A HISTORY OF RHODODENDRON CLASSIFICATION

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ABSTRACT. An account is given of the history of, and the development of ideas in the classification of *Rhododendron* from the time of Linnaeus to the present day.

INTRODUCTION

When Linnaeus published his Species Plantarum in 1753 he included nine shrubs that would now be placed in *Rhododendron*, though he treated five of them as members of *Azalea*. Two other species—now known as *Loiseleuria procumbens* and *Rhodothamnus chamaecistus*—were also included. Linnaeus, therefore, divided nine species of *Rhododendron* between two genera. Today, the eight or nine hundred species are placed in one genus, but are dispersed among about ninety-three groups arranged in a whole hierarchy of categories—sub-genera, sections, sub-sections, series and sub-series. No history has been written of the development during the two hundred years from the simple beginnings of Linnaeus to the present elaborate classification, though several authors touch on it. Zabel (1902), for example, gives a brief summary of the early history; Rehder & Wilson (1921) contribute a more complete history though confined to the azaleas; and Sleumer (1949) presents much concise information. The present account does not seek to record all the details of the tortuous history, which are mainly concerned with the appropriateness of rival names. Here we shall be concerned only with the origin of new ideas which have proved significant in the development of our understanding of the genus. These original ideas have been rather few, and to emphasize them the history is divided into periods, each ending with some major advance.

I. LINNAEUS TO G. DON, 1753–1834

Since the publication of the Species Plantarum by Linnaeus in 1753 is officially recognized as the basis of botanical nomenclature, it forms a convenient beginning for our history. Of course, the alpine rose had been known to European botanists long before, and other species as they became known had been recognized as close relatives. A brief sketch of the earlier history of *Rhododendron* is given by Cowan (1950). Linnaeus presented the species known to him under the two generic headings *Rhododendron* and *Azalea*. This subdivision, which was based on the number of stamens (10 and 5 respectively), has persisted until the present day although the characters used to define the two groups have been revised and the groups have rarely been treated as distinct genera since Salisbury (1805–08) pointed out good reasons for uniting them.

Azalea, as it first appeared, comprised six species. Four of these truly belonged to the azalea group, as we now understand it: one (*Azalea*

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lapponicum) would have been more correctly placed in *Rhododendron*; while the sixth plant is now known as *Loiseleuria procumbens*—the alpine azalea of Scotland and the Continent. There is no longer any doubt that *Loiseleuria* should be excluded, but there are some grounds for the opinion that the *name* Azalea should remain attached to this plant since it was probably the first to bear it. In that event another name is needed for "Azalea". Adanson (1763), therefore, revived Kaempfer's pre-Linnaean name *Tsutsusi* in place of *Azalea* (which he reserved for *Loiseleuria*) and Reichenbach (1827) proposed a new generic name, *Anthodendron*, for the same purpose. However, this is a problem of nomenclature rather than classification, and it is one that need not detain us while the azaleas are retained within *Rhododendron*.

Linnaeus selected *Rhododendron* from a confusion of many previous names such as *Chamaerhododendros* of Tournefort. Five species were listed in the Species Plantarum: 1, *ferrugineum*; 2, *dauricum*; 3, *hirsutum*; 4, *chamaecistus* (now forming *Rhodothamnus*); 5, *maximum*.

For eighty years after Linnaeus the classification of rhododendrons made little progress. Several new species arrived in Europe during this period and botanists were often puzzled by their overall resemblance to *Rhododendron*, combined with peculiarities which did not fit with their idea of the genus. It was unfortunate that the genus was first known from peripheral areas where several aberrant species occur. It was much later that the heart of the genus, in the Himalayas and Western China, became known. Only then did it become possible for the relationships between the anomalous forms to be understood. With so many more species available now we can see how all these forms link together, but at that time the readiest solution to these puzzles was to create new genera to accommodate each peculiarity. In the second edition of his Species Plantarum Linnaeus (1762) created the genus *Rhodora* for a shrub of the north-eastern United States and Canada, its principal distinguishing feature being its two-lipped flower. Several species became known from the Malayan archipelago and these Blume (1826) placed in a new genus *Vireya*, with the rather slight characters of a small calyx and the stamens scarcely included within the corolla. At the same time Blume proposed another genus, *Hymenanthes*, (for the plant now known as *R. metternichii*), which he compared with *Befaria* rather than *Rhododendron*, although we know it to belong to the same series (*Ponticum*) as a species that had already been described by Linnaeus. The fact that its floral parts are arranged in whorls of seven was given great weight at a time when Linnaeus's largely numerical system was in vogue. The name *Hymenanthes* has proved of importance because it was the first generic name to be applied to a species that is neither lepidote nor an azalea. It therefore serves as a useful label for the non-lepidote Rhododendrons, which together form the largest and horticulturally most important part of the whole genus.* A chinese species, *R. farrerae*, was thought by Tate (1831) to provide a link between the azaleas and rhododendrons. He placed it with *R. dauricum* into a section which he named *Brachycalyx*. The existence of this supposed link stimulated him to suggest that the azaleas should be united with *Rhododendron*. He used Kaempfer's name *Tsutsusi* for the azalea section.

* Throughout this account the three major subdivisions of *Rhododendron* will be referred to as, 1) the azaleas (including *Pentanthera*, *Tsutsutsi* and *Azaleastrum*); 2) *Hymenanthes* or the elepidote rhododendrons; and 3) the lepidote species.

These piece-meal changes were coordinated and further developed when George Don wrote his General History of Dichlamydious Plants (1834). In view of the great part the Royal Botanic Garden at Edinburgh was to play in the later development of the genus, it is interesting to learn that George Don's father was Superintendent of the Garden. George Don the younger went south to take charge of the Chelsea Physic Garden, to undertake tropical collecting expeditions, and to publish many botanical articles and books. With the appearance of his "General History" the framework of a system for rhododendrons was established for the first time. His arrangement is summarized in table 1. One important advance was his formal union of the azaleas and rhododendrons, a step foreshadowed by Salisbury (1805–08) and Tate (1831). He failed to unite the poorly known Malayan vireyas and the misapprehended *Hymenanthes*.

A second important advance was his subdivision of the genus into sections, a process that affected the azaleas as well as the rhododendrons in the limited sense. His division of the azaleas (a term he does not use, reserving it for *Loiseleuria*) is clearly on a geographical basis, though this is not stated. He reserves the name *Tsutsutsi* (now so spelled) for Asiatic species, though the species he listed are now considered to be of many types (e.g. Subseries *Obtusum*, *Schlippenbachii*, and *Luteum*). He coined the name *Pentanther* for the North American azaleas, excepting *R. rhodora* (= *R. canadense*) which he left in a section of its own, Sect. *Rhodora*. The characters used to separate the two sections *Tsutsutsi* and *Pentanthera* are the small calyx and narrow flowers of the American species contrasted with the foliaceous calyx and campanulate flowers of the Asiatic.

Even more important is his attempt to subdivide the remainder of the genus. His Section *Lepipherum* clearly foreshadowed the all-important distinction between lepidote and non-lepidote species. While scales are mentioned in the definition, the group appears to be defined principally on the nature of the calyx, so that several lepidote species are in fact placed in his section *Ponticum* (which was much more widely conceived than the present *Ponticum* Series). Although he left the aberrant *R. dauricum* in the *Lepipherum* group, Don was astute enough to see that *R. anthopogon* merited a section of its own (*Pogonanthum*). The vireyas he continued to regard as a distinct genus. His attempt to subdivide the non-lepidote species into two sections, *Ponticum* and *Booram*, was mainly based on the number of cells in the ovary together with features of the calyx. Although this distinction was to influence ideas for a long time, it has not survived into present classifications. It is difficult to understand why he did not include *Hymenanthes* in his section *Booram*.

The section *Chamaecistus* included two very different plants, namely *Rhodothamnus* and *R. camtschaticum*.

In reviewing Don's system it is a remarkable fact that seven out of the eight sections he proposed are still regarded as valid groups, and in addition *Vireya* is still maintained, though as a Section.

II. Don to Maximovicz, 1834–1870

Very little progress was to be made until the revolutionary system of Maximovicz appeared twenty-six years later. Don's scheme served as a

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TABLE I

A COMPARISON OF THREE SYSTEMS

G. Don (1834) (genera)		Maximovicz (1870) (sections)	Sleumer (1949) (sub-genera)
Hymenanthes			
Rhododendron Sect.	Ponticum	Eurhododendron	Hymenanthes
	Booram		
	Chamaecistus	Therorhodion	Therorhodion (genus)
	Tsutsutsi	Tsusia	Tsutsutsi
	Pentanthera	Azalea	Pentanthera
	Rhodora		„ Sect. Rhodora
	Pogonanthum	Osmothamnus	Rhododendron Sect. Pogonanthum
	Lepipherum		„ Sect. Lepipherum
	—	Rhodorastrum	Rhodorastrum
	—		Pseudorhodorastrum
	—	—	Pseudazalea
	—	Keysia	—
Vireya	—	—	Rhododendron Sect. Vireya
	—	Azaleastrum	Azaleastrum

NOTE. The correspondence between the groups of different authors may be only approximate, as they may be defined by different characters (e.g. *Tsutsutsi* as employed by Sleumer includes part of *Azalea* as used by Maximovicz.)

basis for subsequent publications though his influence was less than it might have been since some of his ideas were rejected by De Candolle in the very influential *Prodromus* (1839). De Candolle retained Azalea as a separate genus to include the deciduous species of both the old and new worlds, while he treated the evergreen azaleas as section *Tsutsutsi* of *Rhododendron*. Inexplicably, he places one deciduous azalea (*R. farrerae*) in *Eurhododendron* and another, North American, species in the evergreen Asiatic *Tsutsutsi*. He re-united Don's *Ponticum* and *Lepipherum* sections and together with *Vireya* formed them into a large amorphous group—*Eurhododendron*. De Candolle retained *Hymenanthes* and *Rhodora* as genera and *Booram*, *Pogonanthum* and *Chamaecistus* as sections. He created another genus, *Osmothamnus*, to include species now regarded as members of *Pogonanthum*. It was therefore redundant. Reichenbach's listing (1840) follows De Candolle very closely, as does that of Heynhold (1846).

During this period, increasing numbers of rhododendrons were reaching Europe from the Himalayas, especially as a result of Hooker's expedition to Sikkim, and of Booth's to Bhutan and Assam. Hooker (1849) was aware of relationships among the Sikkim species, but the first attempt to subdivide the main body of the Himalayan species into named groups was made by Nuttall (1853) when reporting on Booth's collections. These were defined principally on the form of the calyx and the number of cells in the ovary, and while none of Nuttall's names has survived into modern use, it is clear that he was in some instances grouping truly related species. Two years later Nuttall was so impressed with the tubular flowers and pseudo-lateral inflorescences of *R. keysii* (he describes and figures them as over-topped by lateral shoots) that he proposed a sub-genus *Keysia* for this species and this continued to be recognised for some years by later authors. Similarly, Klotzsch (1862) considered the magnificent species, *R. argenteum* Hook. f., to be sufficiently distinctive to require a new genus which he named *Waldemaria* after Prince Waldemar whose collections from Bhutan he was naming.

At this time Planchon was interested in the Chinese azaleas. In an account published in 1854 he recognized sub-genera to include, 1) the deciduous azaleas of both the old and the new worlds (*Azalea*); 2) the evergreen "Indian" azaleas (*Tsutsusi*, in which he mistakenly included *R. molle*); and 3), a new group which he named *Azaleastrum*. This was the first recognition of one of the most important features of rhododendron classification, namely, that within the azaleas several atypical groups are to be found. It is unfortunate that he did not recognise the peculiarities of *R. championae*, which he placed in his *Tsutsusi* group, or he would have anticipated Franchet's *Choniastrum* by thirty years.

The classification of rhododendrons took its greatest step forward with the publication of Maximovicz's *Rhododendreae Asiae Orientalis* by the Imperial Academy of Sciences of St. Petersburg in 1870. As curator of the Herbarium of the St. Petersburg Botanic Garden, Maximovicz had made collecting expeditions through Siberia, Manchuria and Japan, so that he knew most of the species he was discussing at first hand in the field.

The most important contribution made by Maximovicz was his use of the position of the flower-buds and their relationship with leaf-buds ("innovations") to define the major sub-divisions of the genus. He realized that the great majority of the species were characterized by terminal flower-buds with

separate leaf-buds below them. Contrasted with these were three other groups. Firstly, there were the "evergreen" or "Indian" azaleas, in which the flower-buds are also terminal but whose innovations spring from among the scales of the floral buds. We have seen that the name *Tsutsutsi* had become restricted to these plants; Maximovicz used it in the form *Tsusia*. Secondly, there were those rhododendrons whose flower-buds are borne laterally (in the axil of the foliage leaves) not terminating the twigs. *Azaleastrum* was found to have this type of flower-arrangement, and to these Maximovicz added *Keysia* (having misinterpreted Nuttall's description) and also another group which he called *Rhodorastrum*, and which included *R. dauricum* and *R. mucronulatum*. The third group whose inflorescence-form contrasted with the normal arrangement he called *Rhododendra Anomala*. This included *R. camtschaticum* and its close relative *R. redowskianum* in which the arrangement of leaves and flowers is unique within the genus. In them the terminal buds produce a shoot which bears leaves below the flowers. Maximovicz gave this group the name *Therorhodion*, and some subsequent authors have thought it better to treat this small section as a distinct genus.

Some of these inflorescence features are difficult to observe and to interpret, so that it is not surprising that Maximovicz failed to take his ideas as far as he might have done. In particular the relationship of the flower-buds and innovations is difficult to interpret in *R. schlippenbachii* and its allies, and it was here that Maximovicz failed to realize that the inflorescence of these species stands nearer to the *Tsutsutsi* type than that of most azaleas.

For the rest, Maximovicz retained the section *Osmothamnus*, but he redefined it and expanded it from its original usage to include virtually all the lepidote species. By merging Don's *Booram* with his *Eurhododendron* this Section comes to include all the non-lepidote species, together with the lepidote *R. formosum* of the *Maddenii* Series.

Maximovicz's insight into the shoot-morphology of the genus was the most important event in the history of rhododendron classification. The fact that some of the other features of his arrangement are not so advanced as those of Don is probably attributable to his concentration on the Far Eastern region. His feeling for the azaleas was remarkable, but the other two major groups, which are represented poorly in that region, were interpreted with less insight.

III. Hooker to Wilson and Rehder, 1870–1921

Hooker's treatment of the Ericaceae in the monumental Genera Plantarum (Bentham & Hooker, 1876) includes a detailed account of *Rhododendron* that follows Maximovicz very closely, and the few changes are for the better. One change is to correct the application of *Osmothamnus* to the original usage (= *Pogonanthum*) with the consequential employment of another name (*Graveolentes*) for the bulk of the lepidote species. Hooker follows Maximovicz in defining *Eurhododendron* by means of bud-scale characters and consequently includes some lepidote species in this group. They are chiefly species of the *Maddenii* and *Edgeworthii* Series and of *Vireya*.

Another improvement is the recognition of a series to include *R. schlippenbachii* and its allies, though this is defined on foliage characters and the nature of the inflorescence buds is still mis-interpreted. The series is therefore

associated with the deciduous azaleas rather than with *Tsutsutsi*. However, the principal contribution of Hooker was his attempt to break down the large number of non-lepidote and lepidote species into several subseries. In this he was taking further the work of Nuttall and, like his, Hooker's groups are largely based on the nature of the calyx and the number of loculi. Hooker does not use Nuttall's names and their respective groups can only be equated very generally.

In 1882 Clarke continued this subdivision by publishing a key to the Indian species, but he proposed no formal classification of groups, at least among the principal lepidote and non-lepidote groups. However, a notable advance was the dependence on the presence or absence of scales for the major cleavage so that for the first time species of the *Maddenii* and *Edgeworthii* Series appear among their lepidote colleagues and the non-lepidote group emerges uncontaminated. Also, Clarke divided *Vireya* into the true vireya's and another group, *Pseudovireya*, characterized by the valves of the capsule not twisting in the manner he considered characteristic of *Vireya*.

When the collecting of the French missionaries began to make known the many species of Yunnan and Szechuan, Franchet rightly remarked that the centre of gravity of the genus had been moved there from the Himalayas. In his treatment of the collections of David and Delavay, Franchet (1886) followed Hooker closely, but found it necessary to make some modifications. In the lateral-flowered subgenus he proposed a new section *Choniastrum* to include *R. stamineum* and he foreshadowed the need to subdivide *Rhodorastrum* by separating *R. racemosum*, *R. scabrifolium*, *R. oleifolium* and *R. virgatum* into a section distinct from *R. dauricum* though he did not formally take this step. It is of interest also that he, mistakenly, included *R. lutescens* in *Rhodorastrum* because many of its fascicles of flowers are borne in the axils of the leaves.

Towards the end of the last century German botany was coming into the ascendancy, and Adolf Engler was bringing out his great work, Die Pflanzenfamilien, which covered the whole plant kingdom and was intended to be even more comprehensive than Bentham and Hooker's Genera Plantarum. In a volume issued in 1891, Otto Drude covered the Ericaceae and included a treatment of *Rhododendron*. This was not as full as that of Hooker, nor so up-to-date. He reverts to a vague distinction between lepidote and non-lepidote species, so that *Edgeworthii* and *Maddenii* are once more misplaced, and again the distinctness of *Pogonanthum* among the lepidote group is lost sight of. Finally, no record is included of the previous attempts to break down the largest groups into series.

There now occurs a long gap in the history which must have been a period of consolidation. Some very good accounts appeared of the species known in cultivation, for example those of Dippel (1889), Koehne (1893), Zabel (1902), and Schneider (1907), and in their Genera Siphonogamarum Dalla-Torre and Harms (1903) give a very complete generic synonymy of all the groups within *Rhododendron*.

During this time more and more species were becoming known. Not a few of these were discovered by Ernest Henry Wilson on his many plant-collecting expeditions to China, first for Veitch's nursery and later for the Arnold Arboretum. When his collections came to be written up the section on Rhododendron was contributed by Alfred Rehder in collaboration with

Wilson himself (1913). The groups recognized mainly agree with those of Maximovicz, though in a different arrangement and with amended nomenclature. A novel feature is a section *Lepidoto* (= *Triflorum*) which is detached from the main body of the lepidote species. In 1921, the same two authors issued a monograph of Azaleas, in which more important innovations appear, and where previous misconceptions and errors are corrected. New features are the introduction of a section, *Sciadorhodion*, to include *R. schlippenbachii* and its allies, and the transfer of the two Asiatic species *R. pentaphyllum* and *R. albrechtii* to the North American section *Rhodora*, a move, as we shall see, that might have been better left unmade. The even more aberrant species, *R. nipponicum*, was also transferred to *Rhodora*, although Matsumura and Nakai had already (Nakai 1916) placed this species in a section of its own (*Viscidula*). It is interesting to note that Nakai also recognized the need for a section to include the relatives of *R. schlippenbachii* and that his name, *Verticillatae*, was published in the year following Rehder & Wilson's Monograph (Nakai, 1922).

The account of this period may conveniently conclude with reference to Schlechter's work on the New Guinea species (1918) and Copeland's treatment of the Philippine species (1929). Both these authors propose subdivisions of the vireyas. Schlechter recognizes five named sections of New Guinea vireyas, mainly defined by features of the corolla. Copeland named five sections from the Philippines, none of which he equated with those of Schlechter. Later (1943) he recognized *Vaccinioides* as a series distinct from *Vireya* (= *Pseudovireya* of Clarke) and proposed a further series, namely *Malayanum*.

Copeland was modest enough to remark in 1943 "Schlechter and I have undertaken the subordinate classification of the representatives (of *Vireya*) within limited areas into groups which should be given the rank of sections. I am afraid that when a comprehensive organization in sections is undertaken these essays will be found to have created more confusion than enlightenment". In fact, when this was done by Sleumer (1949, see below) four of Copeland's five Philippine named sections were retained and Schlechter's groupings also proved of lasting value.

IV. Tagg, Hutchinson and Rehder, 1930

Throughout the previous period the number of species known continued to rise and many were brought into cultivation. The increase in the size of some sections, especially of *Eurhododendron* (= *Hymenanthes*) and the lepidote species, stimulated attempts to break these down into more manageable units. We have already seen how this process began in Britain with Nuttall, Hooker and Clarke.

A sustained attack on this problem was begun at Edinburgh where Professor Isaac Bayley Balfour began to cluster the many species into Series. These appeared with more or less formal, but often informal mention in a sequence of papers in the Transactions of the Botanical Society of Edinburgh (1919) and Notes from the Royal Botanic Garden (1916, 1917, 1919, 1920) together with an account of the *Maddenii* Series by Hutchinson (1919). The greater number of the Series at present accepted were referred to in these

publications, and several were defined and keys to their constituent species were provided. During the next few years a series of Tentative Lists of the Series and their species was circulated among a group of horticulturists interested in *Rhododendron*.

These ideas culminated in the production of a volume, "The Species of Rhododendron", by the Royal Horticultural Society (ed. Stevenson, 1930). It is difficult to assess a book which has been so useful in stimulating interest in and knowledge of the genus, which in several ways advanced knowledge of the genus, and yet at the same time set aside so much of the accumulated knowledge of the best way in which to group the species.

The plan of this work was to place the species into numerous Series without in any way grouping these into larger units. One result is that all the azaleas with their wide-ranging differences form a single Series with no more standing than the smallest Series of, say, the lepidote species, which may differ from another Series by some ill-defined character. Nor is the grouping of elepidote and lepidote Series retained, nor the presence among the latter of the group *Rhodorastrum*. The occurrence of *Azaleastrum* (in the broad sense) is not recorded, though notes under Series *Ovatum*, *Semibarbatum*, *Stamineum* and *Albiflorum* refer to their similarity.

In spite of their failure to present an overall scheme, the three authors, H. F. Tagg of Edinburgh (elepidote), J. Hutchinson of Kew (lepidote) and Alfred Rehder of the Arnold Arboretum (azaleas and their allies), are responsible for several advances. Most of these are concerned with the recognition of the thirteen Series into which the elepidote species are grouped and the twenty-three Series of the lepidote species.

Interesting new sub-divisions are also proposed among the groups with lateral flowers and among the azaleas. In the former, the authors took up a suggestion that we have seen was made by Franchet forty years before, and divided i *R. virgatum*, and ii *R. racemosum*, *R. scabrifolium* and their allies, as groups separate from *R. dauricum*. Among the azaleas they separated *R. albiflorum* and *R. semibarbatum* each into a Series of its own, and they also separated *R. tashiroi* as a sub-series of azalea. The characters of this species appear so similar to those of the section *Tsutsutsi* that its separation is unconvincing.

John Hutchinson (1947) later published a scheme setting out his views on the evolutionary relationships between all the Series, and a year later he discussed their geographical distribution (Hutchinson, 1948). An interesting survey of the occurrence of polyploidy in the various Series was published by Miss Janaki Ammal (1950) and it is hoped that further work in this field will be undertaken, as this would provide reliable evidence on phylogenetic relations within the genus.

The work on the Series which was initiated at Edinburgh by Balfour and continued there by Tagg has been carried further by a sequence of articles in which particular Series are revised. J. M. Cowan & H. H. Davidian, and later Davidian have published revisions of the following series: *Boothii*, *Glaucophyllum*, *Lepidotum*, *Anthopogon*, *Campanulatum*, *Fulvum*, *Thomsonii*, *Lacteum*, *Campylogynum*, *Saluenense*, and *Triflorum* (Cowan & Davidian, 1947; 1948; 1949; 1951; Davidian 1954; 1963; Davidian & Cowan, 1956). At present we are preparing a revision of the *Lapponicum* Series for which much of the research was conducted at Edinburgh.

V. Sleumer: Ein System der Gattung Rhododendron—1949

With the publication of the Species of Rhododendron there were virtually two systems of classification in use. Outside Britain the slowly developed botanical system largely prevailed, but in Britain, especially among horticulturists, the simplicity of many Series, all equivalent in rank (though some were divided into sub-series) was irresistible, especially as no good account of the botanical system had been published in Britain. In any event, the Series provided a more extensive range of pigeon-holes for the many known species. All that was lacking was the grouping of the Series into classes of higher rank. That this should be attempted was suggested by Cowan (1949).

In that year Hermann Sleumer, a life-long research worker on the family Ericaceae, provided the necessary link between the two systems in his "Ein System der Gattung Rhododendron" which appeared in the Botanische Jahrbuch (1949). In this comprehensive treatment he sets out the full botanical hierarchy of groupings as we have seen it develop from the time of Don and provided a key.

Apart from this synthesis of the two classifications, Sleumer continued the long process of refining the recognized groups within the genus. Firstly, he confirmed the view of Small (1914), Hutchinson (1921) and Copeland (1943) that *R. camtschaticum* and its allies should form a genus of their own, *Therorhodion*. Secondly, he divided *R. trichocladum* and its allies from the remainder of the lepidote groups as a new sub-genus (*Pseudazalea*) on the basis of more or less deciduous foliage and precocious flowers. Thirdly, Sleumer took even further the sub-division of the lateral-flowered lepidote species by separating *R. racemosum* from *R. virgatum* and *R. oleifolium*. Finally, he brought together the scattered work on *Vireya*, from Clarke to Schlechter and Copeland, into an orderly system. The nomenclature used in 1949 was subsequently slightly amended (Sleumer 1958; 1964).

VI. Present Trends

From the preceding account it is evident that progress has been made when some new feature of the plant has been brought into use in classification. The most notable instance is the nature of the buds as used by Maximovicz and later by Wilson & Rehder. The scales and other hair types have been given increasing importance. The presence of scales had for long been taken into account, but Clarke finally gave them overriding weight in subdividing the genus. In this he was followed by many others and Cowan (1950) sought to extend their use to defining some series (e.g. *Falconeri* and *Anthopogon*) and also as a means of grouping similar Series. Finally, Seithe (1960) showed how tomentum characters are diagnostic for the three major divisions of the genus, namely the lepidote species, the elepidote species, and the azaleas and their allies. These three major groups she raised to a status above that of Sleumer's subgenera calling them "chori subgenerum".

Other characters have been sought, mainly with a view to strengthening or refining the definition of existing groups. Working at Edinburgh, James Sinclair (1937) discovered a most interesting variation in the way in which the young foliage leaves are held within the winter buds. In all the lepidote species (except Series *Edgeworthii*) the young leaf-blades lie flat, whereas in

all other species (the elepidote and azalea groups) the leaves are tightly rolled back. Secondly, the plant-collector Frank Kingdon Ward (1935, 1947) demonstrated the value of seed-characters and those of the seedling and flower in classification, and Cowan (1949) drew attention to the value of the number of hypodermal layers in the leaf.

Copeland (1943) carried out an anatomical comparison of all genera of the sub-family *Rhododendroideae* as a result of which he concluded that the large genus *Rhododendron* would be more manageable if divided into several genera. Those he recognized were *Rhododendron*, *Azalea*, *Hymenanthes*, *Azaleastrum*, and *Therorhodion*. This proposal has not received support and is subject to the criticism that the genera *Azalea* and *Azaleastrum* both contain groups which are sufficiently distinctive to claim generic rank if this is granted to *Rhododendron* and *Hymenanthes*.

Cox (1948) studied the anatomy of the wood of rhododendrons and concluded that differences existed between the woods of lepidote and elepidote rhododendrons as compared with those of azaleas and that all differed from *Azaleastrum*. Unfortunately the samples compared were too small to allow significant differences to emerge. For this reason some of his conclusions must be erroneous. The wood characters of seven "rhododendrons" were compared with seven "azaleas" (all North American deciduous species) and these with one member of the azaleastrum group, namely, the atypical North American *R. albiflorum*. When Cox found that the wood of *R. lapponicum* agreed with that of his azalea sample rather than with that of the rhododendron sample he proposed its transference to that group in spite of the wealth of characters that show it to be a typical member of the lepidote rhododendrons. Since Cox examined only one other lepidote species, it is clear that he had not established any basis for using wood characters in classification.

In 1968 we studied the pattern of veins entering the leaf from the stem and found variations which corresponded with the major subdivisions. One of us (M.N.P.) in 1970 demonstrated that characters of the cotyledons also showed patterns of variation, mainly affecting pubescence and venation, which also correspond with the major groupings. These seed-leaf characters were also capable of refining the existing classification of some azaleas. The Asiatic members of *Pentanthera*, *R. pentaphyllum* and *R. albrechtii*, were seen to be more correctly linked with *R. quinquefolium* and similar Far Eastern species of the *Schlippenbachii* Series. At the same time, other species of this series formed a distinctive grouping of their own. At the present time we are carrying out, in collaboration with Dr B. F. Palser, a comparative study of embryology within the genus and several characters of the ovary, ovule, and embryo sac show promise of systematic value.

Most of these anatomical characters have not been applied to any formal classification, but belief in the existing system is greatly strengthened by them. We have discussed their implications (1970) and conclude that the lepidote and elepidote groups are coherent and natural, each representing a single evolutionary line, whereas the azaleas and their allies are a more diverse group, probably representing several separate and ancient evolutionary lines.

This conclusion appears to us the most telling argument against splitting *Rhododendron* into separate genera. It would be easy and useful to recognize

the lepidote and elepidote species as distinct genera, but in that event it would be necessary to divide the azaleas into several genera, some of which might comprise a single species. The present rather unwieldy genus seems preferable.

A completely new set of evidence is afforded by the application of chemotaxonomy to *Rhododendron* (Harborne & Williams, 1971, and references therein). For some years these studies have mainly related to flower-pigments, but in their recent paper Harborne & Williams report a survey of flavonoids in the leaves of 206 species of *Rhododendron*, and of the simpler phenols in those of 55 species. Their results generally do not conflict with the accepted classification, but it is interesting that these chemical characters are less constant than any of several independent morphological characters. Trichome characters, for example, were found to correspond closely with the accepted major groups (Seithe, 1960) and could therefore be used for their definition, but it would not be possible to construct a meaningful system on the chemical evidence. The authors point out that the characters are not diagnostic of groups but that some are correlated with them. For example caryatin is confined to the subgenus *Hymenanthes* (except apparently for a variety of *R. occidentale*) and sub-genus *Pentanthera* lacks both gossypetin and coumarins.

This inconstancy of the chemical attributes is disappointing. The closely-knit section *Lapponicum*, for example, clearly has a spectrum of substances that characterizes it (though several other groups within the subgenus *Rhododendron* are very similar chemically) but no compound is listed for all species investigated and several compounds have a very erratic distribution within the group. Intra-specific variation is suggested by the fact that some names listed in this section which we consider to be conspecific proved to possess different combinations of compounds. Since the results are based on extracts from only one or two plants of each taxon, it is possible that a large sample would have shown intra-specific variability to be general. Also, the variability within accepted groupings of species makes it difficult to assess the correctness or otherwise of the placing of a species. The authors point out several examples of species which seem (chemically) out of place in their present series and these will need careful assessment in future revisions.

Harborne & Williams suggest that the pattern of distribution of flavonoids may serve to indicate the main streams of evolution within the genus. More advanced groups may be expected to lack one or more of the primitive flavonoid features which characterize the genus. They consider that the paucity of these flavonoid characters in the only known Australian species, *R. lochae*, confirms its evolutionary advancement. The authors consider it to have evolved in Australia in isolation from the South-east Asian groups, but a more likely history is for it to be a recent immigrant from New Guinea where more than 150 species occur. *R. lochae* is the only member of the section *Vireya* (listed under *Pseudovireya*) which was investigated and since this section is one of the largest in South-East Asia (having about 290 species) the isolation of *R. lochae* cannot be assumed until the vireyas have been sampled more completely.

The presence of what are regarded as primitive flavonoid characters is considered as evidence that *Rhododendron* is an ancient relict genus. Furthermore, the possession of two more unusual flavonoid characters—gossypetin and azaleatin—is thought by Harborne & Williams to indicate the association

of *Rhododendron* with relatively primitive angiosperm groups. However, we cannot agree that *Rhododendron* is a relict genus: it has all the hall-marks of recent vigorous speciation. No doubt some groups in the smaller subgenera are relict within the context of *Rhododendron* but they and the Ericaceae generally must be well removed from the primitive angiosperms.

VII. The Future

Without attempting to predict future developments in this field, it may be of interest to consider areas of study that appear to offer promise. It might be thought that a sufficient factual basis for the construction of a reliable classification already exists, but the very existence of this body of evidence in relation to one group of plants encourages research into other types of evidence within the same group. This is so not only because there is considerable interest in the comparison of independent types of evidence, but also because the correspondence or disparity of the evidence provides additional information on the relationships within the group. For example, we have already seen how well the pattern of leaf-folding in the bud agrees with the distribution of scales, but noted that the correspondence was not exact. The fact that Series *Edgeworthii* does not agree with other lepidote species in this respect is an additional fact of interest and importance. This non-correspondence of characters has been termed non-congruity by Crowson (1953, 1970). Non-congruent characters could form a basis for the construction of possible evolutionary pathways within the genus *Rhododendron*. Phylogenetic hypotheses concerning *Rhododendron* have been few (Hutchinson, 1947), but with the accumulation of evidence from several independent lines such speculation could be placed on a firmer foundation.

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