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CLASSIFICATION OF THE VIREYA GROUP OF RHODODENDRON (ERICACEAE)

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SUMMARY

A new classification of the *Vireya* group of *Rhododendron*, based upon their evolutionary relationships as inferred from analysis of nuclear and plastid DNA sequence data, is presented. *Rhododendron* sect. *Vireya* is not monophyletic and its species are herein placed in three sections within subg. *Rhododendron*, namely sect. *Discovireya*, sect. *Pseudovireya* and sect. *Vireya*, with two subsections recognised within sect. *Vireya*: subsect. *Euvireya* and subsect. *Malayovireya*. Identification keys are provided.

Key words: Ericaceae, *Rhododendron*, *Vireya*, classification, molecular systematics.

INTRODUCTION

Rhododendron L. is a large genus of Ericaceae with an estimated 600–1000 species, the number depending upon the breadth of specific variation accepted by individual workers. The genus is widely and commonly cultivated in temperate and subtemperate regions and this presumably has contributed to its intensive study by systematists as it is the subject of a voluminous literature, especially dealing with the description of new taxa. The contemporary classifications of *Rhododendron* are based upon the seminal publication 'Ein System der Gattung *Rhododendron* L.' (Sleumer 1949). Following Sleumer's publication several authors have conducted more detailed morphological studies of infrageneric groupings and, insofar as implications for disposition within the genus are concerned, these have been synthesised in the classification of Chamberlain et al. (1996). Subsequently, molecular characters obtained by sequencing nuclear and plastid DNA, have made it possible to infer evolutionary relationships within and between the relevant taxa (whether they be species, genera or families). There is little doubt that biological classification has benefited from these investigations. Infrageneric relationships of *Rhododendron* have been the subject of several studies based upon plastid DNA sequence data (Kurashige et al. 1998, 2001). A phylogeny derived from analysis of sequences from the nuclear *RPB2-I* gene (Goetsch et al. 2005) was based on species from all higher-level infrageneric groups of *Rhododendron*. The Goetsch et al. (2005) study is the most comprehensive molecular study of the genus published to date and its results supported the classification of Sleumer (1949) over that of Chamberlain et al. (1996). The classification of the genus proposed by Goetsch et al. (2005) is followed here.

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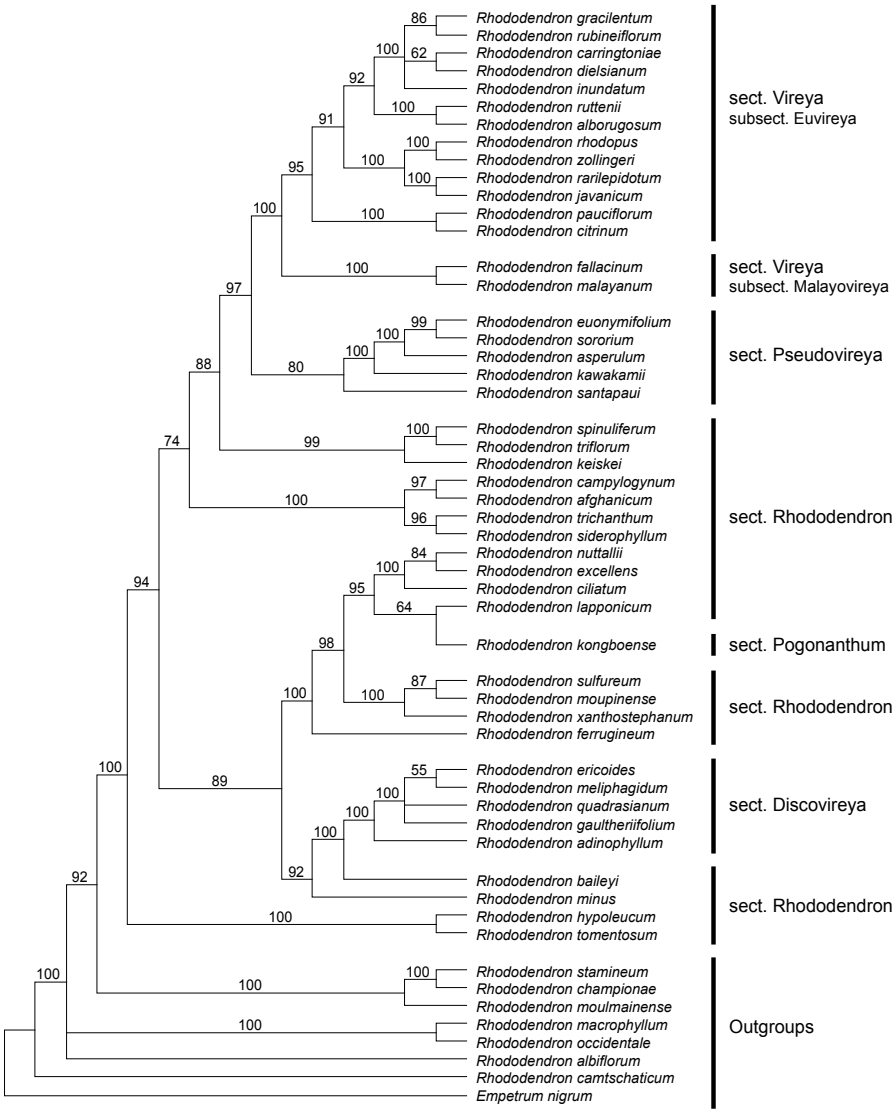

Fig. 1. Maximum parsimony strict consensus tree for *Rhododendron* subg. *Rhododendron* based upon *RPB2-i* sequences. All bootstrap values > 50% are shown. Based on Hall et al. (2006).

The largest section of *Rhododendron* is sect. *Vireya* (Blume) H.F.Copel., as defined by Sleumer (1966). Section *Vireya* contains about 300 species and is divided into seven subsections (Sleumer 1966). The Malesian representatives are divided amongst all seven subsections, while the non-Malesian species of *Vireya* are restricted to only three subsections: subsect. *Euvireya* H.F.Copel., subsect. *Malayovireya* Sleumer and subsect. *Pseudovireya* (C.B.Clarke) Sleumer. Argent (2006) published a new classification of

Vireya sensu Sleumer that raised sect. *Vireya* to subgeneric rank with seven included sections. Within one of these, sect. *Euvireya*, five subsections were recognised. Four of Argent's sections are as circumscribed by Sleumer (1966, as subsections), two comprise species that Sleumer had allocated to subsect. *Pseudovireya*, and one is based on the merger of Sleumer's subsect. *Euvireya* and subsect. *Solenovireya* H.F.Copel. The classification of Argent (2006) is not congruent with that suggested by phylogenetic analyses based on DNA data. Data generated from two cpDNA intergenic spacer regions, *psb*A-*trn*H and *trn*T-*trn*L, indicated that subsect. *Pseudovireya* was paraphyletic, *Malayovireya* and *Siphonovireya* Sleumer were monophyletic, and that the remaining polyphyletic subsections, *Albovireya* Sleumer, *Euvireya*, *Phaeovireya* Sleumer and *Solenovireya*, formed a major clade (Brown et al. 2006a). Similar results were found in the phylogenetic study based on sequences of the ITS region of nuclear ribosomal DNA (Brown et al. 2006b).

Section *Vireya* sensu Sleumer (1966) was identified as polyphyletic based on data from the nuclear gene *RPB2-i* (Hall et al. 2006); this study included greater taxonomic diversity within subg. *Rhododendron* than the previous molecular phylogenetic studies by Brown et al. (2006a, b). Results of Hall et al. (2006) are summarised in Fig. 1 (details of voucher specimens are provided or referenced in Appendix 1). The clade of Asian mainland species of subsect. *Pseudovireya* was sister to a strongly supported clade of the other six subsections of section *Vireya*. The Malesian species of *Pseudovireya* were monophyletic and formed a clade with the North American *R. minus* Michx. and the Asian *R. baileyi* Balf.f. (both species of sect. *Rhododendron*). This clade is sister to an assemblage containing sect. *Pogonanthum* G.Don and representatives of most major subsections of sect. *Rhododendron*.

The results of Hall et al. (2006) have implications for the classification of vireyas, indicating that there are three groups of *Vireya* that should be recognised as separate taxa of equal rank, i.e., the Asian species of *Pseudovireya*, the Malesian species of *Pseudovireya*, and the core vireyas (the remaining six subsections sensu Sleumer). Further research using another nuclear gene (RPC1) confirms the resolution of *Discovireya* and the mainland *Pseudovireya* species into separate clades (Goetsch & Hall unpubl.). The classification proposed by Argent (2006) is rejected because it is artificial (as acknowledged by Argent) and formal classification should always be based upon evolutionary relationships, as far as these are known. Furthermore, it results in an unbalanced classification, as molecular studies clearly show the vireya group is polyphyletic and embedded within subg. *Rhododendron* and therefore cannot be a sister taxon to it as depicted in Argent (2006: 4).

The classification presented below is based on the results of Hall et al. (2006) plus Goetsch & Hall's unpublished data. Relationships within sect. *Rhododendron* are complex and are the subject of ongoing research, hence this section is treated below in its traditional sense following Sleumer (1949) and Chamberlain et al. (1996). The relative positions of the three vireya groups are clear. We agree with Argent's views (Argent 2006) that a practical method is required for dealing with the large number of species involved; there are nearly 300 species within sect. *Vireya* as it is defined here. The most satisfactory way of achieving this end is to treat the relevant subsections sensu Sleumer (1966) as informal groups, thus facilitating identification but not compromising the tenet that formal classification should be based on evolutionary

Table 1. Comparison of the classification by Sleumer (1966) and Argent (2006) of *Rhododendron* sect. *Vireya* (sensu Sleumer 1966) with that of Craven et al. (this paper).

Sleumer 1966	Argent 2006	Craven et al. (this paper)
sect. *Vireya*	subg. *Vireya*	
subsect. *Albovireya*	sect. *Albovireya*	sect. *Vireya* subsect. *Euvireya*
subsect. *Euvireya*	sect. *Vireya* (as *Euvireya*)	sect. *Vireya* subsect. *Euvireya*
subsect. *Malayovireya*	sect. *Malayovireya*	sect. *Vireya* subsect. *Malayovireya*
subsect. *Phaeovireya*	sect. *Phaeovireya*	sect. *Vireya* subsect. *Euvireya*
subsect. *Pseudovireya*[1]	sect. *Discovireya*	sect. *Discovireya*
	sect. *Pseudovireya*	sect. *Pseudovireya*
subsect. *Siphonovireya*	sect. *Siphonovireya*	sect. *Vireya* subsect. *Euvireya*
subsect. *Solenovireya*	sect. *Vireya* (as *Euvireya*) subsect. *Solenovireya*	sect. *Vireya* subsect. *Euvireya*

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.

relationships. Unpublished data of Goetsch & Hall show that subsect. *Malayovireya* is sister to the remainder of the core vireyas and within sect. *Vireya* we have recognised two subsections, i.e., *Euvireya* and *Malayovireya*. Molecular evidence presently does not support taxonomic recognition of the other subsections and series (sensu Sleumer 1966) of the core vireyas, other than *Malayovireya*. It would appear that the core vireya complex is comprised of a large group of actively evolving (including radiating and interbreeding) species, of which the speciose and morphologically ultradiverse New Guinea clade is a notable example. The classifications of Sleumer (1966) and Argent (2006) are compared in Table 1 with that presented below. To facilitate identification of specimens of subg. *Rhododendron* and of informal groups within subsect. *Euvireya*, keys are provided below the classification.

RHODODENDRON

Rhododendron L.

subg. **Rhododendron**

sect. **Rhododendron**

sect. **Pogonanthum** G.Don

sect. **Vireya** (Blume) H.F.Copel. (1929) 136, 151. — *Vireya* Blume (1826) 854. — subg. *Vireya* (Blume) C.B.Clarke (1882) 462. — Type: *Rhododendron javanicum* (Blume) Benn. (*Vireya javanica* Blume).

subsect. **Euvireya** H.F.Copel. (1929) 137, 159. — ser. *Javanica* Sleumer (1960) 176. — Type: *Rhododendron javanicum* (Blume) Benn. (*Vireya javanica* Blume).

sect. *Linnaeopsis* Schltr. (1917) 144. — subsect. *Linnaeopsis* (Schltr.) Sleumer (1949) 541. — Type: *Rhododendron linnaeoides* Schltr.

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

subsect. *Malesia* H.F.Copel. (1929) 136, 151. — Type: *Rhododendron bagobonum* H.F.Copel.
subsect. *Phaeovireya* Sleumer (1949) 539. — sect. *Phaeovireya* (Sleumer) Argent (2006) 21. — Type: *Rhododendron beyerinckianum* Koord.
subsect. *Siphonovireya* Sleumer (1960) 68. — sect. *Siphonovireya* (Sleumer) Argent (2006) 21. — Type: *Rhododendron habbemae* Koord.
subsect. *Albovireya* Sleumer (1960) 107. — sect. *Albovireya* (Sleumer) Argent (2006) 22. — Type: *Rhododendron album* Blume.
ser. *Linnaeoidea* Sleumer (1960) 134. — Type: *Rhododendron anagalliflorum* Wernham.
ser. *Saxifragoidea* Sleumer (1960) 141. — subsect. *Saxifragoidea* (Sleumer) Argent (2006) 22. — Type: *Rhododendron saxifragoides* J.J.Sm.
ser. *Taxifolia* Sleumer (1960) 141. — Type: *Rhododendron taxifolium* Merr.
ser. *Stenophylla* Sleumer (1960) 141. — Type: *Rhododendron stenophyllum* Hook.f.
ser. *Citrina* Sleumer (1960) 144. — Type: *Rhododendron citrinum* (Hassk.) Hassk.
ser. *Buxifolia* Sleumer (1960) 145. — Type: *Rhododendron buxifolium* Low ex Hook.f.

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

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

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

subg. **Hymenanthes** K.Koch

subg. **Choniastrum** (Franch.) Drude

subg. **Azaleastrum** Planch.

subg. **Therorhodion** (Maxim.) Drude

Notes — 1. The name *Rhododendron* ser. *Vaccinioides* Hutch. (Hutchinson 1930: 817) has not previously been lectotypified as far as we are aware. It is here typified with *R. vaccinioides* Hook.f., the first described species of its group.

2. Argent (2006) cited Sleumer as the combining author for the name *Rhododendron* sect. *Pseudovireya* and as the author for the name *Rhododendron* sect *Albovireya*, giving as the references for these names Sleumer (1949: 537) and Sleumer (1960: 107), respectively. In his 1949 publication, Sleumer treats *Pseudovireya* at the rank of subsection and, in his 1960 publication, he treats *Albovireya* also at subsectional rank. We have seen no evidence that Sleumer believed the two taxa should be treated at the rank of section. Argent, whether or not inadvertently, has made the new

combinations because in accordance with Art. 46.4 of the International Code of Botanical Nomenclature (Greuter et al. 2000) the names are to be attributed to him, as given in the classification above.

3. Characteristic features, noting that exceptions may sometimes occur in individual species, that serve to differentiate between the five sections of subg. *Rhododendron* and the two subsections of sect. *Vireya* are as follows:

sect. *Rhododendron* — Scales entire to crenulate; corolla campanulate to funnel-shaped or tubular; stamens 10, exserted, staminal filaments hairy towards the base or glabrous; capsule valves not twisting after dehiscence; seeds without distinct tails.

sect. *Pogonanthum* — Scales incised; corolla salver-shaped; stamens 5–8, included, staminal filaments glabrous or hairy towards the base; capsule valves not twisting after dehiscence; seeds without distinct tails.

sect. *Vireya* — Scales sessile or sometimes stalked, lobed to deeply incised or sometimes entire; corolla campanulate, trumpet-like, salver-shaped, tubular or funnel-shaped; stamens (5–)10(–16), exserted to included, staminal filaments glabrous or hairy from the base; capsule valves twisting after dehiscence; seeds with a distinct tail at each end.

subsect. *Euvireya* — Scales sessile or stalked, scattered or dense, not of two obviously different size classes, lobed to deeply incised (or sometimes entire) and the centre not dark-coloured.

subsect. *Malayovireya* — Scales sessile, dense, of two obviously different size classes, lobed and the centre dark-coloured.

sect. *Pseudovireya* — Scales entire; corolla campanulate; stamens 10, exserted, staminal filaments glabrous proximally and distally and hairy in the middle region; capsule valves not twisting after dehiscence; seeds with a distinct tail at each end.

sect. *Discovireya* — Scales entire to undulate; corolla tubular-cylindric; stamens 10, exserted to included, staminal filaments glabrous or hairy from the base; capsule valves not twisting after dehiscence; seeds with a distinct tail at each end.

4. *Rhododendron* subsect. *Euvireya* contains species 26–74 and 89–276 of Sleumer (1966), species 37–89 and 103–313 of Argent (2006), and the recently described *R. dutartrei* Danet and *R. kogo* Danet (Danet 2007). Subsection *Malayovireya* contains species 75–88 of Sleumer (1966) and species 90–102 of Argent (2006). Section *Pseudovireya* contains species 1–11 of Argent (2006). Section *Discovireya* contains species 1–25 of Sleumer (1966) and 12–36 of Argent (2006).

KEY TO THE SECTIONS AND SUBSECTIONS OF SUBGENUS RHODODENDRON

1a. Seeds without distinct tails 2
b. Seeds with distinct tails 3
2a. Corolla campanulate to funnel-shaped or tubular; scales entire to crenulate . . . . . sect. **Rhododendron**
b. Corolla salver-shaped; scales incised . . . . . sect. **Pogonanthum**

3a. Capsule valves twisting after dehiscence; scales variously incised or rarely entire 4
b. Capsule valves not twisting after dehiscence; scales entire to undulate 5
4a. Scales sessile, dense, of two obviously different size classes, lobed, centre dark-coloured . . . . . sect. **Vireya** subsect. **Malayovireya**
b. Scales sessile or stalked, scattered or dense, not of two obviously different size classes, lobed to deeply incised (or sometimes entire), centre not dark-coloured . . . . . sect. **Vireya** subsect. **Euvireya**
5a. Corolla campanulate; staminal filaments glabrous proximally and distally and hairy in the middle region . . . . . sect. **Pseudovireya**
b. Corolla tubular-cylindric; staminal filaments glabrous or hairy from the base . . . . . sect. **Discovireya**

KEY TO THE INFORMAL GROUPS OF SUBSECTION EUVIREYA

1a. Scales entire . . . . . subsect. **Euvireya 'Siphonovireya'**
b. Scales lobed to deeply incised 2
2a. Scales deeply incised, stalked, each inserted on a distinct and permanent tubercle . . . . . subsect. **Euvireya 'Phaeovireya'**
b. Scales shallowly or deeply incised, sessile or rarely stalked, rarely inserted on an apparently non-permanent tubercle 3
3a. Scales dense, usually overlapping . . . . . subsect. **Euvireya 'Albovireya'**
b. Scales scattered, not overlapping 4
4a. Corolla trumpet-like or salver-shaped, tube narrow, lobes equalling 1/4 or less of the total corolla length and spreading ± at right angles to the tube . . . . . subsect. **Euvireya 'Solenovireya'**
b. Corolla campanulate or tubular or funnel-shaped, tube usually relatively broad, lobes equalling 1/4 or more of the total corolla length and erect to spreading-ascending or rarely ± at right angles to the tube . . . . . subsect. **Euvireya 'Euvireya'**

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APPENDIX 1

Voucher details for the majority of species included in Fig. 1 are given in Goetsch et al. (2005). Details for the other species are: *R. kawakamii*, *Goetsch 93*; *R. gracilentum*, *Goetsch 104*; *R. carringtoniae*, *Goetsch 105*; *R. javanicum*, *Goetsch 106*; *R. pauciflorum*, *Goetsch 107*; *R. euonymifolium*, *Goetsch 108* (all WTU); *R. rubineiflorum*, *Craven & Brown 10373*; *R. inundatum*, *Craven 10481*; *R. ruttenii*, *Craven 10436*; *R. alborugosum*, *Craven 10634*; *R. rhodopus*, *Brown, Craven, Juswara & Ramadanil 129*; *R. zollingeri*, *Brown, Craven, Juswara & Ramadanil 125*; *R. rarilepidotum*, *Craven 10636*; *R. fallacinum*, *Craven 10635*; *R. malayanum*, *Craven & Brown 10371*; *R. ericoides*, *Craven & Brown 10362*; *R. quadrasianum*, *Craven & Brown 10379*; *R. citrinum*, *Binney s.n.*; *R. meliphagidum*, *Binney s.n.*; *R. adinophyllum*, *Binney s.n.* (all CANB).