COTYLEDONS AND THE TAXONOMY OF RHODODENDRON

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ABSTRACT. Cotyledons of species of *Rhododendron* vary in the presence or absence of hairs and of lateral veins and combinations of these are of systematic importance. Cotyledonary hairs are absent in all lepidote groups, although scales may be present. The Subgenus *Rhododendron* is characterized by the absence of both hairs and lateral veins, this combination being found elsewhere only in the two monotypic and isolated Sections *Viscidula* and *Candidastrum*. In contrast, cotyledonary hairs and lateral veins occur in elepidote groups, cotyledonary hairs being present invariably in the large Subgenus *Hymenanthes*, and in most sections of the subgenera forming the Azalea group. The detailed structure of hairs is characteristic and constant in the various groups which possess them. Thus, cotyledonary characters support the three subgeneric groupings of Seithe, which she called "chori subgenerum". The cotyledonary characters of *R. pentaphyllum* indicate that this species is closely related to *R. schlippenbachii* and *R. quinquefolium* and should be excluded from Section *Canadense*. Further, *R. schlippenbachii*, *R. quinquefolium*, *R. pentaphyllum* and *R. albrechtii* form a natural group separate from the species of Section *Brachycalyx* in which the cotyledonary hair is of a different type.

INTRODUCTION

The prevalence of hairs and their great diversity of form within the genus *Rhododendron* has been the subject of a number of investigations, the most comprehensive being those of Cowan (1950) and Seithe (1960). Cowan demonstrated some correlation between the hair types he recognised and the subdivisions of the genus as set out in "The Species of Rhododendron" (Stevenson, 1930). Seithe was able to establish the presence of associations of hair types which were of great taxonomic significance. She proposed three major groupings of subgenera, called "chori subgenerum", viz. i, *Rhododendron* (consisting of all scale-bearing subgenera), ii, *Azalea* (including subgenera *Pentanthera*, *Tsutsutsi* and *Azaleastrum*) and iii, *Hymenanthes* (consisting of a single, large, non-scale-bearing subgenus). This proposal has been upheld by other lines of inquiry, e.g. that of Philipson and Philipson (1968), where the anatomy of the node was found to have taxonomic significance and indicated the same three major groupings.

Investigations on Rhododendron hair types have previously been made on true leaves and plant parts beyond the young seedling stage. The nature of the cotyledons has been neglected. Seithe (1960) records the results of investigations on the indumentum of seedlings, but considers the development of hairs on successively older true leaves, without reference to the cotyledons. Balfour (1919) recorded observations on seedling indumentum but also confined his observations to the epicotyl. He refers to divergences on the epicotyl but dismissed the cotyledons with the remark "the earliest stages of extraseminal development are uniform in the genus". Kingdon-Ward (1947) referred to the presence of scales on cotyledons of some lepidote species, but his further discussion and conclusions were based on the indumentum of the true leaves of the seedling.

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During the raising of seedlings for anatomical study, it was noticed that species differed in the presence or absence of marginal hairs on the cotyledons. This character has been found to have a high degree of taxonomic correlation. Other characters of the cotyledon, especially the venation, also proved of interest, and have some relation to the systematics within the genus.

While these observations were being made, the work of Hedegaard (1968) became available. The numerous illustrations of seedlings published by this author extend the range of my observations on the presence or absence of marginal hairs. Hedegaard, however, does not describe different basic types nor draw attention to the taxonomic implications of his observations.

Scope and Methods

Seedlings of 157 species, representing all subdivisions within the genus except *Choniastrum*, were studied and these are listed in Table 2. Fully expanded cotyledons were examined under both binocular and compound microscopes for the nature of their indumentum and, for most species, also for their venation. To the results of this work have been added those of Hedegaard (1968) who recorded the presence or absence of hairs, but not not venation patterns.

The Indumentum

COTYLEDONARY HAIR TYPES

In those species which bear scales on the true leaves, a few scales may occur on the margin of the cotyledon, especially towards its base, and, more rarely, on the surface of the lamina of the cotyledon (fig. 5a,b,c). These scales are not considered further in this investigation.

The type of indumentum and venation are recorded in Table 2 where each species studied is listed under the subdivisions of the genus as recognized by Sleumer (1949, 1958 and 1964) and also under the serial system as recognized in the Rhododendron Handbook, Part I (Synge, 1967). Data from Hedegaard's (1968) observations are marked by H.

The cotyledons may be entirely glabrous or they may bear one or two of the epidermal appendages described below. With the exception of scales, all the hair-types were confined to the margins of the cotyledons, the only observed exception being the occurrence of some hairs on the surface in *R. rex* and *R. quinquefolium*.

A frequent type of cotyledonary hair consisted of a columnar base of small cells terminating in one to several (often two) elongated transparent cells usually of markedly unequal length (Hair-type I, fig. 1; fig. 5d,e,f). Rarely, these hairs were notched or branched (fig. 5,g), or the terminal cells were undeveloped. Glandular hairs having a similar, but often longer, columnar base, terminated in a dilated multicellular head with a dense appearance (Hair-type II, fig. 1; fig. 5h,i). A third type of hair was finger-like and typically closely appressed to the margin. These hairs frequently contained chloroplasts, especially in the basal cells, and they sometimes ended in short, blunt, subequal, clear cells (Hair-type III, fig. 1; fig. 6a,b). In *R. wadanum* the terminal cells were extremely long and occasionally very sharply pointed (fig. 6c). A limited number of species (*R. scabrifolium*, one species of Section *Pentanthera* and two species of Section *Tsutsutsi*) bore cotyledonary hairs which could not be referred to any of the three types and are accordingly listed in Table 2 under A (anomalous). When marginal hairs occurred on the cotyledons of *R. scabrifolium* the surface of all, or of at least the terminal cells of the hair, bore minute, short striations, arranged parallel to the long axis of the hair (fig. 6d). In addition, one of the terminal cells was always of a distinct and uniform buff colour. *R. japonicum* of the otherwise glabrous Section *Pentanthera* (Subseries *Luteum*) occasionally possessed one or two strong, multicellular, strigose hairs near the base of the cotyledons (fig. 7a). The few hairs found in the predominantly glabrous Section *Tsutsutsi* (Subseries *Obtusum*) were also anomalous. Of those species examined here, cotyledons of a very few seedlings of *R. oldhamii* bore one minute, ill-defined hair (fig. 6e), while those of *R. rubropilosum* had hairs of two distinct forms, namely, very short, stout, glandular hairs and long tapering setae (fig. 6f,g).

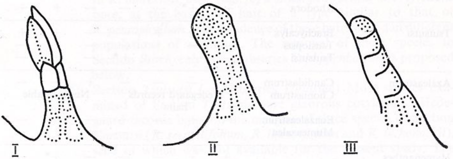


FIG. 1. Hair types on *Rhododendron* cotyledons: type I; type II; type III. Semi-diagrammatic.

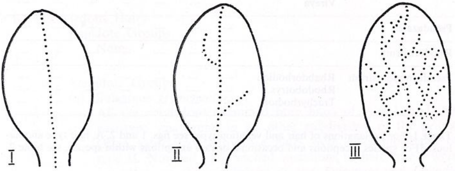


FIG. 2. Venation patterns of *Rhododendron* cotyledons: type I; type II; type III. Semi-diagrammatic.

DISTRIBUTION OF HAIR TYPES

The distribution of these hair-types among the subdivisions of the genus is shown in Table 1. As discussed below, there is a high degree of constancy.

TABLE 1

Systematics of Cotyledonary Characters

Subgenus	Section	Hair Type I	Hair Type II	Hair Type III	Hair Type A	Venation I	Venation II	Venation III
Pentanthera	Pentanthera*	—	—	—	—	—	+	—
	Viscidula	—	—	—	—	+	—	—
	Rhodora	—	+*	—	—	—	+	+
Tsutsutsi	Brachycalyx	—	+	+	—	—	+	+
	Tsusiopsis	—	—	+	—	—	+	—
	Tsutsutsi	—	—	—	+*	—	+	—
Azaleastrum	Candidastrum	—	—	—	—	+	—	—
	Choniastrum	Hedegaard records hairs				Not available		
	Euazaleastrum	—	+	—	—	—	+	—
	Mumeazalea	—	+	—	—	—	+	—
Hymenanthes		+	+	—	—	—	+*	—
Rhododendron	Lepipherum	—	—	—	—	+*	—	—
	Pogonanthum	—	—	—	—	+*	—	—
	Vireya	—	—	—	—	+	—	—
Pseudazalea		—	—	—	—	+*	—	—
Rhodorastrum		—	—	—	—	—	+	—
Pseudorhodorastrum	Rhabdorhodion	—	—	—	—	+	—	—
	Rhodobotrys	—	—	—	—	—	+	—
	Trachyrhodion	—	—	—	+*	—	+	—

TABLE 1. For explanations of hair and venation types see figs. 1 and 2. A, hair type anomalous. *For species exceptions and occasional or rare exceptions within species, see table 2.

A. Cotyledons Glabrous

1. Lepidote Groups
   (a) Subgenus *Rhododendron* (= most lepidote Series)
   (b) Subgenus *Pseudazalea* (= Series *Trichocladum*)
   (c) Subgenus *Rhodorastrum* (= Series *Dauricum*)
   (d) Subgenus *Pseudorhodorastrum* (= Series *Scabrifolium* and *Virgatum*).

   Approximately one quarter of the seedlings in the population of *R. scabrifolium* studied bore a very few hairs of the unique type described above. These were associated with normal scales at the base of the cotyledons.

2. Elepidote Groups
   (a) *Therorhodion* (given generic rank by Sleumer = Series *Camtschaticum*)
   (b) Section *Candidastrum* (= Series *Albiflorum*)

(c) Section *Viscidula* (= Subseries *Nipponicum*)

(d) Section *Pentanthera* (= Subseries *Luteum*). In *R. japonicum* a small proportion of cotyledons bore 1 or 2 hairs at the base (fig. 7a).

(e) Section *Rhodora* (= Subseries *Canadense*) A striking exception among the species of Section *Rhodora* is *R. pentaphyllum* with strongly developed glandular hairs on the cotyledons (fig. 7b). In *R. albrechtii*, also, (fig. 7c) a small proportion of cotyledons bore, at the base, one hair of a type similar to that of *R. pentaphyllum.* The incidence of these hairs varied in different populations of seedlings. The removal of these species to Section *Brachycalyx* (= Subseries *Schlippenbachii*) is proposed below.

(f) Section *Tsutsutsi* (= Subseries *Obtusum*) Most species examined of Section *Tsutsutsi* bore glabrous cotyledons. Hedegaard records hairs on the margins of three species of Section *Tsutsutsi* (*R. serpyllifolium*, *R. linearifolium* and *R. tschonoskii*), seed of which was not available for the present study. The cotyledonary hairs of *R. oldhamii* and *R. rubropilosum* have been described above.

B. Cotyledons Hairy

1. Lepidote Groups

None.

2. Elepidote Groups

(a) Subgenus *Hymenanthes*

All the cotyledons examined bore hairs of type I, and this hair-type was found in no other subdivision of the genus. Often associated with these hairs were glandular hairs of type II. Notched or branched variations of hair type I were prevalent on the cotyledons of the *Falconera* and *Grandia* subsections.

(b) Section *Brachycalyx* (= Subseries *Schlippenbachii*)

The species fell into two groups on the basis of cotyledonary hairs. Although most species bore hairs of type III, *R. quinquefolium* and *R. schlippenbachii* were outstanding in their possession of prominent glandular hairs only (fig. 7d).

(c) Section *Tsusiopsis* (= Subseries *Tashiroi*)

Type III hair present (fig. 6b).

(d) Subgenus *Azaleastrum* (except Section *Candidastrum*)

Of the Sections of this subgenus, seedlings of *Choniastrum* were not available for study; those of *Candidastrum* have already been described as glabrous; and those of the remaining two Sections, *Mumeazalea* and *Euazaleastrum* had glandular hairs only. Whereas the glands of *Mumeazalea* resembled those of *R. schlippenbachii* in having long stalks with globular heads (fig. 7e) those of *Euazaleastrum* were shorter stalked with a more elongate head (fig. 7f).

THE VENATION

This characteristic shows a high degree of constancy (Table 1). A midrib is consistently present in cotyledons, but lateral venation is variable.

The large subgenus *Rhododendron* is characterized by cotyledons lacking lateral veins (fig. 8a,b). Exceptions to this character were found in the two species studied of the Series *Carolinianum* where the cotyledons of the few seedlings available showed lateral venation. Other exceptions occurred in some species of the *Yunnanense* subseries of Section *Triflora*, in a few cotyledons of some species of the Subsect. *Lapponica*, in a few cotyledons of *R. trichostomum* (Section *Pogonanthum*), and in a very small proportion of a population of *R. edgeworthii*. Such exceptional cotyledons showed one or two lateral veins; often this lateral venation was present in only one of the two cotyledons. No large scale examination of cotyledons for venation type was undertaken, but careful scrutiny of a random sample of each of the lepidote species investigated, leaves no doubt that the absence of lateral venation greatly predominates in this subgenus.

In contrast, the other large subgenus, *Hymenanthes*, is defined just as clearly by the presence of lateral veins (fig. 8i,j). They were observed in all species examined, the only exception being two species in the *Campanulata* Subsection.

Most of the sections of Subgenera *Pentanthera*, *Tsutsutsi* and *Azaleastrum* which make up the "chorus subgenerum" *Azalea* of Seithe showed lateral venation which was typically more strongly developed than that found in cotyledons of Subgenus *Hymenanthes* (fig. 8i,j). The two exceptions, Sections *Viscidula* and *Candidastrum*, are monotypic groups (fig. 8p,k). The tendency to the development of strong lateral venation culminated in the three species *R. quinquefolium*, *R. schlippenbachii* and *R. pentaphyllum* where the exceptionally large cotyledons displayed a reticulating system of veins (fig. 8x,u).

The remaining subgenera fall into the "chorus subgenerum" *Rhododendron* of Seithe. In Subgenus *Rhodorastrum* lateral veins were present (fig. 8f); in Subgenus *Pseudorhodorastrum* lateral veins were present in Sections *Trachyrhodion* (fig. 8d), and *Rhodobotrys* (fig. 8e), but absent in Section *Rhabdorhodion* (fig. 8c); and in Subgenus *Pseudazalea* most cotyledons examined of *R. trichocladum* were found to lack lateral veins although they occurred in some of the larger seedlings (fig. 8g).

CELLS OF THE HYPOCOTYL

As seen in profile, the epidermal cells of the hypocotyl, especially those immediately below the insertion of the cotyledons, may be flat, convex or papillate. More or less flat profiles were characteristic of most groups, convex hypocotylary cells being rare in lepidote groups, and convex or even papillate cells occurring only sporadically in *Hymenanthes*. My own observations, supplemented by those of Hedegaard, indicated that projecting cells were characteristic of Section *Brachycalyx* and *R. pentaphyllum*, and, to a lesser extent, of Section *Tsutsutsi*. *R. japonicum* was the only representative of Section *Pentanthera* in which this character was recorded.

LENGTH OF COTYLEDONS

Cotyledons ranged in size from 0·5–8·0 mm. Insufficient measurements were made to obtain the range of size present in individual species, but

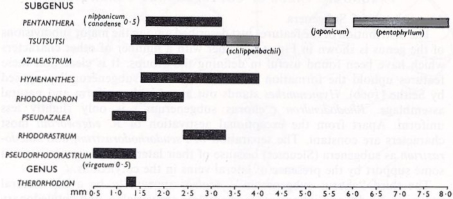
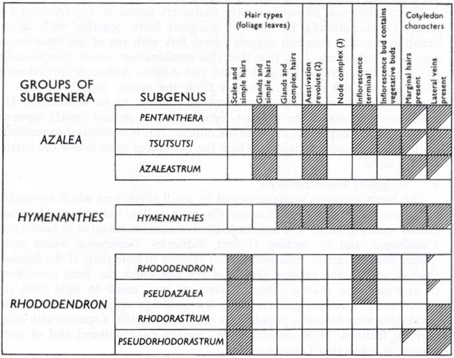


FIG. 3. Subgeneric comparison of cotyledonary length.



GROUPS OF SUBGENERA	SUBGENUS	Hair types (foliage leaves) Scales and simple hairs	Glands and simple hairs	Glands and complex hairs	Aestivation revolute (2)	Node complex (3)	Inflorescence terminal	Inflorescence bud contains vegetative buds	Cotyledon characters Marginal hairs present	Lateral veins present
AZALEA	PENTANTHERA		▨		▨		▨		◩	◩
	TSUTSUTSI		▨		▨		▨	▨	◩	▨
	AZALEASTRUM		▨		▨				◩	◩
HYMENANTHES	HYMENANTHES			▨	▨	▨	▨		▨	▨
RHODODENDRON	RHODODENDRON	▨					▨			◩
	PSEUDAZALEA	▨					▨			◩
	RHODORASTRUM	▨								▨
	PSEUDORHODORASTRUM	▨							◩	▨

FIG. 4. Summary of subgeneric characters. (1) Seithe (1960). (2) Sinclair (1937). (3) Philipson & Philipson (1968).

characteristic differences between the subgenera were apparent and are indicated in Fig. 3.

TAXONOMIC VALUE OF COTYLEDONARY CHARACTERS

A. Groups of Subgenera

The distribution of the features just described among the major subdivisions of the genus is shown in Fig. 4, together with a number of other characters which have been found useful in defining the groups. It is clear that these features uphold the formation of the three "chori subgenerum" proposed by Seithe (1960). *Hymenanthes* stands out as a highly uniform and natural assemblage. *Rhododendron* ("chorus subgenerum") is only slightly less uniform. Apart from the exceptional aestivation of *R. edgeworthii* most characters are constant. The separation of *Pseudorhodorastrum* and *Rhodorastrum* as subgenera (Sleumer) because of their lateral inflorescence is given some support by the presence of lateral veins in the cotyledons.

The third "chorus subgenerum", *Azalea*, appears to be a less natural grouping. Nodal and inflorescence characters are variable, and cotyledonary features further indicate diversity. In particular, the monotypic groups, *Viscidula* (*R. nipponicum*) and *Candidastrum* (*R. albiflorum*) do not conform to the general "*Azalea*" pattern. All other sections are similar in having cotyledons with lateral venation and marginal hairs, but the hairs differ sufficiently to provide diagnostic characters for most of the subdivisions. These will be discussed below.

The combination of cotyledonary characters found in *Therorhodion* (= Series *Camtschaticum*), i.e. lack of marginal hairs, together with lateral venation (fig. 8h), does not suggest a close link with any of the three major groups of subgenera. It is true that this combination occurs exceptionally in "chori subgenerum" Rhododendron and Azalea. Although cotyledonary characters do not clearly exclude it from the genus, the distribution of vascular strands within the hypocotyl may prove to be distinctive. The xylem components of the two cotyledonary traces remain clearly separate throughout the hypocotyl and into the radicle. This is in contrast to seedlings of the genus Rhododendron in which the two traces unite below the cotyledonary node.

B. Subgenus Rhododendron

This large subgenus is characterized by small cotyledons which invariably lack hairs, although they occasionally have scales, and which also lack lateral veins (fig. 8a,b). The only important exceptions occurred in Subsection *Caroliniana*, and in Section *Triflora*, Subseries *Yunnanense* where some species showed lateral venation. It is of interest to note that, of the lepidote rhododendrons, the Section *Triflora* is the one which has been considered to approach the azaleas. Other exceptions may come to light with the examination of further material, as a few seedlings with lateral veins in the cotyledons were found in populations of *R. edgeworthii*, a species with other atypical features, of *R. trichostomum* (Section *Pogonanthum*) and of some species of subsection *Lapponica*.

C. Other Lepidote Subgenera

Pseudazalea, *Rhodorastrum* and *Pseudorhodorastrum* all resemble subgenus *Rhododendron* in their lack of marginal hairs. Section *Trachyrhodion* (*R.*

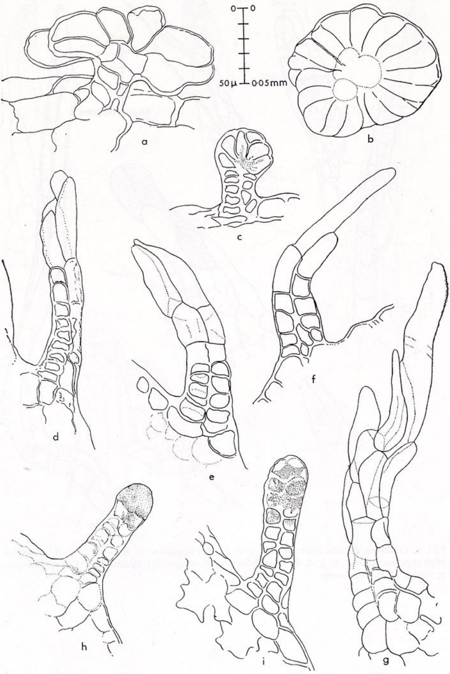


FIG. 5. Trichome details. Scales, a–c: a, *R. polyandrum*; b, scale in surface view of *R. rigidum*; c, *R. trichocladum*. Hair type I, d–g: d, *R. fauriae*; e, *R. dryophyllum*; f, *R. zeylanicum*; g, type I, branched, *R. grande*. Hair type II, h–i (Hymenanthes): h, *R. arboreum*; i, *R. haematodes*.

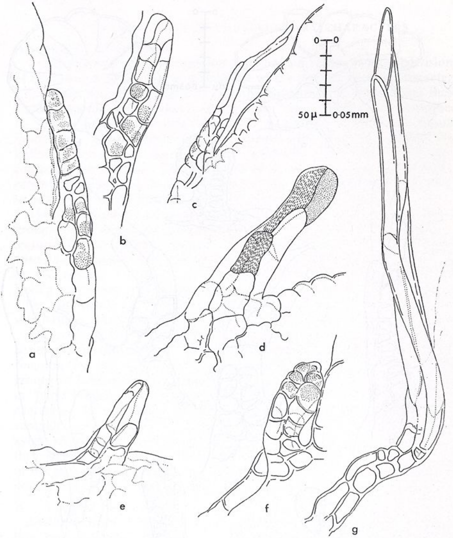


FIG. 6. Trichome details. Hair type III, a–c: a, *R. reticulatum*; b, *R. tashiroi*; c, *R. wadanum*. Hair type anomalous, d–g: d, *R. scabrifolium*; e, *R. oldhamii*; f, (glandular), *R. rubropilosum*; g, (seta), *R. rubropilosum*.

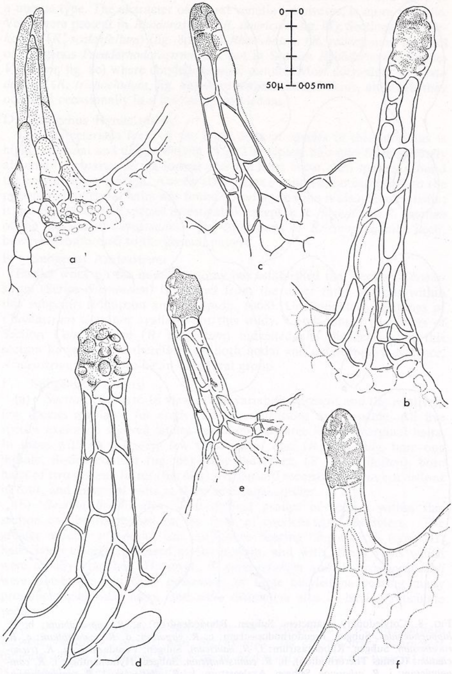


FIG. 7. Trichome details. Hair type anomalous: a, *R. japonicum*. Hair-type II (Azalea), b–f: b, *R. pentaphyllum*; c, *R. albrechtii*; d, *R. schlippenbachii*; e, *R. semibarbatum*; f, *R. leptothrium*.

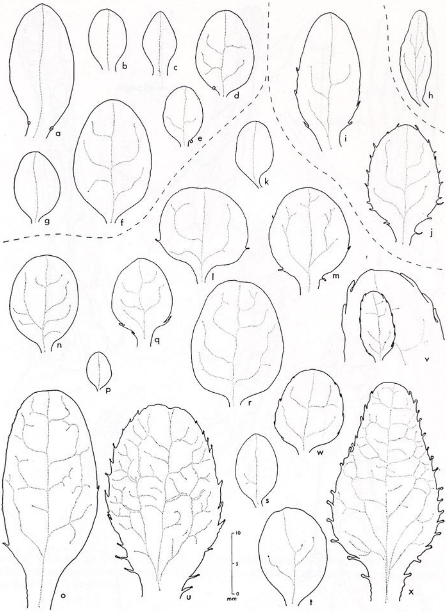


FIG. 8. Cotyledonary characters. Subgen. Rhododendron: a, *R. supranubium*; b, *R. hippophaeoides*. Subgen. Pseudorhodorastrum: c, *R. virgatum*; d, *R. scabrifolium*; e, *R. racemosum*. Subgen. Rhodorastrum: f, *R. dauricum*. Subgen. Pseudazalea: g, *R. trichocladum*; (Genus Therorhodion), h, *R. camtschaticum*. Subgen. Hymenanthes: i, *R. campanulatum*; j, *R. arboreum*. Subgen. Azaleastrum: k, *R. albiflorum*; l, *R. semibarbatum*; m, *R. leptothrium*. Subgen. Pentanthera: n, *R. canescens*; o, *R. japonicum*; p, *R. nipponicum*; s, *R. canadense*; t, *R. vaseyi*; u, *R. pentaphyllum*. Subgen. Tsutsutsi: q, *R. rubropilosum*; r, *R. kaempferi*;v, *R. tashiroi* (with marginal detail); w,*R. reticulatum*; x, *R. schlippenbachii*.

scabrifolium) is exceptional in that some seedlings bore one or two hairs of a unique type. The character of lateral venation, however, is more variable. Veins were present in *Rhodorastrum* (*R. dauricum*, fig. 8f), Sections *Trachyrhodion* (*R. scabrifolium*) (fig. 8d) and *Rhodobotrys* (*R. racemosum*) (fig. 8e) of Subgenus *Pseudorhodorastrum* but not in Section *Rhabdorhodion* (Series *Virgatum*, fig. 8c) where cotyledons were minute. Most cotyledons of *Pseudazalea* (*R. trichocladum*, fig. 8g) were without lateral veins, although they occurred occasionally in a few larger cotyledons.

D. Subgenus Hymenanthes

The characteristic form of the cotyledons of species in this subgenus is highly constant and diagnostic (fig. 8i,j). The typical hair may be moderately abundant or sparse. In the former case the hairs occur, well spaced, around the cotyledonary margin. Among the species examined, no exception to the presence of marginal hairs was found. Lateral venation is also characteristic; it was observed in all species investigated, except in *R. fulgens* and *R. lanatum* of the Subsection *Campanulata*. The cotyledons of *R. campanulatum* itself, however, conformed to the general pattern.

E. Subgenus Azaleastrum

Earlier work on the nodal anatomy has established that Section *Choniastrum* (Series *Stamineum*) is distinct from the other three sections within this subgenus (Philipson and Philipson, 1968). Unfortunately, seedlings of *Choniastrum* were not available for this study. Cotyledonary characters of Section *Candidastrum* (*R. albiflorum*) indicated the distinctness of this section however, and therefore, on both nodal and cotyledonary evidence, *Azaleastrum* appears to be an unnatural group.

F. Subgenus Tsutsutsi

(a) *Section Tsutsutsi.* In view of the variability present and the relatively few species available for study, no generalizations are possible. All five species examined showed lateral venation and three lacked marginal hairs. In those with hairs a very few seedlings of one, (*R. oldhamii*), bore one minute, ill-defined hair (fig. 6e) while the other, (*R. rubropilosum*), bore hairs of two distinct forms (fig. 6f,g). Hedegaard records glabrous cotyledons in four, and marginal hairs in three additional species.

(b) *Section Brachycalyx.* Two distinct groups of species within this section can be recognised on the basis of cotyledonary characters. The greater number of species had cotyledons bearing "finger-like" (type III) hairs lying closely appressed to the margin, and with lateral veins which were usually branched. However, *R. quinquefolium* and *R. schlippenbachii* were outstanding in their possession of large cotyledons bearing many prominent glandular hairs, and were distinctive also in having reticulate venation.

(c) *Section Tsusiopsis. R. tashiroi* has been considered to be intermediate between Sections *Tsutsutsi* and *Brachycalyx*. Its cotyledonary characters indicate clearly its affinity with Section *Brachycalyx*, since the type III hair is confined to these two sections.

G. Subgenus Pentanthera

(a) *Section Rhodora.* The four species of this section fall into two groups both morphologically and geographically. The two species from North America (*R. vaseyi* and *R. canadense*) agree in their glabrous cotyledons, while the Japanese species (*R. albrechtii* and *R. pentaphyllum*) have glandular hairs on the cotyledonary margins. These are abundant and prominent in *R. pentaphyllum* but only occasionally present in some populations of *R. albrechtii*. In addition, the cotyledons of *R. pentaphyllum* were the largest of any species of Rhododendron studied, and were outstanding also in their reticulate venation. These very characteristic features are indistinguishable from those of *R. schlippenbachii* and *R. quinquefolium*. The markedly papillate surface of the hypocotyl of *R. pentaphyllum* and, to a lesser degree of *R. albrechtii*, is in contrast to the flat surface of the hypocotyl of the North American species of Section *Rhodora*. In this feature, however, they are similar to *R. schlippenbachii* and most of its allies.

The great resemblance between the seedlings of *R. pentaphyllum*, *R. schlippenbachii* and *R. quinquefolium*, together with the similarity of mature plants of these species, suggests that they are closely related. At present they are placed in two distinct subgenera, a separation based on the relationship of the vegetative buds to the scales of the terminal inflorescence bud. In *R. pentaphyllum* the new shoots arise from buds below the terminal inflorescence, whereas in *R. schlippenbachii* and *R. quinquefolium* the buds of the new shoots are enclosed within the lower scales of the inflorescence bud. In spite of this morphological difference, the overall resemblance between *R. pentaphyllum* and *R. schlippenbachii* often leads to confusion between the two species. This similarity includes the form of the mature leafy shoot and floral morphology. The two-lipped form of the corolla of the North American species is in contrast to the rotate-campanulate form of the Japanese. Similarity also extends to details of ornamentation of the seed. The testa of *R. pentaphyllum* is unornamented, as is that of *R. schlippenbachii*, in contrast to the high degree of ornamentation of the seed of the North American species of Section *Rhodora* where elaborate projections are developed (Hedegaard, 1968). In *R. albrechtii* the elaboration of the testa is only weakly indicated. This mutual syndrome of characters appears to outweigh the position of the buds on which feature the species have been allocated to different subgenera. It would appear, therefore, that *R. pentaphyllum* (and less certainly *R. albrechtii*) should be classified with *R. schlippenbachii* and *R. quinquefolium* and the three in turn should be separated from the remaining species of Section *Brachycalyx*.

(b) *Section Pentanthera*. This section comprises about fifteen North American species, one Eastern European, and two closely related species in the Far East. Nine of the North American species have been studied and all of these, together with the European *R. luteum* have completely glabrous cotyledons with lateral veins (fig. 8n). Of the two Far Eastern species, only *R. japonicum* was available for study, and here some cotyledons in otherwise glabrous seedling populations bore one or a few stout, multicellular hairs (fig. 8). Also, the cotyledons were very much larger than those of other species in the section, and they showed greater branching of lateral veins which sometimes became reticulate. In addition, the cells of the hypocotyl of *R. japonicum* seedlings were prominently papillate in contrast to those of the European and North American species which had a flat outer surface. This distinction is further upheld by the corolla which is broadly funnel-like in *R. japonicum* and does not show the narrow tubular base characteristic of the other species.

It should be noted that only the Far Eastern species occasionally produces cotyledonary hairs and it is interesting that this situation is parallel to that just described in the Section *Rhodora*.

(c) *Section Viscidula*. The single species in this group, *R. nipponicum*, undoubtedly stands in isolation within the genus on account of its unique, drooping, cylindric flowers with included style and stamens. The isolation is supported by the characteristics of the cotyledons (fig. 8p). The combination of a lack of both hairs and lateral veins occurs elsewhere in the "chorus subgenerum" *Azalea* only in the equally isolated *R. albiflorum* (Section *Candidastrum*).

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TABLE 2

Cotyledonary details of species studied

Sleumer, 1949 & 1958	Handbook, 1967	Species examined	Hair type				Venation		
Subgen. & Sect.	Series & Subser.		I	II	III	A	I	II	III
(Excluded)	Camtschaticum	camtschaticum Pallas	—	—	—	—	—	+	—
Pentanthera	Azalea								
Rhodora	Canadense	canadense (L.) Torrey	—	—	—	—	—	+	—
		vaseyi A. Gray	—	—	—	—	—	+	—
		albrechtii Maxim.	—	(+)	—	—	—	+	—
		pentaphyllum Maxim.	—	+	—	—	—	—	+
Viscidula	Nipponicum	nipponicum Matsumura	—	—	—	—	+	—	—
Pentanthera	Luteum	arborescens (Pursh) Torrey	—	—	—	—	—	+	—
		atlanticum (Ashe) Rehd.	—	—	—	—	—	+	—
		calendulaceum (Michx.) Torrey	—	—	—	—	—	+	—
		canescens (Michx.) Sweet	—	—	—	—	—	+	—
		japonicum Suringar	—	—	—	+	—	+	—
		luteum Sweet (H.)	—	—	—	—	—	+	—
		nudiflorum (L.) Torrey)	—	—	—	—	—	+	—
		occidentale A. Gray	—	—	—	—	—	+	—
		roseum (Loisel.) Rehd.	—	—	—	—	—	+	—
		serrulatum (Small) Millais	—	—	—	—	—	+	—
		viscosum (L.) Torrey	—	—	—	—	—	+	—
Tsutsutsi									
Brachycalyx	Schlippenbachii	amagianum Makino	—	—	+	—	—	+	—
		farrerae Tate	—	—	+	—	—	+	(+)
		mayebarae Nakai & Hara	—	—	+	—	—	+	(+)
		reticulatum D. Don ex G. Don	—	—	+	—	—	+	(+)
		sanctum Nakai	—	—	+	—	—	+	—
		viscistylum Nakai	—	+	—	—	—	+	—
		wadanum Makino	—	+	—	—	—	+	—

		weyrichii Maxim.	—	+	—	—	—	+	—
		quinquefolium Bisset & Moore	—	+	—	—	—	—	+
		schlippenbachii Maxim.	—	+	—	—	—	—	+
Tsusiopsis	Tashiroi	tashiroi Maxim.	—	—	+	—	—	+	—
Tsutsutsi	Obtusum	kaempferi Planch.	—	—	—	—	—	+	—
		kiusianum Makino	—	—	—	—	—	+	—
		linearifolium Sieb. & Zucc. (H)		U				N.A.	
		obtusum (Lindl.) Planch. (H)	—	—	—	—		N.A.	
		oldhamii Maxim.	—	—	—	+	—	+	—
		pulchrum Sweet (H)	—	—	—	—		N.A.	
		rubropilosum Hayata	—	+	—	+	—	+	—
		serpyllifolium Miquel (H)		U				N.A.	
		simsii Planch. (H)	—	—	—	—		N.A.	
		tosaense Makino	—	—	—	—	—	+	—
		tschonoskii Maxim. (H)		U				N.A.	
		yedoense Maxim. (H)	—	—	—	—		N.A.	
Azaleastrum									
Candidastrum	Albiflorum	albiflorum Hook.	—	—	—	—	—	—	—
Mumeazalea	Semibarbatum	semibarbatum Maxim.	—	+	—	—	—	+	—
Choniastrum	Stamineum	moulmainense Hook. (H)		U				N.A.	
Euazaleastrum	Ovatum	leptothrium Balf. f. & Forrest	—	+	—	—	—	+	—
Hymenanthes	Arboreum								
	Arboreum	arboreum Smith	+	+	—	—	—	+	—
		zeylanicum Hort. ex Loud.	+	+	—	—	—	+	—
	Argyrophyllum	argyrophyllum Franch. (H)		+	—	—		N.A.	
		insigne Hemsl. & Wils.	+	—	—	—	—	+	—
	Auriculatum	auriculatum Hemsl.	+	+	—	—	—	+	—
	Barbatum								
	Crinigerum	crinigerum Franch.		U				N.A.	
	Glischrum	habrotrichum Balf. f. & W. W. Sm.		U				N.A.	
	Maculiferum	pachytrichum Franch.	+	(+)	—	—	—	+	—
	Campanulatum	campanulatum D. Don	+	+	—	—	—	+	—

TABLE 2 (*continued*)

Cotyledonary details of species studied

Sleumer, 1949 & 1958 Subgen. & Sect.	Handbook, 1967 Series & aubser.	Species examined	Hair type I	Hair type II	Hair type III	Hair type A	Venation I	Venation II	Venation III
		fulgens Hook. f.	+	—	—	—	+	—	—
		lanatum Hook. f.	+	—	—	—	+	—	—
	Falconeri	falconeri Hook. f.	+	—	—	—	—	+	—
		hodgsonii Hook. f.	+	—	—	—	—	+	—
		rex Lévl.	+	+	—	—	—	+	—
	Fortunei								
	Calophytum	calophytum Franch.	+	+	—	—	—	+	—
	Fortunei	fortunei Lindl. (H)	+					N.A.	
		vernicosum Franch.	+	+	—	—	—	+	—
	Griffithianum	griffithianum Wight	+	+	—	—	—	+	—
	Oreodoxa	fargesii Franch.	+	—	—	—	—	+	—
	Grande								
		grande Wight	+	—	—	—	—	+	—
		coryphaeum Balf. f. & Forrest	+	+	—	—	—	+	—
	Griersonianum	griersonianum Balf. f. & Forrest	+	+	—	—	—	+	—
	Irroratum								
	Irroratum	aberconwayi Cowan	+	+	—	—	—	+	—
	Parishii	cookeianum Davidian		U				N.A.	
	Lacteum	dryophyllum Balf. f. & Forrest	+	(+)	—	—	—	+	—
		phaeochrysum Balf. f. & W. W. Sm.	+	—	—	—	—	+	—
		wightii Hook. f.	+	+	—	—	—	+	—
	Neriiflorum								
	Forrestii	forrestii Balf. f. ex Diels		U				N.A.	
	Haematodes	haematodes Franch.	+	(+)	—	—	—	+	—
	Sanguineum	sanguineum Franch.		U				N.A.	
	Ponticum								
	Caucasicum	brachycarpum D. Don ex G. Don (H)	+	—	—	—		N.A.	
		caucasicum Pallas (H)	+	—	—	—		N.A.	
		chrysanthum Pallas		—				N.A.	

		degronianum Carrière (H)		+				N.A.	
		fauriei Franch.	+	—	—	—	—	+	—
		makinoi Tagg (H)	+	—	—	—		N.A.	
		metternichii Sieb. & Zucc.	+	+	—	—		N.A.	
		ungernii Trautv.	+	—	—	—	—	+	—
		yakusimanum Nakai (H)	+					N.A.	
	Ponticum	catawbiense Michx.	+	—	—	—	—	+	—
		macrophyllum, D. Don ex G. Don (H)		+				N.A.	
		ponticum Linn. (H)	+					N.A.	
	Taliense								
	Roxieanum	bathyphyllum Balf. f. & Forrest (H)	+	+	—	—		N.A.	
		gymnocarpum Balf. f. ex Tagg	+	+	—	—	—	+	—
	Taliense	sphaeroblastum Balf. f. & Forrest	+	+	—	—	—	+	—
	Wasonii	rufum Batal. (H)	+				—	+	—
	Thomsonii								
	Campylocarpum	callimorphum Balf. f. & W. W. Sm.	(+)	+	—	—	—	+	—
		caloxanthum Balf. f. & Farrer	+	+	—	—	—	+	—
		campylocarpum Hook. f. (H)	+					N.A.	
	Selense	dasycladoides Hand.–Mazz. (H)		+				N.A.	
	Souliei	litiense Balf. f. & Forrest		U				N.A.	
		souliei Franch.	+	+	—	—	—	+	—
		wardii W. W. Sm.	+	+	—	—	—	+	—
Pseudazalea	Trichocladum	caesium Hutch.	—	—	—	—	+	—	—
		chloranthum Balf. f. & Forrest (H)	—	—	—	—		N.A.	
		trichocladum Franch.	—	—	—	—	+	(+)	—
Rhodorastrum	Dauricum	dauricum Linn.	—	—	—	—	—	+	—
		ledebouri Pojarkova (H)	—	—	—	—	+	—	—
		mucronulatum Turcz. (H)	—	—	—	—		N.A.	
Pseudorhodorastrum									
Trachyrhodion }	Scabrifolium	pubescens Balf. f. & Forrest	—	—	—	—		N.A.	
		scabrifolium Franch.	—	—	—	+	—	+	—
Rhodobotrys }		racemosum Franch.	—	—	—	—	—	+	—
Rhabdorhodion	Virgatum	virgatum Hook. f.	—	—	—	—	+	—	—
		oleifolium Franch.	—	—	—	—	+	—	—

TABLE 2 (*continued*)

Cotyledonary details of species studied

Sleumer, 1949 & 1958	Handbook, 1967	Species examined	Hair type				Venation		
Subgen. & Sect.	Series & Subser.		I	II	III	A	I	II	III
Rhododendron									
Lepipherum	Boothii								
	Tephropeplum	tephropeplum Balf. f. & Farrer	—	—	—	—	+	—	—
	Campylogynum	campylogynum Franch.	—	—	—	—	+	—	—
	Carolinianum	carolinianum Rehd.	—	—	—	—		N.A.	
		chapmanii A. Gray	—	—	—	—	—	+	—
		minus Michaux	—	—	—	—	—	+	—
	Cinnabarinum	cinnabarinum Hook. f.	—	—	—	—	+	—	—
		concatenans Hutch.	—	—	—	—	+	—	—
		xanthocodon Hutch.	—	—	—	—	+	—	—
	Edgeworthii	edgeworthii Hook. f.	—	—	—	—	+	(+)	—
	Ferrugineum	ferrugineum Linn.	—	—	—	—	+	—	—
		kotschyi Simonk.	—	—	—	—	+	—	—
	Glaucophyllum								
	Glaucophyllum	brachyanthum Franch.	—	—	—	—	+	—	—
		glaucophyllum Rehder	—	—	—	—		N.A.	
		tsangpoense Hutch. & Ward	—	—	—	—	+	—	—
	Lapponicum	chryseum Balf. f. & Ward	—	—	—	—		N.A.	
		edgarianum Rehd. & Wils.	—	—	—	—		N.A.	
		fastigiatum Franch.	—	—	—	—		N.A.	
		fimbriatum Hutch.	—	—	—	—		N.A.	
		hippophaeoides Balf. f. & W. W. Sm.	—	—	—	—	+	(+)	—
		impeditum Balf. f. & W. W. Sm.	—	—	—	—		N.A.	
		rupicola W. W. Sm.	—	—	—	—	+	(+)	—
		russatum Balf. f. & Forrest	—	—	—	—	+	(+)	—
		scintillans Balf. f. & W. W. Sm.	—	—	—	—		N.A.	
		websterianum Rehd. & Wils.	—	—	—	—		N.A.	
	Lepidotum								
	Baileyi	baileyi Balf. f.	—	—	—	—	+	—	—

Lepidotum	lepidotum Wall.	—	—	—	—		N.A.	
Maddenii								
Ciliicalyx	burmanicum Hutch.	—	—	—	—	+	—	—
	ciliatum Hook. f.	—	—	—	—	+	—	—
	cubittii Hutch.	—	—	—	—	+	—	—
	johnstoneanum Watt	—	—	—	—	+	—	—
	supranubium Hutch.	—	—	—	—	+	—	—
Maddenii	crassum Franch.	—	—	—	—	+	—	—
	maddenii Hook. f.	—	—	—	—	+	—	—
	manipurense Balf. f. & Watt	—	—	—	—	+	—	—
	odoriferum Hutch.	—	—	—	—	+	—	—
	polyandrum Hutch.	—	—	—	—	+	—	—
Megacalyx	dalhousiae Hook. f. (H)	—	—	—	—		N.A.	
	megacalyx Balf. f. & Ward	—	—	—	—	+	—	—
	rhabdotum Balf. f. & Cooper	—	—	—	—	+	—	—
	sinonuttallii Balf. f. & Forrest	—	—	—	—	+	—	—
	taggianum Hutch.	—	—	—	—	+	—	—
Micranthum	micranthum Turcz.	—	—	—	—		N.A.	
Saluenense	radicans Balf. f. & Forrest	—	—	—	—	+	—	—
	saluenense Franch.	—	—	—	—	+	—	—
Triflorum								
Augustinii	augustinii Hemsl.	—	—	—	—	+	—	—
	trichanthum Rehd.	—	—	—	—	+	—	—
Hanceanum	hanceanum Hemsl.	—	—	—	—	+	—	—
Triflorum	ambiguum Hemsl.	—	—	—	—	+	—	—
	keiskei Miq.	—	—	—	—	+	—	—
	lutescens Franch.	—	—	—	—	+	—	—
	triflorum Hook. f.	—	—	—	—	+	—	—
Yunnanense	concinnum Hemsl.	—	—	—	—	+	—	—
	— var. pseudoyanthinum (Balf. f. ex Hutch.) Davidian	—	—	—	—	—	+	—
	davidsonianum Rehd. & Wils.	—	—	—	—	—	+	—
	oreotrephes W. W. Sm.	—	—	—	—	+	—	—
	rigidum Franch.	—	—	—	—	—	+	—
	stereophyllum Balf. f. & W. W. Sm.	—	—	—	—	—	+	—

TABLE 2 (*continued*)

Cotyledonary details of species studied

Sleumer, 1949 & 1958 Subgen. & Sect.	Handbook, 1967 Series & Subser.	Species examined	Hair type I	Hair type II	Hair type III	Hair type A	Venation I	Venation II	Venation III
		tatsienense Franch.	—	—	—	—	+	—	—
		yunnanense Franch.	—	—	—	—	+	—	—
	Uniflorum	ludlowii Cowan	—	—	—	—	+	—	—
		patulum Ward	—	—	—	—		N.A.	
Pogonanthum	Anthopogon	cephalanthum Franch.	—	—	—	—	+	—	—
		trichostomum Franch.	—	—	—	—	+	(+)	—
Vireya	Vaccinioides	aurigeranum Sleum.	—	—	—	—	+	—	—
		beyerinkianum Koorders	—	—	—	—		N.A.	
		christianae Sleum.	—	—	—	—	+	—	—
		commonae Foerster	—	—	—	—	+	—	—
		gracilentum F. v. Muell.	—	—	—	—	+	—	—
		invasorium Sleum.	—	—	—	—		N.A.	
		jasminiflorum Hook. (H)	—	—	—	—		N.A.	
		javanicum Reinw.	—	—	—	—	+	—	—
		laetum J. J. Smith	—	—	—	—	+	—	—
		leptanthum F. v. Muell.	—	—	—	—	+	—	—
		lochae F. v. Muell.	—	—	—	—		N.A.	
		macgregoriae F. v. Muell. (H)	—	—	—	—		N.A.	
		retusum (Bl.) Benn. (H)	—	—	—	—		N.A.	
		saxifragoides J. J. Smith	—	—	—	—	+	—	—
		yelliottii Warb. (H)	—	—	—	—	+	—	—
		zoelleri Warb.	—	—	—	—	+	—	—

TABLE 2. For explanations of hair and venation types see figs. 1 and 2. A, hair-type anomalous (see figs. 6d, e, f, g and 7a). (H) data from Hedegaard (1968). U, hairs present, type unknown (data from Hedegaard) N.A., venation pattern not available.

REFERENCES

BALFOUR, I.B. (1919). Observations on Rhododendron seedlings. *Trans. Bot. Soc. Edinb.* 27: 221–227.

COWAN, J. MACQUEEN (1950). *The Rhododendron leaf. A Study of the epidermal appendages.* Oliver & Boyd, Edinburgh and London.

HEDEGAARD, JOHANNES (1968). Beiträge zur Kenntnis der Morphologie von Rhododendron-Samen. *Rhod. u. immergr. Laubgeh. Jahrb. Deutsche Rhod.-Gesellsch.* Bremen.

KINGDON-WARD, F. (1947). Observations on the classification of the genus Rhododendron. *Rhod. Yearb.* 99–114.

PHILIPSON, W. R. & PHILIPSON, M. N. (1968). Diverse nodal types in Rhododendron. *Journ. Arn. Arb.* 49: 193–217.

SEITHE, ALMUT, geb. v. HOFF (1960). Die Haarformen der Gattung Rhododendron L. und die Möglichkeit ihrer taxonomischen Verwertung. *Bot. Jahrb.* 79: 297–393.

SINCLAIR, J. (1937). The Rhododendron bud and its relation to the taxonomy of the genus. *Notes R.B.G. Edinb.* 19: 267–271.

SLEUMER, H. (1949). Ein System der Gattung Rhododendron L. *Bot. Jahrb.* 7: 511–553.

— (1958). The genus Rhododendron L. in Indochina and Siam. *Blumea*, suppl. 4: 39–59.

— (1964). Ericaceae of Malesia, suppl. 2. *Ibid.* 12: 339–347.

STEVENSON, J. B. Ed. (1930). *The species of Rhododendron.* Rhod. Soc., London. 2nd ed. 1947.

SYNGE, P. M. Ed. (1967). *Rhododendron handbook* (Part I). R.H.S., London.

Plant life at its ecological limits. This book* considers plants which grow under special conditions in localities where at least one ecological factor is not optimal. The author uses numerous examples to illustrate the various correlations between vegetation and locality at those places where there is a limit to plant life—both phanerogamic and cryptogamic. After defining his subject, Prof. Lötschert has chapters on the following topics: vegetation of hot springs such as solfataras; vegetation of mobile soils; plants on soils with mineral deficiencies; bog plants; heath vegetation on podsols; mangroves; epiphytic vegetation. As this list of contents shows, there are two aspects of the subject that are not included: the problems of tree limits in mountainous and arctic regions and the limits of vegetation in the arid conditions of desert.

The author deals with his subject clearly and in detail. Many of his examples are from the region of Central America, such as Cuba and San Salvador, where he has undertaken several investigations. The book is well illustrated with diagrams and photographs and there are very useful lists of further references. It can be recommended to all who are interested in this subject; one only hopes that the author will continue his work and write a similar book dealing with those aspects not dealt with in this one.

S.-W. BRECKLE.

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* Pflanzen an Grenzstandorten. W. Lötschert. Pp. 167, 124 figs., 1 colour tab., 21 tables. Gustav Fischer Verlag, Stuttgart. 1969. 42 DM.