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SHOOT MORPHOLOGY IN RHODODENDRON

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ABSTRACT. As the characteristics of leaf and flower buds have been used for the definition of subgeneric categories, a full understanding of them is desirable. The species range in habit from tall trees to moss-like shrublets. The architecture of their branching can be related mainly to Leeuwenberg's model, though exceptions occur. The differentiation of lateral appendages into foliage leaves and cataphylls (perulae) and the unequal development of internodes frequently results in characteristic pseudowhorls. Two distinct forms of vernation and several patterns of nodal anatomy correspond very closely with established classification. The separation of vegetative and floral buds in most species, and the occurrence of compound buds in a few groups has been given prominence in the classification of the genus, as has the arrangement of these buds in relation to each other. Careful developmental studies are needed to determine the arrangement of buds in some cases which remain doubtful. It appears that development may be subject to variation in some species. A recent tendency to place less emphasis on these characters is therefore justified.

The form and stature of rhododendrons range from prostrate subshrubs to moderately large trees. In spite of this they display comparatively little variation in their basic architecture. I shall be speaking of several features of the stems, leaves and buds of rhododendrons, seeking to understand how they affect the habit of the plants, and also to relate them to the classification of the genus.

Possibly most of us think of the typical habit as a rounded shrub bearing evergreen leaves in clusters at the ends of the shoots. So long as the plant remains vegetative the branches increase in length and the shoots are monopodial, with side branches at intervals. Since the inflorescences are terminal (with exceptions to be considered later) once the plant becomes reproductive, the branching is sympodial. Even when the flower buds are all lateral the growth pattern may remain the same because the terminal buds often abort. However, species which always (*R. virgatum* Hook. f.) or occasionally (*R. leptothrium* Balf. f. & Forr.) retain monopodial branching into maturity are known. Such exceptional species will be referred to in greater detail later.

Modifications of size and relative importance of branches, and the retention of monopodial growth by the main stems even when the laterals have come to flower, leads to the formation of trees with a single trunk which may reach a height of 20m. At the other extreme are prostrate shrubs or even cushion and mat plants (e.g. *R. saxifragoides* J. J. Smith) and the trailing habit of many epiphytes (e.g. *R. rarum* Schlecht.).

A limitation of what I have referred to as the typical growth form of rhododendrons is that the foliage (i.e. the photosynthetic surface) is displayed to sunlight as a single outer surface. This may have advantages, for example the suppression of competitors, but the branches are effective vegetatively only at their tips. A broader view of the genus shows that other growth habits are common. A densely leafy shrub is produced in *R.*

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ovatum (Lindley) Maxim. by continued growth and the retention of leaves. A more open type of growth with diffuse presentation of leaves can be achieved by spindly uneven growth with retention of leaves (usually in pseudowhorls) throughout several flushes of growth. This habit is characteristic of several North American azaleas, of sect. *Choniastrum* and of many vireyas. This tendency is taken further in several vireyas (e.g. *R. nummatum* J. J. Smith) by a differentiation between main branches and smaller lateral branches so that something approaching a frond-like display of foliage results (e.g. *R. pusillum* J. J. Smith). Perhaps the species that comes closest to the differentiation of long and short shoots is the deciduous *R. albiflorum* Hook., in which the main branches may remain leafy for years by the production of successive tufts of leaves each spring on short lateral branches.

If we attempt to interpret the growth-forms of rhododendrons in terms of the architectural models published by Hallé and Oldeman (1970) what I have called the typical rhododendron habit conforms clearly to their Leeuwenberg's model (Fig. 1A). Modifications with a tree form result from the retention of vegetative growth by principal branches—a habit conforming to Scarrone's model (Fig. 1B). This habit is also prevalent in shrubby species, being characteristic of the lax growth of many vireyas. Intermediate states between these two models occur as branches become more or less vigorous. Finally, those species with lateral flowers and a persistent vegetative apex (e.g. *R. virgatum*) belong to the very different model of Rauh (Fig. 1C). For a genus the size of *Rhododendron* to display only three models indicates that it is not very adventurous in this respect.

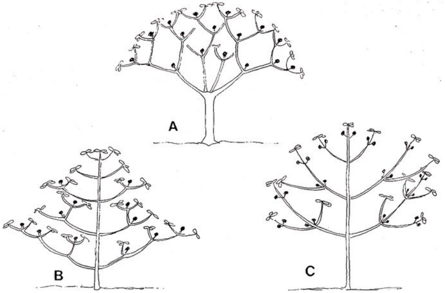


FIG. 1. Diagrammatic representation of the growth form of rhododendrons according to the models of Hallé and Oldeman. A, Leeuwenberg's model with branches ending in inflorescences and growth renewed by lateral buds; B, Scarrone's model, with retention of vegetative growth by principal axes; C, Rauh's model, with lateral inflorescences and persistent vegetative apices.

Another respect in which rhododendrons cannot be regarded as versatile is in the production of offshoots. The great majority of species are spot-bound, but the drooping branches of shrubs may reproduce by layering, and cushion or mat species (e.g. *R. camtschaticum* Pallas) root as they spread. Species which spread underground are rare, the most well-known being *R. atlanticum* (Ashe) Rehd.

Clearly there is some relation between habit and habitat. Alpine species, even though unrelated, may approach one another in form. The greatest distinction in habit within the genus is the division between deciduous and evergreen groups. This corresponds in a general way with the distribution of the north temperate forests on the one hand and the tropical forest and alpine species on the other. It seems probable that this cleavage within the genus is very old and enduring.

I may refer briefly to variation in the size and shape of leaves. As regards shape the extremely narrow (*R. stenophyllum* Hook. f.) and the rotund (*R. orbiculatum* Ridley) fairly represent the range for the whole genus. As regards size the small leaf of *R. anagallifolium* Wernh. (6mm long) certainly approaches the lowest limit of the whole genus—though some species of sect. *Tsutsusi* may equal it. The largest leaves reported are for *R. sinogrande* Balf. f. & W. W. Smith (70cm long). In most species the leaves are petiolate, but sessile leaves do occur, even with auriculate bases closely wrapped around the stem (e.g. *R. carrii* Sleumer and *R. rhodoleucum* Sleumer).

Another feature of the leaves which shows surprisingly good correspondence with the major sub-divisions of the genus is the pattern of veins entering the leaf from the stem. In the Ericaceae (to which family *Rhododendron* belongs) a unilacunar node is almost universal. In *Rhododendron,* however, there is a good deal of variation and this variation forms a pattern consistent with Sleumer's classification (Philipson & Philipson, 1968). Stated briefly, *Hymenanthes* stands apart from all other rhododendrons because its nodal anatomy is more complex—often surprisingly complex, especially in the large-leaved species. All the sub-genera except *Hymenanthes* have the simple node typical of the Ericaceae, though in sect. *Choniastrum* it may tend towards the condition in *Hymenanthes*. These findings relate to the pattern at the junction of stem and leaf, they do not take into account any pattern of vascular strands within the petiole.

The arrangement of the foliage on the stems is always spiral. In some species the leaves are spaced along the branches (e.g. *R. womersleyi* Sleumer) but it is more common for them to be arranged in apparent whorls. This whorled appearance is due to the very short internodes between leaves towards the ends of growth increments. I know of no extensive study of the phyllotaxis in the various species but the well-known difference between the '3-leaved' and '5-leaved' azaleas is based on a difference in their phyllotaxis—2/5 in *R. schlippenbachii* Maxim. (*Sciadorhodion*) and 2/3 in *R. reticulatum* G. Don (*Brachycalyx*). These two sections were formerly united, but some years ago the separation of *Sciadorhodion* as a section of subgen. *Pentanthera* on the grounds of cotyledonary characters was advocated (Philipson, M. N., 1970) and this opinion is also supported by their different hair-types. These have been assumed to approach the broad scaly hairs of the evergreen azaleas, but those of *Sciadorhodion* are similar to those of subgen. *Pentanthera* whereas those of *Brachycalyx* are flattened narrow ribbons approaching those of the sect. *Tsutsusi*.

In addition to foliage leaves, the shoot apex also produces appendages which develop into scale leaves. These enclose resting buds, whether vegetative or reproductive. In some tropical vireyas this character is almost absent (e.g. *R. stenophyllum*). The bud-scales are closely imbricated, with the inner scales longer and more membranous than those to the outside. The inner scales frequently increase in length considerably as the bud opens and may become even more conspicuous by bright colouration and by being carried up by the elongation of the internodes between them. The outer scale leaves are rarely persistent (cf. *R. roxieanum* Forr.) but the inner mostly fall early. In species with many well-shaped inner scales, this produces the bare base of the current shoot which is so typical of many rhododendrons. The internodes between the foliage leaves, on the other hand, often do not elongate, resulting as we have seen in the typical pseudo-whorl. An intermediate condition is found in e.g. *R. ovatum* in which growth increments show bud-scale scars at the base often without marked internodes, followed by scattered leaves along the stem and a terminal pseudo-whorl.

An interesting variation is found in the shoots of most species of sect. *Tsutsusi*, where the current season's shoots bear two kinds of leaves: (i) those borne spaced out along the stems; (ii) those clustered in a pseudo-whorl at the ends of the shoots. The latter are more coriaceous and persist through the next season, whereas the former are more delicate and fall off before or during their first winter. In their position, their thinness and their deciduousness, they incline towards inner bud-scales, and they may be thought of as appendages intermediate between foliage and inner scales.

Before leaving the topic of buds I should refer to one other feature: the arrangement of the young leaves while compacted together in the bud. The occurrence of different vernation types within a genus is known in a number of genera (e.g. *Primula* (Pax & Knuth, 1905), *Prunus* (Clarke, 1976), *Nothofagus* (Philipson & Philipson, 1979)) where they are found to correspond with other characters in defining subgeneric taxa. This is also true in *Rhododendron* (Sinclair, 1937). In about half the genus the margins of the foliage leaves are revolute, though the cataphylls enclosing them are imbricate (Fig. 2A). This occurs in all the non-lepidote species—i.e. all the subgenera except *Rhododendron* with the exception of *R. camtschaticum* (and presumably the other two species in subgen. *Therorhodion*). On the other hand all lepidote species and also *R. camtschaticum* have imbricate (Fig. 2B) vernation with again a single exception, the subsect. *Edgeworthia*, in which the young leaves are revolute.

There may also be interesting differences in the way in which flowers are enclosed by their bud scales, but no extensive study of this feature has been made. Two types were pointed out in a recent paper published in Japan (Kaku, Iwaya & Kunishige, 1980). In one, the individual flowers are subtended by substantial scales which may form part of the outer

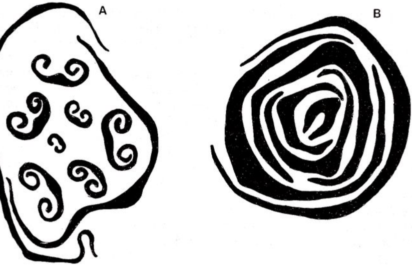


FIG 2. Vernation in foliage buds. A, *R. albiflorum* with revolute foliage and imbricate cataphylls; B, *R. trichostomum* with foliage and cataphylls both imbricate.

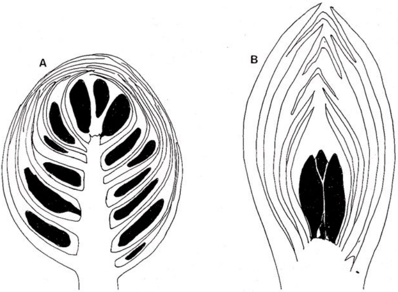


FIG. 3. Diagrams of arrangement of flowers in inflorescence buds. A, *R. microphyllum* with flowers in a raceme between prominent cataphylls; B, *R. kiusianum* with flowers central and enclosed by reduced cataphylls.

covering of the bud (*R. micranthum* Turcz. is an extreme example of this type; Fig. 3A), while in the other type the flowers form a central cluster with very delicate scales between them, this cluster being enclosed by the outer bud scales (e.g. *R. kiusianum* Makino; Fig. 3B).

One of the most important features of the shoot morphology of the genus is the relationship of leaf-buds and flower-buds. In most flowering plants the flowers or inflorescences occur on the same shoots as the leaves but, as is well known, the inflorescence buds of *Rhododendron* are separate from the buds which give rise to new leafy shoots. The typical arrangement in *Rhododendron* is for the flower bud to terminate a branch and to be surrounded at its base by a few vegetative buds (Fig. 4A). These vegetative buds usually occur in the axils of leaves (or reduced leaves) below the terminal inflorescence bud, but occasionally the upper lateral buds will also be reproductive with vegetative buds occurring in the axils of lower leaves (Fig. 4B).

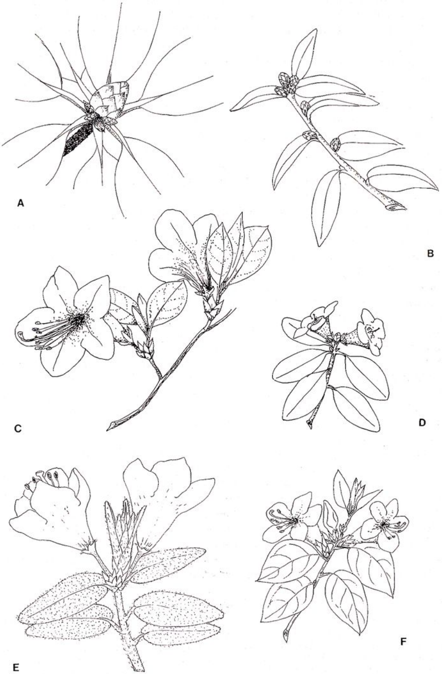
A more striking variation is for the vegetative buds to develop in the axils of the outer cataphylls of the floral bud—that is, the buds are compound (Fig. 4C). It should be noted, however, that the flowers and leaves are still produced by separate buds, on different axes. Indeed, the distinction between the various cases so far described is sometimes difficult to define, as the upper leaves may be so reduced they resemble cataphylls, and conversely the lower cataphylls may be enlarged and loosely applied to the bud so that they approach foliage leaves.

A simple deviation from the typical condition is the abortion of the terminal inflorescence bud—e.g. in *R. dauricum* L. the terminal flower bud aborts, but otherwise the arrangement of the buds conforms to the normal (Fig. 4D). A more significant deviation is for the inflorescences to arise only from lateral buds—the terminal bud either continues vegetatively (e.g. *R. virgatum, R. scabrifolium* Franch.; Fig. 4E) or aborts. In the latter event vegetative growth is resumed by lateral buds immediately *above* the inflorescences (e.g. subgenera *Azaleastrum, Candidastrum* and *Mumeazalea*; Fig. 4F). It is not always easy to decide whether vegetative innovations are terminal or pseudoterminal. Sleumer (1980) considers that the renewed growth is always pseudoterminal. Careful developmental studies will be needed to resolve this question, but my observations confirm that growth in *R. virgatum* is terminal and this appears to be true also of *R. scabrifolium* and at least sometimes in *R. leptothrium* and *R. ovatum.*

The value of these bud characteristics in classification has been accepted ever since they were first recognized by Maximovicz (1870). He divided the genus into two unequal parts, namely *'Rhododendra apiciflora'* and the much smaller *'Rhododendra lateriflora'*. Franchet (1886) extended this idea, and Sleumer (1949) adopted it as the first cleavage in his key to the genus.

The character of lateral inflorescence buds with vegetative renewal above them is certainly valuable in defining the three non-lepidote subgenera *Azaleastrum, Candidastrum* and *Mumeazalea.* In addition to

FIG. 4. The relationship between floral and vegetative buds. A, *R. ponticum*, the most general arrangement with a terminal floral bud and vegetative buds below it; B, *R. racemosum*, with several lateral floral buds below a terminal floral bud—vegetative buds in lower axils; C, *R. nudipes* with compound buds—the vegetative buds being in the axils of the outer scales of the floral buds; D, *R. dauricum* in which only lateral buds flower, the terminal floral bud aborts; E, *R. scabrifolium* in which the floral buds are lateral, the terminal bud being vegetative; F, *R. ovatum* in which the flower buds are lateral, the terminal bud either as in *R. virgatum*, or aborting, in which case (as figured) the new growth is pseudo-terminal.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these Sleumer recognized two small lepidote subgenera on the basis of inflorescence/vegetative bud relationships (*Rhodorastrum* and *Pseudorhodorastrum*) but Cullen (1980) realized that a better treatment of these groups is obtained by downgrading the inflorescence character so that these groups may be integrated with the lepidote sections to which they appear closely akin. This treatment receives support from the variable condition of the terminal bud found among the species of Sleumer's *Pseudorhodorastrum*: floral in *R. racemosum* Franchet (at least sometimes), vegetative in *R. virgatum* and *R. scabrifolium* (? always), and aborted (from either the floral or vegetative state; according to several authorities).

Another example of the value of bud characters in classification is provided by the compound buds so characteristic of all sections of subgen. *Tsutsusi*. The occurrence of similar compound buds in the two species *R. schlippenbachii* and *R. quinquifolium* Bisset & Moore resulted in their being included in this complex. But many features conflict with this association so that we (M. N. Philipson, 1970; W. R. Philipson, 1980) took a similar stance to that taken later by Cullen (1980) and downgraded the importance of bud characters in relation to these two species.

In spite of the great importance that has been given these characters in the classification of the genus, they have not been carefully and completely documented, considerable difference of opinion still persists, and clarification of several points is needed. For example, Sleumer believes (1949, 1980:3) that the terminal bud of shoots with lateral flowers never grows on but aborts, yet terminal renewal-shoots appear to be the general rule in *R. virgatum* and *R. scabrifolium*, and are at least occasional in *R. leptothrium* (and no doubt other species of sect. *Azaleastrum*). Another doubtful case is provided by *R. racemosum* which is generally regarded as having lateral flower buds with an abortive terminal bud. However, plants with well-developed terminal flower-buds occur.

The nature of the inflorescence in another group of species has also been the subject of much debate. This group is subgen. *Therorhodion*, including *R. camtschaticum*. The inflorescence has been thought so distinctive that the species have sometimes been removed from *Rhododendron* as a separate genus—*Therorhodion*. However, as we have seen is usual in *Rhododendron*, the flowers arise from buds which are distinct from those which form the new vegetative shoots by which the growth of the plant is continued. The whole of the shoot that arises from the inflorescence bud dies after fruiting is over (Fig. 5A). It has been claimed that in *R. camtschaticum* the top-most flower is terminal, whereas in other rhododendrons the raceme ends in an aborted apex, but a careful study of young inflorescence buds shows that the upper flower primordia and the apex abort as in other rhododendrons (Fig. 5A). It has also been claimed that the inflorescence of *R. camtschaticum* is borne at the ends of leafy shoots and this claim has some justification. However, the leaves below the flowers are different in shape and texture from the foliage leaves (a distinction more evident in living plants than in herbarium specimens) and in my opinion correspond to the perulae found on the peduncle of all species of the genus (Fig. 5B). In the final analysis the sole distinction between *Therorhodion* and *Rhododendron* is that the inner

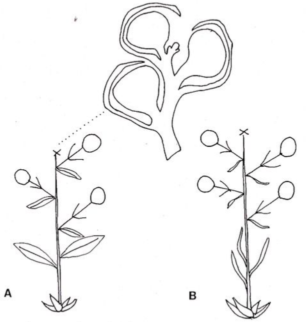

FIG. 5. Diagrammatic comparison of inflorescence of *R. camtschaticum* and of a typical rhododendron. In both the inflorescence arises from a special bud and the whole structure dies after fruiting. A, *R. camtschaticum*, with reduced leaves below the raceme (enlarged view of apex with aborted flower primordia and apex); B, truss of a typical species with perulae below the raceme.

perulae of the inflorescence buds are more leaflike. As this appears too slight a distinction I prefer to return *Therorhodion* to its former position as part of the main genus.

Fig. 6 illustrates how some characters agree very well with the subgeneric limits—they are said to be congruent. For example, the congruence of scales and vernation is striking, though even with them some exceptions do occur. *R. edgeworthii* combines scales with revolute vernation, and *R. camtschaticum* combines imbricate vernation with glandular hairs. Such incongruities give clues to evolution within the genus. I do not wish to speculate on the original nature of the genus, which is obviously in a state of active speciation at present, but there is one conclusion I would arrive at from this table, as an example of what can be deduced.

The type of nodal anatomy which predominates in the Ericaceae is the simple node, and this also predominates within *Rhododendron*. The complex nodal anatomy found in all the species of *Hymenanthes* investigated, and in no other group, in my opinion provides conclusive evidence that *Hymenanthes* is a derived group, and that it cannot be regarded as resembling the ancestral form of the genus. This is in direct opposition to the view put forward many years ago by my one-time colleague and fellow Northumbrian, the late John Hutchinson. I doubt if he would mind this difference of opinion. In the 35 years since his suggestion was made additional lines of evidence have been investigated.

SUB-GENERA	SECTIONS	FLOWER AND LEAF BUDS	LEAF FOLDING	SEED	HAIR TYPES		NODE	COTYLEDON
					SCALES OR GLANDS	SIMPLE OR BRANCHED		
HYMENANTHES	(MANY ELEPIDOTE)							
RHODODENDRON	RHODODENDRON (MOST LEPIDOTE)	*	*	*				*
	POGONANTHUM (ANTHOPOGON)							
	VIREYA							
PENTANTHERA	RHODORA (CANADENSE)							
	PENTANTHERA (LUTEUM)							*
	VISCIDULA (NIPPONICUM)							
	SCIADORHODION							
TSUTSUSI	TSUTSUSI (OBTUSUM)							*
	BRACHYCALYX (SCHLIPPENBACHII)	*						
	TSUSIOPSIS (TASHIROI)							
AZALEASTRUM	CHONIASTRUM (STAMINEUM)						*	
	AZALEASTRUM (OVATUM)							
CANDIDASTRUM	CANDIDASTRUM (ALBIFLORUM)							
MUMEAZALEA	MUMEAZALEA (SEMIBARBATUM)							
THERORHODION	THERORHODION (CAMTSCHATICUM)							

FIG. 6. A summary of some characteristics of the subgenera and sections. The symbols are not exact portrayals of the features, but are generalized diagrams. In those representing flower- and leaf-buds, floral buds are in solid black and vegetative bud in outline. An asterisk denotes that one or a few exceptions occur. (Modified from Philipson, M. N. & Philipson, W. R., 1971).

It would be disheartening if no new and more definite conclusions could be reached.

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