Vireya Rhododendrons in Borneo

by G. C. G. Argent

Abstract. Results are presented of several recent collecting expeditions to Sarawak and Sabah with field observations of hybrids, possible pollination strategies of the species and habitat preferences. Some re-assessment is made of the subsectional taxonomic groupings with implications for the section Vireya as a whole.

INTRODUCTION

Borneo, with about 46 Rhododendron species, is much less rich than New Guinea which has about 167. Nevertheless Borneo contains the second largest number of species of any island with about one sixth of the 300 or so Vireya Rhododendron species known. This situation maybe explained in broad terms by two somewhat opposing factors: firstly Borneo is relatively accessible to the south-east Asian mainland where rhododendrons have their centre of origin and which has meant a fairly broad genetic input in the geological past; but secondly the island has fewer, relatively old and predominantly declining mountains. Thus the land form in Borneo of green peaks contrasts with the jagged bare rocks of New Guinea with its tectonic instability and rapid mountain building. Mt. Kinabalu is of course the exception which 'proves the rule' for Borneo, having arisen very rapidly as a 'young giant' of not much more than 1 million years and which carries a quite disproportionate number of the Bornean rhododendrons with about half the total known species occurring on its slopes.

The first observations on Bornean rhododendrons referred to in this paper came from a visit by the author to the Gunong Mulu National Park as a guest of the Sarawak Forestry Department on the Royal Geographical Society's 'Mulu' expedition. It was only on working up this material that several taxonomic problems presented themselves and on a return visit more careful collections and observations were made. A marvellous opportunity to follow up this initial study came with an invitation from the Sabah National Parks

Department to produce a handbook of the rhododendrons of Kinabalu which was subsequently expanded to an account of the rhododendrons of Sabah (Argent et al,. 1988). This was backed with very generous field assistance to gather specimens and observations on several short visits which combined well with the excellent facilities provided by the Royal Botanic Garden in Edinburgh to grow many of the species collected successfully as living plants. This has enabled the study of several aspects of these plants which were not obvious to casual observation in the wild. Some taxonomic problems have been solved by this study but probably as many new ones have arisen.

TAXONOMIC PROBLEMS

Of the first group of species that have been very problematic are those closely related to R. javanicum (Bl.) Benn., particularly R. brookeanum Low ex Lind., R. moultonii Ridley, R. retivenium Sleumer and R. lowii Hook. f. According to Sleumer (1966) R. javanicum does not occur in Borneo although the distribution (Peninsula Malaysia, Sumatra, Java, Bali, Sulawesi and Philippines) encircles the island. A number of characters are used to separate R. javanicum from R. brookeanum, including presence or absence of simple hairs on the ovary, leaf shape and flower size, but none are clear cut. Flower size is a very difficult character to deal with in the herbarium because corolla tissue shrinks and the dimensions of the dried flowers to a large extent reflect the degree of pressure to which the flowers have been submitted in the drying process. Leaf shape is highly variable and the dimensions of Bornean collections of this group of species undoubtedly covers most of the range of size found in R. javanicum. Presence or absence of simple hairs on the ovary breaks down, with hairs occurring in R. javanicum var. teysmannii (Miq.) K. & G., whilst populations showing variation in this indumentum character have been discovered in at least two places in Borneo. In fact R. moultonii only differs from R. brookeanum on the basis of glabrous ovary and for this reason has been reduced to subspecific status (Argent, 1982). Other variable characters in the Bornean populations of R. javanicum (sensu Argent, 1982) are the degree of overlap of the corolla lobes, the leaf shape, leaf venation, ovary shape and flower colour, which all show quite remarkable variations that

are often correlated in local populations but which do not correlate well over the whole of Borneo. Thus the distinctive form of R. brookeanum subsp. moultonii (Ridley) Argent from G. Api in Sarawak has short sulcate leaves and elegantly quilted and overlapping corolla lobes but a plant from Kalimantan exhibits the same flower shape but totally different leaf form. Given that the ecology of this group of species is mainly lowland, there are therefore potential intermediates in the forests between the different sites of collection and for this reason a much broader view of the taxonomic units has been taken, at least for the time being, than for the montane species which are much more absolutely isolated because of the island nature of the high ground to which they are restricted. This is not a totally satisfactory resolution of the problem but until more information is obtained on many of the populations it at least gives a practical interim solution.

Of the last two species in this problematic group, R. lowii is almost totally isolated because of its montane ecology but R. retivenium depended on ovary indumentum and its scented flowers for the maintenance of a separate identity. Ovary indumentum in this group, for the reasons stated above, was already slightly questionable, whilst the presence of scent could not be accepted as a sufficiently good character, even in the living state, let alone the herbarium. This was an instance where cultivation of the plants provided a new character which has proved very reliable and has redefined R. retivenium as a distinct and highly maintainable species. This character is the expansion of the new leaves in a revolute manner unlike all the other related species which have leaves which expand with straight or upturned edges. This is not pyxis (the folding of the leaves in the bud) but the aspect of the very young expanding leaves. It correlates well with ecology, general aspect and, to a very large extent, with the scented flowers, and is very easy to see in cultivated material at the right stage of growth. It will always distinguish this species even in the herbarium although it does have the limitation of not working for herbarium specimens with only mature leaves present. R. longiflorum Lindley is another widespread species occurring in several colours and at least two corolla forms which may represent incipient evolution

favouring different pollinators. R. commutatum Sleumer and R. subcordatum Becc. have been reduced to synonymy with this species (Argent, 1982) and in Borneo the species is now easily identified, although there is some evidence of hybridization between R. longiflorum and R. brookeanum in Sarawak which needs more investigation. Whilst dealing with R. longiflorum it is perhaps best to mention R. praetervisum Sleumer and R. subcordatum Becc. have been reduced to synonymy with this christened by Professor Sleumer when he described the species (Sleumer, 1973). Sleumer discovered indumentum characters in the pistil which in the herbarium neatly separated this species from R. longiflorum under whose name specimens had for long resided. What was surprising when these species were studied in the field, was that they had ever been confused. They grow in different altitudinal zones; they have different flower colours and whereas R. longiflorum holds its flowers erect, R. praetervisum displays vertically hanging flowers. However, in the herbarium ecological notes were too imprecise to be of use, flower colour was lost and rarely accurately reported, and quite amazingly the posture of the flowers was often lost. Specimens of R. longiflorum were obviously pressed after having been so badly wilted that the flowers hung down or occasionally R. praetervisum had been slapped down on a sheet so that the flowers apparently stood erect. Those who have collected in the wild however, will sympathize with collections which are sometimes less than perfect but one must salute Professor Sleumer's beautifully critical detective work, which enabled him to separate these species from herbarium material alone.

Another group of species which has raised interesting problems is R. nervulosum Sleumer, R. stenophyllum Hook. f. ex Stapf and R. exuberans (Sleumer) Argent. R. nervulosum was considered to be a rare species described from Marai Parai on Kinabalu. Specimens agreeing with the original description were first collected from the Mesilau Cave area of Kinabalu and have been grown at the RBG Edinburgh. Subsequent isolated collections with similar leaf morphology but rather widely varying flowers were collected from other locations in 1980 and 1981; in all these cases R. stenophyllum and R. crassifolium Stapf were growing in abundance close by and it looked very

much as if R. nervulosum was a hybrid between these two species. Early in 1982, however, R. nervulosum was collected and studied in G. Lotong in southern Sabah. Here this 'species' was to be found in some numbers as a population rather than isolated individuals; there was plenty of R. crassifolium present but no R. stenophyllum was seen or has been recorded from this mountain. This posed a problem: whereas all the signs elsewhere were clearly that R. nervulosum was a hybrid, on G. Lotong the population was behaving much more like a species and to maintain the theory of hybrid origin one must speculate that either R. stenophyllum occurs on part of G. Lotong close by the sites examined but remains as yet undetected, or that it once existed but has been hybridized out of existence and leaves only the population of R. x nervulosum in evidence. Further field work on G. Lotong and the artificial crossing of R. crassifolium with R. stenophyllum remains to be done to solve this enigma. R. exuberans also intrudes into the problem of R. nervulosum, and was formerly described as a variety of this species (Sleumer, 1963). R. exuberans occurs on a number of mountains, but is never very common. It has almost identical flowers to those of R. stenophyllum and must hybridize with it if it occurs in close proximity. The problem would then be to separate these hybrids from 'typical' R. nervulosum. R. stenophyllum appears to rather easily hybridize with several species and always seems to strongly imprint its progeny with its distinctive narrow leaves.

The final group of problem species that I wish to deal with are in subsect. Malayovireya Sleumer. In this group great variability is encountered on the broad scale, while local populations of the species are very uniform. R. malayanum Jack itself is the most widespread and probably the most difficult species taxonomically. It is distributed from Thailand down through Peninsula Malaysia to Sumatra, Java, Borneo and on to Sulawesi and Seram. Sleumer (1966) recognizes seven subspecific taxa but variation seems to be reticulate, making neat hierarchical classification impossible. R. micromalayanum Sleumer should perhaps be a microspecies rather than a full species. It is a small-leaved, montane form of R. malayanum that occurs in a rather restricted area of three adjacent mountains in Borneo. R. malayanum itself can look

very similar to R. micromalayanum in the western end of its range where it is montane (but has rather different inflorescences) but looks strikingly different in its lowland kerangas (heath forest) form which has enormous leaves.

Further careful work may enable R. malayanum to be split into several more species although any tendency to broaden its concept by 'a lumper' would be in danger of swallowing up many, if not most of the other Malayovireya species.

HYBRIDS

Several references have been made to hybrids and hybridization in the wild and some general observations on this phenomenon can be made. We know from numerous artificial hybridization experiments that any Vireya rhododendron appears capable of crossing with any other species within the group at least within the proximity of an area like Borneo. Hybrids are very difficult to detect in the herbarium but in the wild they can be, and generally are, very obvious to the careful observer. The parents usually grow in the immediate vicinity and the hybrid plant is generally clearly intermediate in morphology between that of its parents. Hybrids are in fact quite common in Borneo but they usually occur as just occasional plants in large populations, appear to be transient, and do not usually backcross to give hybrid swarms.

Presumably there are selective mechanisms operating against such hybrids which maintain relative purity of the species. Notable exceptions to this in Borneo are the case of R. x nervulosum on G. Lotong already referred to, and the much clearer hybrid swarms to be found on Kinabalu, most notably between R. buxifolium Low ex Hook. f. and R. rugosum Low ex Hook. f. (x coriifolium Sleumer) and R. abietifolium Sleumer and R. buxifolium (x sheilae Sleumer). In these last two cases populations of intermediates exist in substantial numbers with great variation indicating backcrossing probably to both parents. It is interesting that Kinabalu, as has already been mentioned, is the exceptional Bornean mountain in that it is actively growing - it is also by far the highest peak. The vegetation in the upper montane zones is still in a

process of colonization and stabilization due to the recent disappearance of an ice cap and the large bare areas of the granite dome appear to favour the establishment of hybrids in the same way that artificially disturbed areas do. It appears that these high altitude species are still in a state of flux with a high potential for producing new species to fill the vacuum of a largely open environment.

POLLINATION SYNDROMES

Pollination syndromes or the general associations between flower types and specific groups of pollinators is something which we have few observations on in the case of Bornean rhododendrons. Parallels can be found for most of the types which have been described by Stevens (1976) or van Royen & Kores (1982) for New Guinea, although absent are bat-types with thick, fleshy corollas, increased numbers of parts and strong scent. Since Stevens' (1976) paper perhaps the most notable discovery is that of R. yongii Argent with handsome dark red flowers which have the anthers dorsally arranged in the mouth of the flower. All other red flowered Bornean species have them either grouped ventrally or regularly disposed around the tube. R. buxifolium, another red flowered species, is also of interest. Apart from being one of Kinabalu's most handsome rhododendrons, it does not neatly fall into the standard pollination categories. Although bright red (bird colour), it has a medium corolla tube with broad, spreading corolla lobes which provide a good insect landing-platform. Furthermore, it is scented with a strong sweet smell and produces copious nectar. Its flowers are frequently visited by birds, especially by the mountain blackeye (Chlorocharis emiliae Sharpe), but they have no sense of smell and cannot therefore be attracted by the scent. It is tempting to speculate that insects are attracted by the scent and nectar, find shelter in the corolla from what can be an unpleasant climate, and the flowers are then sought by birds, not primarily for the nectar but for the sheltering insects. This may seem a complicated explanation but it would account for flowers apparently attracting two quite different groups of animals. Moths probably pollinate the long, white, tubular flowered species such as R. stapfianum Hemsley ex Prain and R. suaveolens Sleumer but there are no

direct observations to confirm this for Borneo. Several observations of butterflies visiting rhododendrons have been made in Sabah: the insects particularly favouring those having bright red or orange flowers with prominent anthers, such as R. crassifolium, R. polyanthemum Sleumer and R. fallacinum Sleumer. As in New Guinea, yellow flower colour is common in the lowland species such as R. brookeanum and R. nieuwenhuisii J. J. Smith which are both probably visited by insects. Self pollination would appear to be rare, although we have no direct evidence for this.

TAXONOMIC GROUPING WITHIN SECTION VIREYA COPELAND f.

The subsectional groupings of Bornean rhododendrons as found in Sleumer's account (1966) are by no means natural. Woods (1978) drew attention to the anomaly of putting R. stenophyllum with three totally unrelated New Guinea species. The divisions of subsect. Vireya (Euvireya) into ser. Buxifolia Sleumer and ser. Javanica Sleumer purely on the size of the leaves is no more than an arbitrary division and the use of flower shape at subsectional level is also questionable given the strong selective pressure which may be exerted on this character making it insufficiently conservative.

In regrouping the Bornean rhododendrons it must be stressed that it is a provisional arrangement which is perhaps no real advance on that of Sleumer (1966) particularly as very little cognizance is taken of relationships outside the island. Subsect. Solenovireya Copel. F., based on salver-shaped (hypocrateriform) corollas, has been abandoned so that all the subsections could be uniformly defined without using corolla shape. The epidermal scales (multicellular hairs) have been given due prominence and studies with the scanning electron microscope have given new information on many of the species. The divisions into scale type has broadly followed Sleumer's (1966) analysis into four main groups but the new grouping, ser. Dendrolepidon Argent, Lamb & Phillipps (Argent et al., 1984), is proposed for species with dendroid or stellate hairs similar to those of subsect. Phaeovireya Sleumer of New Guinea except that they do not sit on epidermal tubercles as in that subsection. Further work is needed to establish the relationship between

species in Dendrolepidon and Phaeovireya. The species of subsect. Solenovireya Copel. f. have been distributed according to scale type between subsects Vireya and Dendrolepidon.

While observing a large number of the Bornean species over several years in cultivation, new characters have been constantly sought that might help with grouping the species in a more natural fashion. Two characters have been observed which are thought to be particularly useful. The first is whether the floral bud scales (perulae or sterile bracts) are fringed with minute simple hairs or not. Of the Bornean species examined, all those in Sleumer's subsections Malayovireya and Pseudovireya (Clarke) Sleumer have a fringe of hairs whilst all those in subsections Vireya and Solenovireya except for R. buxifolium do not (although they are often fringed with 'scales'). Correlated with this character is the general development, or lack of development, of vegetative buds and bud scales. These are well developed in Vireya which generally exhibits prominent resting buds with sheathing bud scales, whilst in Malayovireya and Pseudovireya bud scales are virtually absent, the young shoots developing in a naked manner (which is not rare amongst tropical plants) or at most having subulate cataphylls at the base of developing shoots.

Thus for the Bornean species two major groupings are proposed, each of which is again subdivided into two.

Section	Subsection	Series
		Vireya
	Vireya	Dendrolepidon
Vireya		
	Pseudovireya	Pseudovireya
		Malayovireya

Even close examination of the structure of the epidermal scales supports this division, as in series Vireya and Dendrolepidon. The scales have small point-like centres with broad peripheral flanges and it is really a matter of degree

whether these flanges are lobed as in ser. Vireya or dendroid / stellate as in ser. Dendrolepidon. In series Pseudovireya and Malayovireya the individual scales in both cases have a broad central cushion and again differ as to the degree of development of the marginal flange - this being narrow in Pseudovireya and broad in Malayovireya. The actual difference in development of the numbers of scales between these last two groups exaggerates the difference between them but there is nevertheless an underlying similarity of structure in the scales. What relevance these groupings have outside Borneo has not yet been studied and even for Borneo they remain tentative. The species showing greatest potential to upset the neatness of this scheme is R. buxifolium. It is placed by Sleumer (1966) in subsect. Euvireya (Vireya) where it superficially appears at home with its large flowers with broad corolla lobes. Examination of the floral bud scales shows them to be partly (but not fully) fringed with simple hairs and to have the unusual feature (at least for Bornean rhododendrons) of having the abaxial face partially covered in short simple hairs. Close examination of the scales shows clearly that although very small, they have large central cushions. For these two reasons this species has been transferred to ser. Pseudovireya where it resides rather unhappily with the small flowered species of that section. It is hoped chemical taxonomy may shed more light on the various groupings within Vireya in the future and, together with further morphological observations on more species, a both workable and reasonably natural classification can be achieved.

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