

# 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 Papuasian flower types, are the main characteristics of floral variation in West Malesian species. Preliminary geographic analyses emphasise the richness of the Papuasian *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 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.) 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 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.

Table 1. Distribution of *Rhododendron* sect. *Vireya* in Malesia.

Subsection	West Malesia	Celebes-Moluccas	Papuasia	SE Asian Mainland	Australia	Total
Pseudovireya	11	4	14	6		32
Siphonovireya			7			7
Phaeovireya		2	39			41
Malayovireya	15	1				15
Albovireya	5	4	6			14
Solenovireya	8	4	26			38
Euvireya series						
Linnaeoidea			12			12
Saxifragoidea			1			1
Taxifolia	1					1
Stenophylla	1		3			4
Citrina	1					1
Buxifolia	16	4	23			43
Javanica	40	15	32	2	1	87
Total	98	34	163	8	1	296

Notes.

*R.lindaueanum* = Papuaasia / Celebes

*R.quadrasianum* = Celebes / West Malesia

*R.malayanum* = Celebes / West Malesia

*R.zollingeri* = Celebes / West Malesia

*R.zoelleri* = Papuaasia / Moluccas

*R.javanicum* = West Malesia / Celebes

## 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 portions. Kores & van Royen (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 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, 1988). 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. beyerinckianum* 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, 1985). 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, 1985), 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 pseudoverticillate.

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. 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 Papua. 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 Papua (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 these 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 Papua, with species with red corollas being commoner at higher elevations. In Papua 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 Papuaasia, and in Papuaasia 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 Papuaasia 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 Papuasia 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 Papuasian 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 Malaysian region, and over half the species 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 Papuasian 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 tubes are not found at the highest altitudes (Stevens, 1976).

There is evidence, albeit tentative and mostly coming from Papuasia, 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





























