Buxifolia* from ser.

*Javanica* (Sleumer, 1973; Stevens, 1976, 1981; Woods, 1978; see also changes in series composition in Kores & van Royen, 1982). As has been noted (Stevens, 1976; Woods, 1978) the New Guinea and Bornean species of ser. *Stenophylla* have nothing else in common apart from their leaf shape, and similarly narrow leaves crop up sporadically in other groups (subsects *Pseudovireya*, *Phaeovireya* and *Malayovireya*) without being accorded taxonomic recognition.

Careful study of even these 'classic' characters will doubtless yield more information of taxonomic importance, but there are other characters that may be used. Although the distinctive epidermis/hypodermis complex seems to be ubiquitous in the group, other aspects of the anatomy, such as the distribution of sclereids in stem and petiole, the shape of the petiole and midrib bundles (e.g. they are open in *R. quadrasianum* and closed in *R. zoelleri*) may be of interest (cf. Breitfeld, 1888). Even nodal structure shows variation. Philipson and Philipson (1968) considered the basic structure in the section to be one trace from a single gap, although the trace might briefly fragment before fusing in a few species. Three bundles were found in the petiole of *R. commonae*, *R. leucogigas*, and *R. culminicola*. I have seen three bundles in the petiole of *R. beyerinkianum* and *R. citrinum*, and five bundles in that of *R. intranervatum*. In view of the importance of nodal anatomy in the major classification of the genus, these observations should be extended. Foliar stomata are generally unorientated, but in narrower-leaved taxa such as *R. taxoides* and *R. quadrasianum* are orientated parallel to the axis of the blade.

*Vireya* rhododendrons all grow in a similar way. Inflorescences terminate the stem, and are overtopped by replacement shoots arising from buds in the axils of leaves below the inflorescence (Stevens, 1981; Philipson, pp. 161–171). However, within this basic pattern, there is much variation in how much growth there is per flush, how the leaves are disposed along the flush, and how they are held; *Rhododendron saxifragoides* has erect leaves even as a seedling (Rouse, pp. 99–115), although seedling leaves are usually held more or less horizontally. The reaction of the stems to gravity also varies, thus some species have erect branches (of these, some are small and form hummocks, whilst others are almost trees) and others have spreading branches and form small shrubs. Argent's work also suggests that there are some exciting characters in the vegetative bud, with some species in subsects *Malayovireya* and *Pseudovireya* having few and inconspicuous reduced leaves at the beginning of the flush. Young plants of *R. himantodes* at Edinburgh seemed to have completely naked vegetative terminal buds and to lack reduced leaves entirely, expanded leaves being scattered more or less regularly along the stem, however, in herbarium specimens there are a few reduced leaves at the beginning of each growth innovation and the leaves are strongly pseudovercillate.

There has been little detailed study of the seeds of *Vireya* rhododendrons, although they tend to be superficially similar. Fruit size may sometimes be useful in distinguishing between taxa (e.g. Sleumer, 1973). Preliminary evidence suggests that chromosome number is uniform in the group (Jones & Brighton, 1972).

For the purposes of this paper, subsects *Malayovireya*, *Phaeovireya*, and

*Albovireya* (all as delimited above) are tentatively accepted as useful units in the ensuing evolutionary and biogeographic discussion. However, all the Papuan species of subsect. *Euvireya*, and perhaps those of subsect. *Siphonovireya* as well, form a single group which at this stage cannot be divided into subgroups that have phylogenetic coherence. Thus *R. saxifragoides*, placed in the monotypic series *Saxifragoidea*, is just a Papuan *Euvireya* rhododendron with a particularly distinctive growth form. To include the West Malesian *Euvireya* rhododendrons (possibly excluding *R. citrinum*) in this group would also be a reasonable expression of our ignorance about relationships. We could then approach the critical question of the nature and number of the relationships between species in West Malesia and Papuasias. For instance, are some of the species with large, funneliform, orange-yellow corollas in West Malesia (e.g. *R. javanicum*) more closely related phyletically to comparable species in Papuasias (e.g. *R. zoelleri*) than to other species in the *Euvireya* group; and is subsect. *Solenovireya* monophyletic, with a comparable direct West Malesian-Papuan relationship? Also, and particularly to the point here, how often did some of the more distinctive flower types evolve? The distribution of these flower types in the currently recognized separate supraspecific taxa tells us little about such questions.

#### FLOWER TYPES IN VIREYA RHODODENDRONS

Stevens (1976) divided flower colours into basically red, basically white, and basically yellow-orange. There was a clear correlation between altitude and flower colour in Malesian rhododendrons, and especially in Papuasias, with species with red corollas being commoner at higher elevations. In Papuasias nearly 50 red-flowered species grow above 3000m; only nine species with flowers of other colours grow much above this altitude. About 28 species grow only at or above 3000m; 24 of these have red-coloured flowers, the rest have yellow, orange or greenish flowers. Red-flowered species are clearly becoming proportionally more numerous than species with other flower colours by 2000m (Stevens, 1976, fig. 2A), but there is a definite peak of abundance above 3000m. The same general correlation holds for the Celebes-Moluccas region and for the Borneo-Sumatra area, although the relative absence of non-volcanic habitats above 3000m (see below) means that any secondary peak of abundance above 3000m would not be detected (Stevens, 1976, fig. 3B-D).

In addition, although there is a great variety of flower types throughout the whole region, such flower types are not distributed at random either geographically or altitudinally. In Papuasias, and in Papuasias alone (with but a single exception—see below), there are c.36 species with red, tubular, zygomorphic, scentless flowers. There are an additional c.40 species with similar flowers that show little if any zygomorphy of the tube, although the stamens may be placed on one side of the corolla. This flower type occurs in several species in the Celebes and in some species throughout the rest of Western Malesia. The first flower type is not particularly correlated with altitude, other than the general correlation shown by red-coloured flowers. Kores (pers. comm.) suggests that the

second may be; this is perhaps because it frequently occurs in small leaved species that tend to grow at high altitudes.

Another very common flower type is that with a white corolla and a long, narrow tube; the corolla has walls of unexceptional thickness and the flower is scented. About 30 species in New Guinea have flowers of this type, as do four, or perhaps six, in the Celebes-Moluccas region, and seven or eight in the rest of Malesia. The other common white flower type is large, funneliform, and scented, and has long lobes; the corolla tends to be rather thick and the flowers themselves more than 5-merous. This flower type is represented by perhaps 11 species in Papuasias and three from the Celebes-Moluccas region, but appears to be absent from West Malesia.

The commonest yellow-orange flower type is also more or less funnel-shaped and has corolla lobes about half the length of the corolla; it may or may not be scented. About 10 species from Papuasias have flowers of this type; red flowered versions of it are rare.

In Western Malesia, the majority of species have funnel-shaped to campanulate, long-lobed, variously coloured flowers; species with red, short-tubular flowers and white, long-tubular flowers are uncommon; a single species with red, zygomorphic flowers has recently been described from Sabah (*R. yongii*, see Argent, 1982). The relatively long corolla lobes of these West Malesian species should be emphasized (see also Stevens, 1976). Perhaps 35% of Papuan species have flowers with lobes one third (or more) the length of the whole corolla; this figure is 43% in the Celebes-Moluccas region, but fully three quarters in the West Malesian region, and over half the species there are lobed to half way or more. In addition, flower colour there is notably variable at the infraspecific level (infraspecific variation in flower colour in Papuan rhododendrons is perhaps greater than earlier allowed for—see Kores & van Royen, 1982). Again, there does not seem to be any particular restriction of a given flower type to altitudinal zones other than those that might be expected from the flower colour, although species with red flowers and particularly long corolla lobes are not found at the highest altitudes (Stevens, 1976).

There is evidence, albeit tentative and mostly coming from Papuasias, of association of particular flower types with particular pollinators. The two common red tubular flower types are probably bird-pollinated by members of the Meliphagidae\*, of which representatives of four nectar-eating genera (*Ptiloprora*, *Melidictes*, *Myzomela* and *Oreornis*) occur above 3000m (Stevens, 1976). This agrees with the general theory of the tendency of such pollinators to predominate at high altitudes (Cruden, 1972); birds will remain active at all temperatures, whereas many insects will become torpid in the cool, cloudy conditions so often occurring there. Beehler (1981) has recently shown that the nectar-eating niche in birds proportionally increases at high altitudes in New Guinea. The Ericaceae generally may form a very important nectar source for such birds, but details of the general behaviour and feeding of the high-altitude Meliphagidae are sparse. As is becoming increasingly clear, birds feed on

\*Although the Meliphagidae is predominantly an Australian-Papuan group, its relationships are uncertain (Sibley, 1970; Cracraft, 1981).

many flowers that do not have the obvious characters of ornithophily (e.g. Snow & Snow, 1980). At least some rhododendrons flower in flushes (Kores, 1978; Smith, 1980; Kores & van Royen, 1982; van Royen & Kores, 1982; Argent, pers. comm.); this may increase the need of the Meliphagidae for additional food sources unless the flowering flushes are asynchronous.

Butterflies have been observed to visit a few species with large, orange-yellow, broadly funnel-shaped flowers, and also some red-flowered species, e.g. *R. christi* (Stevens, 1976). This latter case is interesting; although aspects of the floral syndrome of *R. christi* are those of a bird-pollinated flower, it has a yellow tube and red lobes (see also *R. glabriflorum*); yellow surrounded by red is an attractive colour combination for butterflies (Bierzchudek, 1981; see also below). The long tubular white flower type is probably pollinated by sphingids, and the funneliform white flower type is probably pollinated by bats (Kores, pers. comm.).

Whatever the floral syndrome, nectar robbing may be quite common. This is clearly shown in several of the excellent photographs in Kores & van Royen (1982). In addition, especially with the current level of knowledge, floral types should not be considered as the exclusive preserve of one particular class of pollinator.

In West Malesia even circumstantial evidence is almost absent when attempting to assign flower types to pollinators; available evidence shows no clear trends (Stevens, 1976). Argent (pp. 53–61) notes butterflies visiting flowers with a red/yellow combination (e.g. *R. javanicum* subsp. *brookeanum* var. *kinabaluensis*). The more open flowers of species from the area makes the nectar apparently less well concealed, but the base of the tube is often pouched, and in species like *R. himantodes* access to the nectar seems to be restricted to five small areas (cf. the aptly-named 'revolver' flowers: Proctor & Yeo, 1973).

#### GENERAL DISTRIBUTION OF RHODODENDRON SECT. VIREYA IN MALESIA

In addition to the unreliability of some of the major taxonomic groups mentioned above one has to remember that the species are morphological species with no necessary phylogenetic unity; a few are almost certainly occasional hybrids, perhaps representing chance and evolutionarily unimportant events. How species concepts affect geographic problems is aptly shown by the changes in circumscription of *R. vitis-idaea* and *R. yelliottii* proposed by Kores & van Royen (1982) which result in the apparent disappearance of a disjunct distributional pattern (that of *R. saruwagedicum*) and the loss of one of the very few 'point endemics' in the Central Highlands of Papua New Guinea (*R. vandeursenii*). Hence, when talking about distributions, one has to try and avoid talking about pseudoproblems. In addition, the imperfection of distributional data even in a so well-known, conspicuous, and apparently well-collected genus as *Rhododendron* will be immediately apparent to anybody who has strayed even a little way from those few beaten paths that exist in Malesia (cf. Stevens, 1981).



We can better comprehend the distribution of species and subsections when we realize that the very great changes in both vegetational limits and composition during the Quaternary are central to an understanding of both the distribution and the evolution of *Rhododendron* in Malesia, and some late Tertiary history is also germane. Because of the differing histories of Papuasia, West Malesia, and the Celebes-Moluccas region, I shall discuss them, to a large extent, independently.

The mobile belt, which now forms the middle part of New Guinea, is believed to have become emergent with elevations up to 1500m or more in the Miocene, 15 million years B.P. (Axelrod & Raven, 1981). However, the mountainous chain that today makes up the spine of New Guinea seems to have reached elevations close to those current only early in the Pleistocene (Löffler, 1981). The tree-line today is up to 4000m elevation in places, although generally somewhat lower, especially on isolated mountains. However, during the last glaciation (until some 10–11000 years ago) the tree-line was down to about 2300m (e.g. Walker & Flenley, 1979; Walker & Hope, 1981; Hope & Peterson, 1975). Such a lowered tree-line may have been common through much of the Pleistocene. Equally interestingly, Walker & Flenley (1979) and Walker & Hope (1981) suggested that the current subalpine forest represents a post-Glacial synthesis of elements that has developed only over the last few thousand years and cannot be said to be a stable community; there are varying degrees of ecological affiliation of taxa and of community constancy over time.

One effect of the lowering of vegetational limits can be readily seen. There was a vast area of land above 2000m that would probably have supported vegetation in the glacial periods of the type in which species of *Rhododendron* now growing only above 3100m and perforce only on isolated peaks could grow; such land was continuous for great lengths of the island (Fig. 1). Within this area, there were obviously places in which conditions were too harsh for arborescent growth—thus Hope & Peterson (1975) estimate that there was 55000km<sup>2</sup> of alpine grassland. Also, part of the chain may be drier than it is now because of the exposure of the broad Arafura shelf; Walker & Flenley (1979) note that vegetational limits may have been slightly higher in western than in eastern New Guinea.

This clearly has important implications for distributional studies. As Kalman & Vink (1970) noted in their study of the ericaceous flora of the Doma Peaks and Mt Giluwe, Mt Wilhelm, and the Kubor Range, local endemism does not seem to be high (but see below); this might be expected with a vegetational history such as that discussed above. Many of the main blocks of land above 2000m altitude have species of *Rhododendron* (Table 2) restricted to them. These main blocks include the mountains of the northern part of the Vogelkop, the glacial period 'subalpine' vegetation of which would be almost confluent. The Maoke Range (Snow Mountains), which almost joins with the Eastern Highlands of Papua New Guinea and other blocks, and so forms an almost continuous chain of land above 2000m altitude over 1200km long, forms by far the largest block of high elevation vegetation. The Owen Stanley block especially is now rather effectively isolated, since Mt Amungwiwa, which is the most northerly high mountain of this block, is relatively far



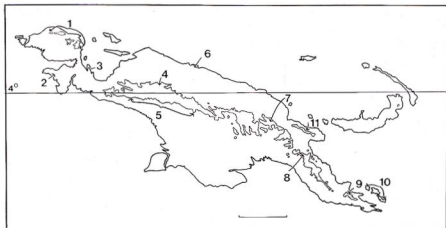


FIG. 1. Land above 2000m altitude in the New Guinea region (enclosed by line) Bar represents 300km. Numbers (see also Table 2): 1, The Vogelkop; 2, Fak-Fak; 3, Wandammen Peninsula; 4, Mt Doormantop; 5, Maoke Range; 6, Cycloop Mountains; 7, Mt Wilhelm; 8, Owen Stanleys; 9, The south-eastern mountains; 10, D'Entrecasteaux archipelago; 11, Saruwaged-Finisterre range.

TABLE 2  
Some endemic species of New Guinea rhododendrons

1. The Vogelkop (numbers refer to Fig. 1).  
*R. brachypodarium*, *R. erosipetalum*, *R. hatamense*, *R. hirtolepidotum*, *R. mollianum*, *R. papuanum*, *R. phaeochristum*, *R. porphyranthes* (mostly species of moderate altitudes).
2. Fak-Fak.  
*R. vinkii* (a low altitude species).
3. Wandammen Peninsula.  
*R. asperrimum* (a low altitude species).
4. Mt Doormantop.  
*R. extrorsum*, *R. lamii*, *R. simulans*, *R. subulosum*, *R. taxoides*. The mountain itself is fairly isolated, and is formed of serpentine rocks. The number of apparent endemics is exceptional for a single mountain.
5. Maoke Range (Snow Mountains).  
There are about 20 species restricted to it, including several species of the small-leaved ser. *Linnaeoidea*, but the whole range is much undercollected.
6. Cycloop Mountains.  
*R. bryophilum*, *R. dianthosmun*, *R. laetum*, *R. wightianum* var. *cyclopense*. An isolated area of not very high hills; again serpentine occurs here.
7. Mt Wilhelm.  
No endemics, although Mt Wilhelm is the highest mountain in Papua New Guinea and is also non-volcanic.
8. Owen Stanleys.  
The arrow points to Mt Amungwiwa. *R. comptum*, *R. giulianettii*, *R. detznerianum*, and *R. spondylophyllum* occur only on the Owen Stanleys.
9. The south-eastern mountains.  
*R. archboldianum*, *R. armitii*, *R. rhodoleucum*, *R. truncicola*. None of these species grows at the highest elevations on Mt Suckling, the highest mountain in the area.
10. D'Entrecasteaux archipelago.  
*R. goodenoughii*, *R. wightianum* var. *insularum*. *R. goodenoughii* is a member of a taxonomically difficult group (cf. Hunt, 1981); *R. wightianum* var. *wightianum* is a widespread taxon.
11. Saruwaged-Finisterre range.  
*R. hellwigii*, *R. pachycarpon*, *R. rhodostomum*.

to the south; this mountain has a very interesting vegetation. Both the Saruwaged-Finisterre block, and especially the Suckling-Dayman block, are isolated from the other main high altitude blocks. New Britain has a very small area of land at about 2000m elevation, some is volcanic, some not; there are five species of *Rhododendron* known from there.

Species of *Rhododendron* today growing above 3000m are generally restricted to single major high altitude blocks. However, *R. womersleyi* and *R. gaultheriifolium* var. *gaultheriifolium* are spread rather more widely and grow only slightly below 3000m; in addition, high altitude blocks in the Eastern and Western Highlands of Papua New Guinea are much fragmented, and species like *R. hooglandii* and *R. atropurpureum* occur on more than one block. Although it seems that geographical isolation has affected the spread of some species growing at lower altitudes (Table 2), a more sophisticated analysis of distributions when they are better known will probably qualify this statement. Thus *R. carringtoniae* occurs on the Suckling-Dayman block and on the Owen Stanleys; *R. rubellum* and *R. alticola* occur mainly on the Owen Stanleys, but with individual stations to the west, whilst with *R. womersleyi*, *R. pleianthum*, *R. maius*, and *R. christi* the relationship is reversed—these latter taxa, it should be emphasized, are all found in the Mt Amungwiwa-Bulldog Road area in the Owen Stanley Block, only *R. maius* being reported from further south.

There are some distributions which suggest that long-distance dispersal or extinction has produced anomalous distribution patterns; a selection of these is given in Table 3. Distributions like those of *R. hooglandii*, *R. atropurpureum*, and *R. villosulum* are particularly perplexing. *Rhododendron atropurpureum* shows local differentiation in the two areas in which it is known to occur (Stevens, 1974); although both it and *R. hooglandii* occur on the Kubors, the former grows on Mt Wilhelm and the latter on Mt Kerigomna. Mt Kerigomna is adjacent to Mt Wilhelm and reaches almost 3900m in altitude; the difference in rhodoendrons (and species of other genera) on the two mountains is inexplicable.

Kalkman & Vink (1970) found that, broadly speaking, the similarity of ericaceous flora between two mountains was affected by the distance between the mountains, but there were numerous species occurring on only a single mountain of those that they studied. To a certain extent, this finding has to be modified when the total ranges, habitats, and altitudinal preferences of the species compared are examined; thus *R. saxifragoides* is a bog-dwelling species in the eastern part of its range, and its absence from mountains to the east of Mts Hagen and Giluwe might be connected with the scarcity of appropriate habitats or the barrier to dispersal to the east that may exist (cf. Smith, 1975). Broadly speaking, however, most species have fairly coherent geographic ranges, and 'point' endemics are not notably common. Several species known only from a single locality occur on the Maoke Range (but see Table 2); endemism of herbaceous alpine plants is highest there (and on the Owen Stanleys; Smith, 1975).

There are a few widespread Papuan species. *Rhododendron culminicola* occurs at high altitudes in many available habitats throughout New Guinea, and *R. beyerinckianum* comes close to this, being absent only from the Vogelkop. A few species like *R. lindaueanum*, *R. nummatum*, *R. zoelleri*, *R. konori* and *R. macgregoriae* all have wide

TABLE 3

Distribution of some New Guinea species of *Rhododendron* on selected mountains

	Giluwe	Kerigomna	Wilhelm	Kubors	Amungwiwa	Saruwageds	Elsewhere
<i>R. saxifragoides</i>	+	—	—	—	—	—	To west
<i>R. hooglandii</i>	—	+	—	+	—	—	Central Highlands
<i>R. atropurpureum</i>	—	—	+	+	—	—	Total range
<i>R. womersleyi</i>	+	+	+	+	+	+	Central Highlands
<i>R. vitis-idaea</i>	—	—	+	—	+	+	Mostly eastern
<i>R. yelliottii</i>	—	—	+	+	+	+	Central Highlands and Owen Stanleys
<i>R. villosulum</i>	—	—	+	—	—	—	Irian Jaya

distributions, although the first two do not quite extend the length of the island; these species also grow at quite low altitudes. *R. superbum* grows east of Mt Doormantop, and it also occurs in the Bismarck and Louisiade Archipelagoes (note that what is apparently a small form of *R. konori* has been collected very recently from Misima Island).

In West Malesia and the Celebes-Moluccas area the situation is different. Although the total land area is much greater, the area above 2000m elevation is much less and much more disjunct (Figs 2 & 3; land above 1000m is, however, of wide extent—see Walker, 1982, fig. 30.1). There is also relatively little land suitable for subalpine species of *Rhododendron*, i.e. above 3000m altitude, in the whole region, and many of the highest peaks are active volcanoes. The highlands of the Malay Peninsula are non-volcanic, although reaching no great altitude; Mt Kinabalu in Sabah, Mt Losir in northern Sumatra, and mountains in the Celebes are the only non volcanic peaks substantially above 3000m elevation. In addition, the depression of the tree-line in West Malesia is believed to be considerably less than in Papuasia; Whitmore (1981) indicates a depression of 350m in Sumatra. Thus there will be less tendency for those highland areas of vegetation that exist to become confluent during the interglacials. Not surprisingly, we see a very different pattern of distribution.

Here we have to distinguish between the Celebes-Moluccas area and 'the rest'. The Celebes-Moluccas area, although small, and in part perhaps notably drier during the glacial periods (e.g. Whitmore, 1975; Walker, 1982, and refs therein), nevertheless supports a fairly rich flora of some 34 species of *Rhododendron*, of which 28 are endemic (most of these occur on the island of Sulawesi itself). Although Sulawesi is not a large island, at least compared to Sumatra, Borneo, and New Guinea, it has a substantial area above 2000m altitude, and this is highly broken up (Fig. 2). Interestingly, the relative diversity of *Rhododendron* contrasts with the lack of diversity of the flora and much of the fauna as a whole (e.g. Whitmore, 1981; Dransfield, 1981).

The Celebes-Moluccas region is clearly intermediate between West Malesia and Papuasia. Although no species in the area have the distinctive Papuanian zygomorphic flower type, there are species (*R. lomphoense*, *R. buruense*, perhaps *R. impositum*) with the large broadly funnel-shaped white flower type that occurs in a number of Papuanian species. Overall consideration of flower types suggests an intermediate position, perhaps tending to be closer to Papuasia (Stevens, 1976). *R. lagunclicarpon* is close to *R. yelliottii* (Papuasia), and *R. zoelleri* and *R. lindauanum*, both Papuanian species, occur in the Celebes-Moluccas area. However, the West Malesian *R. quadrasianum*, *R. malayanum*, *R. zollingeri*, and *R. javanicum* also occur there; the first two have a basically north-western Malesian distribution, the second two have a basically southern distribution (Sunda Islands, but also the Philippines).

There are only some 98 species in the whole of the rest of Malesia, of which 12 are restricted to the Phillipine Islands. Many of these 98 species occur on Mt Kinabalu, in Sabah, or near it, but currently only some six species are restricted to it. Mt Kinabalu is the highest mountain in the whole area, and it has been suggested that lower ranges nearby may once

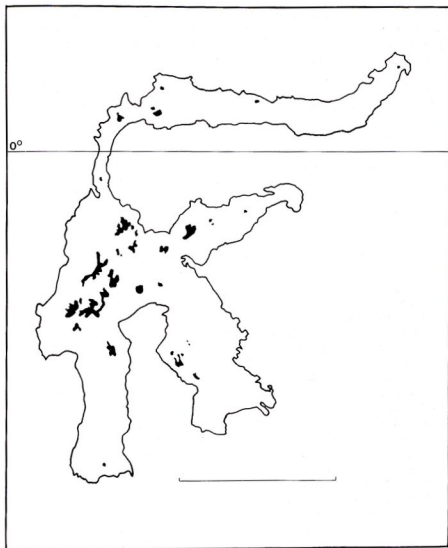


FIG. 2. Land above 2000m altitude on Sulawesi (shaded black). Bar represents 300km.

have been higher and carried a more microtherm flora (Van Steenis, 1964). The central range of Borneo consists of old, eroded mountains, but as can be seen from Fig. 3, areas of land currently above 2000m are small and widely scattered. It is perhaps worth noting that 20% of the species in West Malesia have varieties, whilst the figure in Papuasia is only 6%. These figures should be treated with great caution, but may indicate this greater isolation (or age) of populations of *Rhododendron* in West Malesia. Nevertheless, there are a few widespread West Malesian species—*R. javanicum*, *R. jasminiflorum*, *R. longiflorum* and *R. malayanum*. Although there is quite a long pollen record for northwest

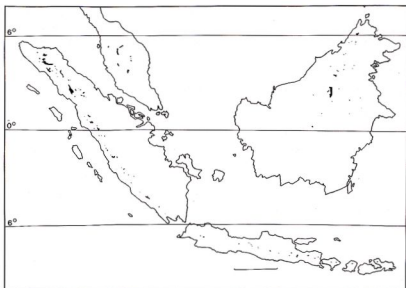


FIG. 3. Land above 2000m altitude in Borneo, Sumatra, Java and the Malay Peninsula (shaded black; many areas barely visible at this reduction). Bar represents 300km.

Borneo, it, too, is not one that suggests a static flora at higher elevations. The montane elements in that record from the Oligo-Miocene differs considerably from that of the Plio-Pleistocene; ericaceous pollen is recorded in the latter (Müller, 1972).

#### DISCUSSION

It is unclear how the marked floral differences between species that grow together throughout Malesia have been involved in diversification and are even today involved in the maintenance of that diversity. The diversity of floral types and possible pollinators would seem strong evidence for their importance in the prevention of hybridization in taxa growing together. The details of the interaction between the plants and their pollinators remain to be worked out; Stiles (1981) and Snow & Snow (1980) suggest the complexity of the interactions possible in a neo-tropical situation. There are few known barriers to crossability between Malesian species of sect. *Vireya*, and it is possible to cross apparently very different species, 'bulldog/chihuaua' problems perhaps only excepted (Sleumer, 1966, 1973; Stevens, 1974, 1976); even the distinct subsect. *Malayovireya* hybridizes with members from other groups (Sleumer, 1966). In general, so long as the habitat is undisturbed, hybridization does not seem to be that frequent.

However, the oscillations in vegetation distribution and composition discussed above were surely accompanied by comparable oscillations in the fauna, and this considerably increases problems when species are considered as entities existing through at least part of the Quaternary: are the relationships between species and pollinators or other aspects of their

ecology that we see today of long standing? Variation in leaf and habit discussed above may also help in ecological isolation, although this is pure surmise. Thus, although in Papua New Guinea *R. saxifragoides* is characteristically a denizen of tussock bogs, in Irian Jaya it has been collected in ridge vegetation where it is less caespitose. It has been suggested that comparable flexibility helps in the maintenance of diversity during periods of environmental change or stress (Stevens, 1981), but it may do this by breaking down some of the apparent ecological barriers between taxa. Our current knowledge of the biology of the group is too simplistic to deal effectively with the problems posed by past ecological change.

Despite these uncertainties, one can reasonably suggest in the case of subjects *Phaeovireya* and *Malayovireya* in particular that there has been great evolution in vegetative and floral characters since these two groups diverged. Three of the most distinctive flower types, zygomorphic red, long tubular white, and large funneliform white, have almost certainly evolved more than once, as have distinctive leaf shapes. All three are probably derived types, emphasizing that species with more than 5-merous flowers are not necessarily representative of an ancestral condition.

Although it is uncertain how long *Vireya* rhododendrons have been in West Malesia, they have almost certainly entered Papuasia from the west within the last 20 million years when the Australian plate, possibly including the eastern part of the Celebes as an outlier, came in contact with SE Asia-Malesia (including the western part of the Celebes: Hamilton, 1979; Audley-Charles, 1981). Much of the diversification of *Rhododendron* in Papuasia, at least, has probably been within the last five million years (the existence of an island chain to the north of the advancing Australian plate complicates the argument, but *Rhododendron* does not seem a particularly aggressive colonist of islands, especially low ones). The distributions of many species seem to be limited by land below 2000m altitude, and the extreme relief and geological diversity of the areas has probably aided speciation. Walker (1982) considered the Papuanian flora to be less saturated than that of West Malasia, and that this, coupled with the extremely unstable nature of the hill country in particular, would tend to favour species with r-type reproductive characteristics. *Rhododendron* sect. *Vireya*, although woody and a slow grower initially, nevertheless can self-fertilize (Rouse, pp. 99-115), each capsule producing large numbers of seeds, and many species are noted colonizers of exposed ground, so it has some of these characteristics, and this may have accentuated its speciation rate.

Malesia has at present, and probably always has had, numerous areas which would appear to act as barriers to the distribution of montane or even colline taxa—thus many islands in the Philippines, the Celebes-Moluccas, the Bismarck Archipelago, the Solomon Islands, and New Guinea itself, have always been isolated by water for groups coming from the west, and there are large areas, especially in West Malesia, and also that between New Guinea and Australia, that would support strictly lowland vegetation even in interglacials. Nevertheless, there has clearly been movement of species across the gaps. It is perhaps interesting that in the Celebes region such well-defined groups as subjects *Malayovireya* and



*Phaeovireya* reach their limits, eastern and western respectively. Although this area seems to be the main dividing line in the distribution of the Ericaceae generally (Stevens, 1981), and of many other groups, too, it is only in this case of a barrier that has been more or less difficult to cross for 20 million years, and it is unlikely to represent an area where rhododendrons, originally isolated on two continental blocks, met.

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