



Vireya Rhododendrons: their monophyly and classification (*Ericaceae*, *Rhododendron* section *Schistanthe*)

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classification
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Abstract Further investigation into the evolutionary relationships of the vireya group of *Rhododendron*, utilising nuclear DNA sequence data, has demonstrated that this group of species is monophyletic, and a revised classification is presented. The name *Vireya* is predated at sectional level by several other valid names and the correct name for the section is now *Schistanthe*. Within *Schistanthe*, four subsections are recognised: *Discovireya*, *Euvireya*, *Malayovireya* and *Pseudovireya*. Revised identification keys are provided. Some morphological features of value for classification and/or species delimitation are briefly discussed.

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INTRODUCTION

Rhododendron L. is one of the larger genera of *Ericaceae* and contains between about 600 and 1 000 species, depending upon the species concept accepted by individual workers. One of the largest of its several sections is *Schistanthe*, a group of c. 300 species primarily found in south-eastern Asia and Malesia. A very concise account of the classification of the genus, especially in the context of molecular evidence, is given in Craven et al. (2008). As with that paper, the classification of the genus proposed by Goetsch et al. (2005) is followed here. Based on analysis of sequence data from the nuclear gene *RPB2-i*, Hall et al. (2006) found sect. *Schistanthe* Schltr. (previously *Vireya* (C.B. Clarke) H.F. Copel.) to be polyphyletic. The Malaysian species of subsect. *Pseudovireya* (C.B. Clarke) Sleumer (sensu Sleumer 1966) formed a clade nested with several clades of sect. *Pogonanthum* G. Don and sect. *Rhododendron* species. The Continental Asian species of *Pseudovireya* were sister to a clade representative of all the other vireya species and these two clades were in a clade with two other clades of sect. *Rhododendron* species. The Sumatran species *R. vanderbiltianum* Merr. was included by Sleumer (1966) in subsect. *Pseudovireya* but this species is considered by Argent et al. to belong in sect. *Rhododendron* (Argent 2006: 37, as sect. *Maddenia*). DNA sequence evidence is equivocal with respect to *R. vanderbiltianum* which appears to be placed near the borderline between sections *Rhododendron* and *Schistanthe* (Goetsch et al. in press). To obtain a more clear assessment of the relationships of *R. vanderbiltianum*, this species should be included in any future comprehensive phylogenetic studies of sect. *Rhododendron*. Drawing on the findings of Hall et al. (2006), Craven et al. (2008) proposed that the vireya species be accommodated in three sections, *Discovireya* (Sleumer)

Argent, *Pseudovireya* (C.B. Clarke) Argent and *Vireya*, and presented a classification to this effect.

Further sequencing of nuclear genes by B.D. Hall and L.A. Goetsch for a comprehensive investigation into the relationships of subsect. *Euvireya* H.F. Copel. species has shown, however, that the vireyas are monophyletic (Goetsch et al. in press). The phylogeny shown in Fig. 1 was obtained from analysis of data from three nuclear genes (*RPB2-i*, *RPC1* and *RPB2-d*) drawn from a reduced number of species, but giving a similar pattern of relationships to that found by Goetsch et al. (in press). Two species, *R. perakense* King & Gamble and *R. santapau* Sastry, Katakai, P.A. Cox, P.B. Cox & Hutchison, are not placed with the species that they would be expected to group with on the basis of morphological evidence, i.e., *Discovireya* and *Pseudovireya* respectively. These two species, and several others that gave interesting results, are discussed by Goetsch et al. (in press). Taking into account the clades recovered in the three nuclear gene phylogeny shown in Fig. 1, together with morphological data, we conclude that four clades should be given taxonomic rank. As there are close phylogenetic relationships between the vireya group of species and sections *Pogonanthum* and *Rhododendron* (Hall et al. 2006, Goetsch et al. in press), it is appropriate that the vireya group be classified within subg. *Rhododendron*, as placed by Craven et al. (2008), but ranked at sectional level as the vireyas nest within the subgenus. Subsectional status is warranted for the four vireya clades recovered for which the following epithets are applicable: *Discovireya*, *Euvireya*, *Malayovireya* and *Pseudovireya*. The morphological features that define these four subsections are given in the key following the classification below. Goetsch et al. (in press) found that there was no support for recognition at any rank for the following taxa recognised by Sleumer (1966) and Argent (2006): *Albovireya*, *Phaeovireya*, *Siphonovireya* and *Solenovireya*. It must be noted, however, that only two representatives of *Siphonovireya*, *R. herzogii* Warb. and *R. inundatum* Sleumer, were included in the DNA sampling by Goetsch et al. (in press) and that it is possible that *R. inundatum* is not a biologically distinct species. *Rhododendron inundatum* recently has been rediscovered near its type locality in a mosaic of introgressive hybrids with *R. herzogii*, *R. macgregoriae* F. Muell. and *R. × psammogenes* Sleumer, the last-named being a

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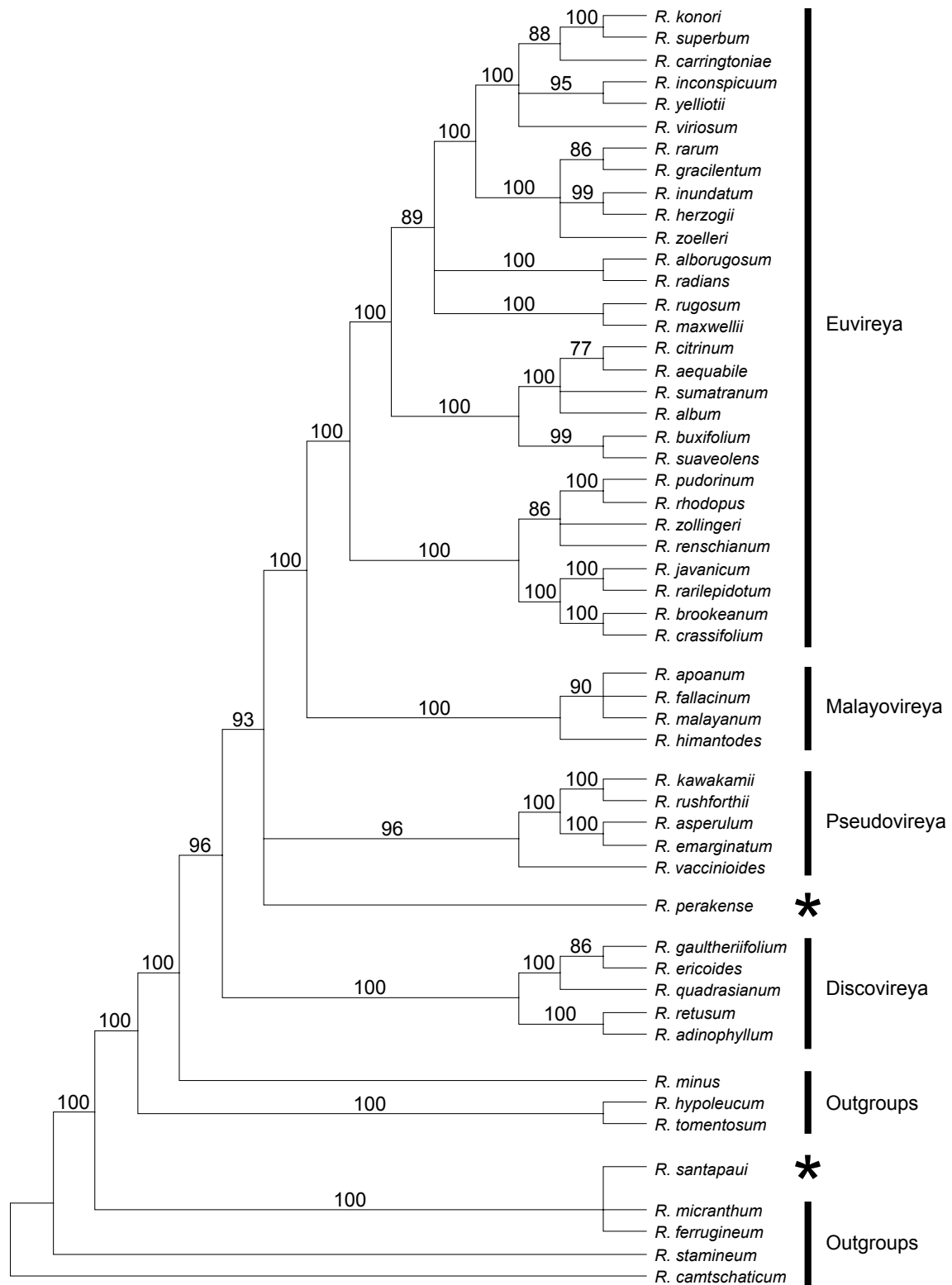


Fig. 1 Inferred phylogeny of *Rhododendron* sect. *Schistanthe* based upon *RPB2-i*, *RPB2-d* and *RPC1* sequence data. The numbers indicate bootstrap support. See text for discussion of the placement of *R. perakense* and *R. santapau*.

putative hybrid between *R. herzogii* and *R. macgregoriae*, i.e., *R. × inundatum* appears to have resulted from a backcrossing between *R. herzogii* and *R. × psammogenes* (Danet, unpubl. data). The respective classifications of Sleumer (1966), Argent (2006) and Craven et al. (2008) for the vireya group of *Rhododendron* are contrasted in Table 1 with the classification proposed in this paper.

Significant changes to plant names are never well received and it is regretted that, under the International Code of Botanical Nomenclature (McNeill et al. 2006), the name sect. *Vireya*

cannot be maintained for the vireya group as a single, inclusive taxon. Craven et al. (2010) discussed the issue and accepted sect. *Schistanthe* as the correct name for the section. The name change arises because the prior, valid publication of five sections by Schlechter (1917), all of which have nomenclatural priority over sect. *Vireya*, was not taken into account by subsequent authors who worked on the taxonomy of the vireya group. For clarity, and simplicity in referencing, in the text of this paper *Schistanthe* is used in lieu of *Vireya* when referring to pre-2010 literature.

Table 1 Comparison of the classifications by Sleumer (1966), Argent (2006) and Craven et al. (2008) of *Rhododendron* sect. *Schistanthe* with that of Craven et al. (this paper).

Sleumer 1966	Argent 2006	Craven et al. 2008	Craven et al. (this paper)
sect. <i>Vireya</i>	subgenus <i>Vireya</i>	sect. <i>Vireya</i>	sect. <i>Schistanthe</i>
subsect. <i>Albovireya</i>	sect. <i>Albovireya</i>	sect. <i>Vireya</i> subsect. <i>Euvireya</i>	sect. <i>Schistanthe</i> subsect. <i>Euvireya</i>
subsect. <i>Euvireya</i>	sect. <i>Vireya</i> (as <i>Euvireya</i>)	sect. <i>Vireya</i> subsect. <i>Euvireya</i>	sect. <i>Schistanthe</i> subsect. <i>Euvireya</i>
subsect. <i>Malayovireya</i>	sect. <i>Malayovireya</i>	sect. <i>Vireya</i> subsect. <i>Malayovireya</i>	sect. <i>Schistanthe</i> subsect. <i>Malayovireya</i>
subsect. <i>Phaeovireya</i>	sect. <i>Phaeovireya</i>	sect. <i>Vireya</i> subsect. <i>Euvireya</i>	sect. <i>Schistanthe</i> subsect. <i>Euvireya</i>
subsect. <i>Pseudovireya</i> ¹	sect. <i>Discovireya</i>	sect. <i>Discovireya</i>	sect. <i>Schistanthe</i> subsect. <i>Discovireya</i>
	sect. <i>Pseudovireya</i>	sect. <i>Pseudovireya</i>	sect. <i>Schistanthe</i> subsect. <i>Pseudovireya</i>
subsect. <i>Siphonovireya</i>	sect. <i>Siphonovireya</i>	sect. <i>Vireya</i> subsect. <i>Euvireya</i>	sect. <i>Schistanthe</i> subsect. <i>Euvireya</i>
subsect. <i>Solenovireya</i>	sect. <i>Vireya</i> (as <i>Euvireya</i>) subsect. <i>Solenovireya</i>	sect. <i>Vireya</i> subsect. <i>Euvireya</i>	sect. <i>Schistanthe</i> subsect. <i>Euvireya</i>

¹ As Sleumer (1966) was dealing with the Malesian region only, the group of species that includes the type of subsect. *Pseudovireya* was not treated by him. Subsection *Pseudovireya* sensu Sleumer (1966) represents *Discovireya* of Argent (2006), Craven et al. (2008) and Craven et al. (this paper).

MORPHOLOGY

Goetsch et al. (in press) note the radiation of *Euvireya* species and the extensive variation in their floral morphology. Although limited supporting data are available, there are several features that might be considered key innovations in the evolution of the diversity found within the vireya group as a whole. Given that *Rhododendron* is dry-fruited and that both fruit and seeds (the latter because of their very small size) are not likely to be attractive to frugivorous and/or seminivorous animals, a non-animal-mediated explanation for the wide dispersal of the vireya group across numerous sea barriers must be found. Seeds of a broad range of *Rhododendron* species, covering much of the taxonomic diversity within the genus, are well illustrated by Hedegaard (1980). Commonly in *Rhododendron*, the seeds have the testa produced into very short tufts at each end of the seed, or extended as a narrow marginal flange around the seed, or both; seeds of these types may well adhere easily to terrestrial mammals and most of the relevant species themselves are terrestrial. Such small seeds may be adapted for dispersal through adhesion to terrestrial mammals. It should not be discounted, however, that those *Rhododendron* seeds with a well-developed wing may be wind-dispersed. A broad wing would assist in making the seed more buoyant in air and thus more readily transported by wind. A terrestrial dispersal strategy would not benefit dispersal of species of *Schistanthe* rhododendrons as they mostly occur on the islands of the Malesian archipelago and successful dispersal has had to overcome the saltwater barriers, thus ruling out dispersal by terrestrial mammals. Additionally, most *Schistanthe* species are found in montane regions and deposition of their seeds in lowland tropical forest would not result in their successful establishment. Even when the present islands of the Sunda shelf were connected, mammal-mediated dispersal from montane region to montane region would have been very unlikely. *Schistanthe* seeds are characterised by possession of a long tail at each end of the seed; the tail being a very long extension of testal tissue. Hedegaard (1980: 366–367) illustrates only a single example of *Schistanthe*, i.e., *R. lochiai* F.Muell., but this is sufficient for comparison with the other species of the genus. A great many vireya species are epiphytes and thus have little opportunity for interactions with mammals but they often occur in open, airy situations. Conventionally, it is thought that the seed tails facilitate dispersal of the seeds by wind but there is little empirical data. An initial study of the behaviour of vireya seeds in a current of air was undertaken by Blenkin (2005). Blenkin's experimental work was hindered due to electrostatic effects when real seeds were used and models had to be constructed. Nevertheless, the results showed that the tailed models floated in air better than did tailless models; this area of research is worth revisiting.

Another feature that may have been advantageous in the radiation of *Schistanthe* species, especially those evolving to fill

epiphytic niches, is the occurrence of idioblasts, giant cells present in and below the upper leaf epidermis of vireya species (Nilsen 2003, Nilsen & Scheckler 2003). The function of idioblasts within vireya leaves is not well understood but it is believed likely they may have a role in leaf water balance, glandular secretion, light penetration or herbivore defence (Nilsen 2003, Nilsen & Scheckler 2003). If leaf water balance is found to be a major function of idioblasts then this would be of value to epiphytic plants when subjected to periods of drying, enabling them to control water movements.

A dense indumentum in plants conventionally is thought to provide one or more benefits, such as a defence against herbivores, protection from desiccation by sheltering the stomata, or reducing potentially harmful effects of radiation until the leaf has matured its epidermis and cuticle. In many *Schistanthe* species, the leaf trichomes (in subg. *Rhododendron* these conventionally are termed scales) may be very dense and especially so in the younger stages when the leaves are expanding. Nilsen & Webb (2007) concluded that scales in *Schistanthe* species generally were not associated with stomata and that scales in these species had little significance for reduction in water use. In all examined species of subsect. *Malayovireya*, however, Nilsen & Webb found that stomata were clustered in crypts below the scales and considered this would be advantageous during periods of drought. For *Malayovireya*, the occurrence of stomata in scale-associated crypts may be a key innovation. Nilsen & Webb (2007) also discussed the high altitude, New Guinean *R. saxifragoides* J.J.Sm., the only amphistomatous species they had found in over 200 examined species of *Rhododendron*. Argent (2006) used this feature together with a compact habit as the basis of his subsect. *Saxifragoidea*. The ecophysiological basis for the occurrence of stomata on each side of the leaf in *R. saxifragoides* may be due, at least in part, to the habit and habitat of the species. *Rhododendron saxifragoides* is a cushion plant occurring in high altitude bogs. If its leaves were orientated more or less at right angles to the stem, as is usual in *Rhododendron*, the typically stomata bearing abaxial surface of the leaf would be held against the ground. As can be seen in the photographs in Argent (2006: 153, 154) and Sleumer (1966: 374), the leaves of *R. saxifragoides* are held erect, i.e., at an acute angle to the stem. It may be that the leaves in this species are functionally isobilateral in which case amphistomaty would not be unexpected; having stomata on each leaf surface would maximise air exchange and transpiration.

Of the four subsections of *Schistanthe*, three are of medium content: *Discovireya*, (c. 25 species), *Malayovireya* (c. 12 species) and *Pseudovireya* (c. 10 species). *Euvireya*, on the other hand, consists of c. 270 species. The corollas of *Discovireya* and *Pseudovireya* species are relatively invariant as to form and colour. *Discovireya* corollas are generally tubular in shape and yellow, orange or red. *Pseudovireya* corollas are usually rotate-campanulate and white or yellow. *Malayovireya* corollas are more variable, ranging from tubular, tubular-campanulate,

funnel-shaped, campanulate to rotate-campanulate and may be white, pinkish orange, yellow, red or bicoloured. It is in *Euvireya* that the greatest diversity is found and a selected range of flower types is illustrated in Goetsch et al. (in press; Fig. 1). Flowers in *Euvireya* species may be white, pink, red, cream, yellow, orange or green. Bicoloured flowers are not unusual and one species has mauve-pink corollas. Corolla form may be tubular, tubular-campanulate, campanulate, rotate-campanulate, funnel-shaped, salver-shaped or suburceolate, and straight or curved. Many species have zygomorphic flowers but in some species the flowers are actinomorphic (e.g., *R. tinnabellum* Danet). In size, the flowers of *Euvireya* species range from 12 by 7 mm (*R. caespitosum* Sleumer) to 80–190 by 70–150 mm (*R. konori* Becc.). The diversity in flower colour and form suggests that the pollinators are likely to be equally diverse. A propensity to adapt to new and diverse pollinators through modification in floral attributes may be a key innovation enabling *Euvireya* species to evolve to fill the many niches available to them. Species may be terrestrial or epiphytic and occur in montane rainforest at mid or high altitudes, subalpine shrubberies, intermountain basins, bogs, and even low altitude woodlands and lowland rainforest.

The use of bark as a taxonomic character for circumscribing species of *Rhododendron* is little used. Perhaps this is partly because data on bark characteristics are rarely noted by field collectors and hence not available to taxonomists in the herbarium. Additionally, many species of the genus are small to medium shrubs and field collectors usually do not collect bark data from shrubs, especially from small shrubs that may have the bark of the trunk and major stems obscured by bryophytes and other organisms. For example, in the account of *Rhododendron* in Flora of China (Mingyuan et al. 2005), bark is described for only about 45 of the 571 species treated. Bark features were used by Craven (2009) to support the recognition, at species rank, of *R. wariatum* Schltr., a taxon that had been reduced to varietal rank within *R. leptanthum* F.Muell. by Argent (1995) and later placed by Argent (2006) in the synonymy of *R. leptanthum* without taxonomic recognition. It is possible for bark data to be collected from competently identified, mature, cultivated plants and Craven (2009) outlines one approach that could be taken to collect such data.

CLASSIFICATION OF VIREYA RHODODENDRONS

Rhododendron L.

subg. *Rhododendron*

sect. *Rhododendron*

sect. *Pogonanthum* G.Don

sect. *Schistanthe* Schltr. (1917) 140. — Lectotype: *R. hansemannii* Warb. ('*hansemanni*'), designated by Sleumer (1960: 176). This species is now included in *R. macgregoriae* F.Muell.

subsect. *Discovireya* Sleumer (1949) 539. — sect. *Discovireya* (Sleumer) Argent (2006) 21, 37. — Type: *R. retusum* (Blume) Benn. (*Vireya retusa* Blume)

subsect. *Euvireya* H.F.Copel. (1929) 137, 159. — *Vireya* Blume (1826) 854, nom. illeg., non Raf. (1814). — subg. *Vireya* C.B.Clarke (1882) 462. — *Rhododendron* L. § *Vireya* (C.B.Clarke) Hook.f. ex Drude (1897) 36. — sect. *Vireya* (C.B.Clarke) H.F.Copel. (1929) 136, 151. — ser. *Javanica* Sleumer (1960) 176. — sect. *Euvireya* (C.B.Clarke) Argent (2006) 22, 140, nom. superfl. — Type: *R. javanicum* (Blume) Benn. (*Vireya javanica* Blume)

sect. *Hadrnanthe* Schltr. (1917) 140. — Lectotype: *R. hellwigii* Warb., designated by Sleumer (1960: 71)

sect. *Hapalanthe* Schltr. (1917) 140. — Lectotype: *R. zoelleri* Warb., designated by Sleumer (1960: 176)

sect. *Linnaeopsis* Schltr. (1917) 140, 144. — subsect. *Linnaeopsis* (Schltr.) Sleumer (1949) 541. — ser. *Linnaeoides* Sleumer (1960) 134. — Type: *R. linnaeoides* Schltr.

sect. *Zygomorphanthe* Schltr. (1917) 140. — Lectotype: *R. keysseri* F.Först., designated by Sleumer (1960: 176). (This species is now included in *R. culminicola* F.Muell.)

subsect. *Leiovireya* H.F.Copel. (1929) 137, 167. — Type: *R. crassifolium* Stapf

subsect. *Linearanthera* H.F.Copel. (1929) 137, 159. — Type: *R. vidalii* Rolfe

subsect. *Malesia* H.F.Copel. (1929) 136, 151. — Type: *R. bagobonum* H.F.Copel.

subsect. *Solenovireya* H.F.Copel. (1929) 136, 158. — Type: *R. jasminiflorum* Hook.

subsect. *Phaeovireya* Sleumer (1949) 539. — sect. *Phaeovireya* (Sleumer) Argent (2006) 21, 70, nom. superfl. — Type: *R. beyerinckianum* Koord.

subsect. *Astrovireya* Sleumer (1949) 539. — Type: *R. commonae* F.Först.

subsect. *Schizovireya* Sleumer (1949) 538. — Type: *R. macgregoriae* F.Muell.

subsect. *Siphonovireya* Sleumer (1960) 68. — sect. *Siphonovireya* (Sleumer) Argent (2006) 21, 62. — Type: *R. habbema* Koord.

subsect. *Albovireya* Sleumer (1960) 107. — sect. *Albovireya* (Sleumer) Argent (2006) 22. — Type: *R. album* Blume

ser. *Saxifragoidea* Sleumer (1960) 141. — subsect. *Saxifragoidea* (Sleumer) Argent (2006) 22, 153. — Type: *R. saxifragoides* J.J.Sm.

ser. *Taxifolia* Sleumer (1960) 141. — Type: *R. taxifolium* Merr.

ser. *Stenophylla* Sleumer (1960) 141. — Type: *R. stenophyllum* Hook.f.

ser. *Citrina* Sleumer (1960) 144. — Type: *R. citrinum* (Hassk.) Hassk.

ser. *Buxifolia* Sleumer (1960) 145. — Type: *R. buxifolium* H.Low ex Hook.f.

ser. *Dendrolepidon* Argent, A.L.Lamb & Phillipps (1984) 117. — Type: *R. rugosum* H.Low ex Hook.f.

subsect. *Malayovireya* Sleumer (1958) 48. — sect. *Malayovireya* (Sleumer) Argent (2006) 21. — Type: *R. malayanum* Jack

subsect. *Pseudovireya* (C.B.Clarke) Sleumer (1949) 537. — subg. *Pseudovireya* C.B.Clarke (1882) 464. — ser. *Vaccinioides* Hutch. (1930) 817. — sect. *Pseudovireya* (C.B.Clarke) Argent (2006) 19. — Type: *R. vaccinioides* Hook.f.

Notes — Blume's genus *Vireya* (Blume 1826) is illegitimate being a later homonym of *Vireya* Raf. (1814, *Gesneriaceae*).

Characteristic morphological features, noting that exceptions may sometimes occur in individual species, that serve to differentiate between the four subsections of sect. *Schistanthe* are as follows:

subsection. *Discovireya* — Scales entire to undulate; corolla tubular; staminal filaments glabrous or hairy from the base; capsule valves not twisting after dehiscence.

subsection. *Euvireya* — Scales sessile or stalked, scattered to very dense, not of two obviously different size classes, lobed to deeply incised (or sometimes entire) and the centre not dark-coloured; corolla tubular, tubular-campanulate, campanulate, rotate-campanulate, funnel-shaped, salver-shaped or suburceolate, and straight or curved; staminal filaments glabrous or hairy from the base; capsule valves twisting after dehiscence.

subsection. *Malayovireya* — Scales sessile, dense, of two obviously different size classes, lobed and the centre dark-coloured; corolla tubular, tubular-campanulate, funnel-shaped, campanulate to rotate-campanulate; staminal filaments glabrous or hairy from the base; capsule valves twisting after dehiscence.

subsection. *Pseudovireya* — Scales entire; corolla rotate-campanulate; staminal filaments glabrous proximally and distally and hairy in the middle region; capsule valves not twisting after dehiscence.

KEY TO THE SECTIONS OF SUBGENUS RHODODENDRON AND SUBSECTIONS OF SECTION SCHISTANTHE

1. Seeds with a distinct tail at each end 2
1. Seeds without distinct tails 5
2. Capsule valves twisting after dehiscence; scales variously incised or sometimes entire 3
2. Capsule valves not twisting after dehiscence; scales entire to undulate 4
3. Scales sessile, very dense, very unequal in size, lobed, centre dark-coloured
. *R. sect. Schistanthe* subsection. *Malayovireya*
3. Scales sessile or stalked, sparse to very dense, subequal in size, lobed to deeply incised (or sometimes entire), centre not dark-coloured (very rarely mixed indumentum with scales of two types, and in *R. heterolepis* Danet the scales very unequal in size and rounded and sessile or deeply incised and stalked) *R. sect. Schistanthe* subsection. *Euvireya*
4. Corolla rotate-campanulate; staminal filaments glabrous proximally and distally and hairy in the middle region
. *R. sect. Schistanthe* subsection. *Pseudovireya*
4. Corolla tubular; staminal filaments glabrous or hairy from the base *R. sect. Schistanthe* subsection. *Discovireya*
5. Corolla campanulate to funnel-shaped or tubular; scales entire to crenulate *R. sect. Rhododendron*
5. Corolla salver-shaped; scales incised
. *R. sect. Pogonanthum*

Note — Rarely, species of sect. *Schistanthe* lack the long-tailed seeds that are characteristic of the section, e.g., *R. ericoides* Low ex Hook.f. and *R. eymae* Sleumer.

KEY TO THE INFORMAL GROUPS OF SUBSECTION EUVIREYA

1. Scales entire, sessile 'Siphonovireya'
1. Scales lobed to deeply incised, sessile or stalked (very rarely the indumentum with both entire and deeply incised scales) 2

2. Scales deeply incised, stalked, each inserted on a distinct, permanent, small protuberance 'Phaeovireya'
2. Scales shallowly or deeply incised, very rarely entire, sessile or rarely stalked, rarely inserted on an apparently non-permanent, small protuberance 3
3. Scales very dense, usually overlapping 'Albovireya'
3. Scales sparse or dense, not overlapping 4
4. Corolla salver-shaped, tube narrow, lobes equalling 1/4 or less of the total corolla length and spreading \pm at right angles to the tube 'Solenovireya'
4. Corolla tubular, tubular-campanulate, campanulate, rotate-campanulate, funnel-shaped or suburceolate, tube usually relatively broad, lobes equalling 1/4 or more of the total corolla length and erect to spreading-ascending or rarely \pm at right angles to the tube 'Euvireya'

Notes — Subsection *Euvireya* contains c. 270 species and it would be a distinct advantage if a formal classification of the subsection could be devised. Presently, however, it is not possible to propose a credible classification of these species based upon monophyletic groups. The informal groups in the key above do provide a framework to both make species identification more easy and give a basis for discussion of the relevant species groups. These groups are based solely upon phenotypic characters and, as is evident from the inferred phylogenies given in Fig. 1 and Goetsch et al. (in press), should not be thought of as reflecting evolutionary relationships and thus should not be given formal taxonomic recognition. As far as included species are concerned, these informal groups equate to the subsections of the same name in Sleumer (1966) and the sections of the same name in Argent (2006) with one exception: Argent's subsection. *Solenovireya* equates to our informal group 'Solenovireya' and the balance of his sect. *Euvireya* equates to our informal group 'Euvireya'.

'Phaeovireya' could readily be re-defined into informal groups on the basis of floral morphology. Those species with relatively small, apparently non-fragrant, pink or red corollas with a curved corolla tube form one clear cut group to which the name 'Phaeovireya' should be applied as the type species of subsection. *Phaeovireya*, *R. beyerianum*, has flowers of this type. The species group with relatively large, often fragrant, white to pink or red corollas with a straight tube (i.e., *R. hellwigii* Warb., *R. konori*, *R. leucogigas* Sleumer, etc.) would then comprise a second group (perhaps with the name 'Hadranthe' as *R. hellwigii* is the type species of sect. *Hadranthe*). *Rhododendron leucogigas* is best placed in this part of the 'Phaeovireya' group as its leaves do have some of the scales inserted on protuberances (although the majority of the scales certainly are sessile); it is on floral features that its affinities are best assessed. Florally, *R. eymae* is very different from the preceding two species groups with its small, yellow corollas with a straight tube and this Sulawesi species might be better placed in its own group, the other species of 'Phaeovireya' all being New Guinean with the exception of *R. psilanthum* Sleumer which also occurs on Sulawesi but may not be phylogenetically close to the New Guinea species.

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