A Survey of the Anatomy of the Rhododendron Leaf in relation to the Taxonomy of the Genus

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(*With Plates* I–XI)

Explanation of the aim and scope of this Investigation

It may be explained, at the very outset, that this investigation into the anatomy of the leaves of Rhododendrons was undertaken with a very definite purpose and that it is accordingly limited in its scope.

The object in view was to ascertain whether the modifications of leaf structure observed in the genus Rhododendron can be regarded as diagnostic criteria of value, and how far these criteria might serve as an aid in classification by clarifying the relationships of species where these are at present obscure.

To go beyond the defined limits, either to explore the anatomy of the leaf in its minutest detail, or to examine the leaves of all the many species from every aspect was not our intention. Difficulties connected with the classification of Rhododendrons explain the aim of this survey and define its scope. At a recent Rhododendron Conference, held by the Royal Horticultural Society in London in 1949 (Rhododendron Year Book, 1949, pp. 29–58), stress was laid upon the desirability of surveying the genus from every point of view with the object of finding new criteria for the arrangement and separation of certain groups of related species which, as they stand, are somewhat confused assemblages. The leaf anatomy, one important aspect which seemed to offer a profitable line of enquiry, is the subject of this paper.

The work connected with this investigation fell naturally into two main parts. Firstly, a preliminary survey by which to discover characters that are subject to modification and which will, at the same time, meet the requirements of the taxonomist in that they are readily observed under the low power of a microscope, in sections cut by hand; secondly, a general survey (when the characters which comply with the above requirements had been determined) to discover how far these characters confirm or run counter to the sub-divisions of the present system of classification, and further to note special features of the leaf anatomy which would appear to have a bearing upon the relationships of the species and their taxonomic arrangement.

A long time ago variations in the structure of the leaves of different species of Rhododendron were observed and recorded and these were shown to have a definite systematic significance.

The subject was investigated by the French and German botanists, Vesque and Breitfeld, who published the results of their respective researches in 1885 and 1888. Although the enormous number of new species added to the genus during the present century has invalidated their work, which is now of little practical value, nevertheless it is highly suggestive.

Both these authors showed not only that there is a considerable diversity in the anatomical structure of Rhododendron leaves, but that such variations may form a basis for classification. They both, in fact, attempted to classify the genus, providing analytical keys to the species they described, based upon modifications of leaf structure together with varying types of leaf appendage. Vesque described eighteen species and Breitfeld about seventy. Subsequently their work has been disregarded by taxonomists; in any case, when the classification of the genus came to be revised in 1930 and "The Species of Rhododendron" was published, their keys were too incomplete to have much value.

None the less their work is significant and our task has been largely to test and amplify these early observations. We have described and illustrated the more outstanding types of structure observed in different Rhododendron leaves; we have recorded the variations met with in the anatomy of the leaves of different species and finally we have discussed the taxonomic significance of various modifications.

In this enquiry we have followed the arrangement set out in "The Species of Rhododendron" and modified in later papers. Detailed investigation has been limited to the scope of that work, because available material of species other than those described was insufficient for a complete survey; the leaf anatomy of species in every series has, however, been studied and the leaves of no less than 587 of the 608 species in the forty-three series (97 %) have been critically examined. Miss E. R. Stott cut and prepared many of the sections, the great majority from living material.

Earlier Investigations

The work of Vesque, to which reference was made above, is historically interesting, not only as being the first comparative study of the anatomy of the leaves of Rhododendrons, but also as one of the earliest attempts to use anatomical characters as systematic criteria. His paper appeared in the Annales des Sciences Naturelles (Ser. 7, Vol. 1, 1885, pp. 238–240) and is concerned with the anatomical characters of the principal families of the Gamopetalae.

The genus Rhododendron is discussed in the chapter on Ericaceae and to the eighteen species with which he is concerned, Vesque, as we have already stated, gives an analytical key, based partly upon the anatomical structure of the leaf and partly upon the structure of the epidermal appendages. As far as the leaf anatomy is concerned he selects for systematic criteria, variations of the epidermis—particularly with regard to the stomata and the number of cell layers; of the palisade tissue; of the spongy mesophyll and of the structure of the midrib. Vesque's work is, however, not representative of the genus as a whole and, although he records noteworthy variations, the value of these as systematic criteria cannot be assessed without investigation in a much wider field.

Breitfeld's paper which was published in Botanische Jahrbücher (Vol. 9, pp. 319–379, 1888) dealt specifically with the genus Rhododendron. It is divided into several parts and, in the first part, he enlarges upon Vesque's work to which he makes frequent reference. Breitfeld describes the anatomy of the leaves of some seventy species in detail under the heads and sub-heads: (1) the epidermis, with the four sub-headings: (*a*) the cuticle, (*b*) the epidermal cells, (*c*) the stomata, (*d*) the trichomes; (2) the palisade parenchyma;

(3) the spongy parenchyma; (4) the vascular bundles and (5) crystals and cell inclusions. He comments upon the variations which may be observed in different species, and associates these with different systematic groups. He also discusses the physiological significance of the leaf anatomy.

The whole of the second part of his paper is devoted to the study of the structure of the leaves in relation to the systematic arrangement of the species. In the third part he gives an analytical key to the Rhododendrons based upon the anatomical structure of the leaf and its epidermal appendages. The final sections of his work are concerned mainly with the leaf anatomy in its relation to the geographical distribution of species and the phylogeny of the genus.

In view of the handicaps under which Breitfeld worked, much credit is due to him—he had to rely entirely on dried material. We have found that, even with the improved methods of microtechnique which are available to-day, it is not easy to prepare sections of leaves from dried herbarium specimens in such a way that a critical examination can be made. Having examined the leaves of many species, Breitfeld arranged the anatomical characteristics which he had observed in the following order of importance from the systematic point of view: (1) the number of cell layers in the epidermis; (2) the size of the epidermal cells—whether the cells of each layer are approximately equal or greatly differ in size; (3) the thickness of the cuticle combined with the extent of the development of the palisade parenchyma; (4) the vascular bundle—whether or not it is supported by bands of sclerenchymatous tissue, and (5) the stomata—whether they are level with the epidermis or definitely raised above it. The significance of all the above variations he discusses in considerable detail and we may note the points upon which special emphasis is laid.

He remarks, as to the thickness of the cuticle, that nearly all species of Rhododendron possess a strongly developed cuticle on the upper side of the leaf. But contrary to this general rule, he cites a number of exceptions with a poorly developed cuticle, for example, R. *grande* Wight, and R. *lepidotum* Wall.

He next points out that, while the cuticle shows little differentiation in its structure, the cell formation of the epidermis is varied and complex. He stresses a marked distinction between Rhododendrons in which the epidermis consists of a single cell layer and those in which it is composed of two or more cell layers. Generally, the first type is characteristic of Azaleas and related groups, while the second type is characteristic of the group Eurhododendron. He comments also upon the variability in the size of the epidermal cells in different species and upon the unusual structure of the epidermis in species of the Vireya group, where the epidermis consists of two layers, the lower layer being composed of exceptionally large cells.

In discussing the palisade parenchyma Breitfeld discriminates between species in which the width of the palisade varies, being less than, equal to, or greater than the width of the mesophyll tissue. Moreover he draws attention to the presence of water storage cells in the mesophyll tissue.

With regard to their vascular bundles he divides the Rhododendroideae into two main types—firstly, those in which the sclerenchymatous tissue, which forms the bundle sheath, is produced in a band upwards and downwards to meet the upper and lower epidermis; and secondly, those in which the vascular bundles are associated with no such development, but are completely surrounded by parenchymatous tissue.

From the brief resumé of Breitfeld's work given in the foregoing paragraphs it will be seen that, although his investigations extended only to about one-twelfth of the species now known, they covered a wide and varied field. In his survey he includes, in fact, species which are representative of all the more outstanding types of leaf structure which may be seen in the much larger number of species that are available for examination at the present time.

Since Breitfeld's paper appeared, little of importance with regard to our subject has been published and the work of later investigators does not call for further comment in great detail.

Solereder's "Systematic Anatomy of the Dicotyledons" published in 1908, so far as it is pertinent, is largely a reiteration of Breitfeld's earlier observations and views. From the more general standpoint he remarks (Vol. I, p. 480), "Numerous anatomical characters of the leaf structure have been determined and these can be employed for special diagnosis. Among these are: the varied thickness of the cuticle . . . the varied structure of the walls of the epidermal cells, the formation of epidermal papillae on the lower side of the leaf (Rhododendron, etc.), the gelatinisation of the epidermis, a many-layered epidermis (*Diplycosia*, *Gaultheria*, *Pernettya* and *Rhododendron*), various types of leaf structure which are often curious in the ericoid forms . . . branched spicular cells in the tissue of the leaf (*Rhododendron jasminiflorum* Hook.) and other features which will be discussed. . . ."

The subsequent discussion is (with due acknowledgment) based largely upon Breitfeld's observations and Solereder disagrees with him only with regard to one species, R. *gracile* Low. "This species", he remarks (p. 481), "has a simple epidermis, contrary to Breitfeld's description, the structure in question having been quite incorrectly interpreted by him in the species of Rhododendron mentioned, and perhaps also in other species of the section Vireya."

Again, from a general standpoint Solereder further remarks that the cuticular ridges very common in the Ericaceae are apparently wanting in the Rhodoreae, that the strong thickening of the internal cell wall of the cells of the epidermis which occur in some Ericaceae are not observed in Rhododendrons and that the reticulate thickening reported by Simon in other genera is also absent. In another paragraph he notes that gelatinisation of the cell walls is not uncommon in the Ericaceae, but occurs in the tribe Rhodoreae, for example in R. *retusum* Benn. Elsewhere he remarks upon a similar gelatinisation of the internal membranes of the cells of the second epidermal layer in R. *jasminiflorum* Hook.

One other work ought now to be mentioned, namely that of Copeland—"A Study, Anatomical and Taxonomic, of the Genera of Rhododendroideae", which was published in 1943 (American Midland Naturalist, Vol. 30, No. 3, pp. 533–620). Copeland like Solereder comments at some length upon Breitfeld's observations. He does not, however, make use of leaf anatomical characters in his outline of classification though he describes the anatomy of two species R. *californicum* Hook. and R. *micranthum* Turcz.

Microscopic examination of the Leaf

Let us turn now from the earlier works, which form our background, to the present investigation where we are concerned in the first place with the general features of the Rhododendron leaf and the main variations in structure that may be observed in the leaves of different species.

The Rhododendron leaf, if we consider the genus as a whole, though it varies greatly in shape and size, may be described as a normal dorsiventral leaf, with the following general features as seen, when examined under a microscope, in transverse section: (1) an upper epidermis—the dermal layer is a single layer of cells or more than one layer of cells in thickness,* (2) the typical mesophyll consisting of palisade parenchyma cells and of spongy parenchyma often with sclereids, (3) the midrib and secondary nerves, (4) a lower epidermis—a single layer of cells to which the stomata are confined.

The Upper Epidermis

The cuticle is normally well developed. In certain groups of species, however, it is very thin; in others on the contrary it is very thick, but every gradation between these two extremes will be observed when a sufficiently large number of species is examined.

When the epidermis is simple, consisting of a single cell layer (Pl. I and II), the cells are either square in outline or frequently rectangular, elongated to a lesser or greater extent in a transverse direction. The cell walls are thin, moderately thick, or rarely very thick.

When the epidermis is multiple, the dermal layer consisting of two (Pl. III and IV), three (Pl. V and VI), or occasionally four layers of cells, the leaf falls into one of two distinct categories. In the first category the cells of each layer are equal or approximately equal in size, or those of the lower layer or layers are, at the most, only slightly larger than those of the upper layer. In the second the cells of the lower layer or layers are always much larger than those of the upper layer (at least twice as large). Much variation is observed in the thickness of the cell walls of the cells of the upper layer; the walls of the cells of the lower layers are occasionally strongly thickened, but are more frequently very thin and such cells obviously constitute a water storage endodermis.

The Mesophyll

The palisade cells of the mesophyll vary very considerably in different species. Individual cells differ in length and the number of cell layers is inconstant. The palisade tissue is often interrupted by "girders" of strongly sclerosed cells, which connect the upper epidermis with the bundle sheaths of the lateral veins. The spongy mesophyll differs greatly in its degree of aeration; the intercellular spaces are extremely large in some species, but are small in others.

Water tissue, in the form of groups of very large thin-walled storage cells, occurs in certain groups of species, but cells of this kind are altogether absent in others. Water tissue when present, as for example in R. *argyrophyllum* Franch., lies in the spongy mesophyll between the lateral veins of the lamina.

The Midrib and Secondary Nerves

The vascular bundle of the midrib, in its simpler form, is a single, shallowly concave bundle with a poorly or moderately well developed bundle sheath.

* It is unnecessary for our purpose to discriminate between epidermis and hypodermis. Thick walled cells in the lower dermal layer or layers serve to reinforce the epidermis, but, in many species, doubtless serve also for water storage.

No ambiguity arises by describing the epidermis as biseriate or multiseriate and referring to the several dermal layers.

Such a simple type of midrib is characteristic of the Azaleas. In most other species of Rhododendron the midrib in section shows two vertically opposed bundles; the lower bundle is the larger and is concave above, thus forming a concavity in which lies the smaller upper bundle, which is inverted. According to its size the upper bundle fills the concavity to a lesser or greater degree. In rare instances the upper bundle is large enough completely to fill the cavity of the lower bundle and a single amphiphloic bundle is formed. Occasionally the upper bundle is split in two. The bundle sheath is nearly always well developed both above and below the bundle and is frequently produced upwards to meet the epidermis. From the bundle sheath, on the underside, numerous chain-like filaments, composed of small thickened cells linked in a loose network, spread out through the parenchymatous tissue to its outer edge, where they unite with sclerosed cells to form layers of collenchyma in contact with the lower epidermis. Within this network large thin-walled water storing cells are frequently present. This structure characteristic of many species is illustrated in Plate III.

Sclerenchymatous tissue, where it occurs in the tissue of the lamina, is associated with the secondary vascular bundles.

The secondary nerves, like the midrib, are enclosed in a bundle sheath. In many species it will be observed that from the bundles (and particularly the larger bundles) the sclerenchymatous tissue of the bundle sheath is extended to meet the upper epidermis. These extensions act as strengthening layers collectively known as a " girder system ". Such a " girder system " is more or less strongly developed in various species and is well illustrated in R. *arboreum* Sm. (Pl. IX). The corresponding tissue below the midrib is, in the leaves of Rhododendrons, rarely developed into definite strengthening bands to connect the vascular bundles with the lower epidermis.

The tissue between the secondary bundles and the lower epidermis is in certain species undifferentiated parenchyma; in others the cell walls are thickened and a connecting band of collenchyma is formed, very rarely some degree of lignification may be observed; in others again the tissue, functioning as transfusion tissue, takes the form of a group of vertically elongated hyaline cells with pitted walls.

The " girder system " in Rhododendrons is usually therefore incomplete; strongly sclerosed bands are developed only above the bundles. A complete " girder system " connecting the upper and lower epidermis (as may be seen for example in *Phormium tenax* Forst.) is only in rare instances developed in Rhododendrons as for example in species of the Arboreum Subseries.

In close proximity to the vascular bundle of the midrib, both sclereids (stone cells) and compound crystals of calcium oxalate are usually present in the parenchyma; occasionally they are to be found in the spongy mesophyll of the lamina.

The Lower Epidermis

The lower epidermis is invariably composed of a single layer of cells. The individual cells are usually square in outline. The outer edge of the epidermis is commonly straight although not infrequently it is sinuous. In lepidote species the scales are often sunk in deep pits or depressions in the epidermis. In other species again, both lepidote and elepidote, the

outer cell walls are produced into long or short, dome-shaped or conical protruberances or papillae (Pl. X). To draw a clear line of distinction between species with papillae and those without is, however, difficult, for every gradation can be observed, from what is no more than a mere convexity of the cell wall to papillae so well developed that they may accurately be described as short epidermal hairs.

The cuticle varies in thickness, in different species, as does the cuticle of the upper epidermis.

The stomata (which are confined to the lower epidermis in Rhododendrons) are, in elepidote species, commonly raised above the surface of the epidermis but in lepidote species they are more or less level with the surface (Pl. X). In species in which the scales are sunk in definite depressions, there is a tendency for the stomata to be restricted to the walls of the pits.

Anatomical characters as diagnostic criteria

These then are the outstanding anatomical features of the Rhododendron leaf and in the course of our preliminary survey it became evident that the characters most likely to be of diagnostic value were, in fact, those that had already been noted and used by both Vesque and Breitfeld.

Bearing in mind that the main object of this survey was to find readily discernible characters which would be of use in the classification of the genus, we drew up a list of the main criteria in their apparent order of importance:

(1) The number of cell layers of the upper dermis.
(2) The relative size of the cells of the different dermal layers.
(3) The thickness of the cuticle in relation to the depth of the outer cells of the dermal layer.
(4) The presence or absence of water tissue.
(5) The presence or absence of papillae.
(6) The depth of the palisade mesophyll in relation to the total thickness of the leaf.
(7) Variation of the vascular bundles and associated sclerenchyma.
(8) The degree of development of sclereids and crystals.

Later in the course of this investigation it became evident that some reassessment of this order was called for. It was seen that the two characters of primary importance are (1) the number of cell layers of the upper dermis and (2) the size of the cells of the dermal layers. The thickness of the cuticle, the occurrence of water tissue and the presence or absence of papillae were found to be criteria of distinctly lesser value. The remaining two characters, the depth of the palisade and the presence or absence of sclereids were seen to have no general significance. It was observed that the depth of the palisade is not constant in many species and that the number of cell layers of the palisade is variable or indeterminate within the limits of a single species. With regard to the development of sclerenchyma associated with the vascular bundles, great variation was observed (even in a single leaf when sections were taken from different regions along the midrib), and to standardise the position in the lamina at which sections should be taken was found to be impracticable. A useful comparison of the anatomy of the midrib of different species could not therefore be made.

As to sclereids and crystals, these were found to be present in the great majority of species and with no noticeable variation which could be correlated with any particular group of species indicating relationship.

In accordance with the facts set out in the preceding paragraphs, it was decided, when extending the survey to cover the whole genus in detail, to limit the observations to be made to the first five above mentioned criteria. These criteria, the salient features of the leaf anatomy of importance from a taxonomic point of view, may be exemplified by selecting representative species.

In order that the main differences in the anatomy of the leaves of Rhododendrons may be clearly understood we shall describe in detail the leaves of four such species. The first three species R. *chloranthum* Balf. f. et Forrest, R. *argyrophyllum* Franch. and R. *bullatum* Franch. have respectively a single, double and triple layered epidermis and serve to illustrate the types of leaf structure common in the great majority of the species listed in " The Species of Rhododendron ". But in addition to these three types, a fourth distinctive type of leaf structure is common to many Javanese species of the Vireya section as well as to species of the Vaccinioides Series (species of the subgenera Vireya and Pseudovireya of the Flora of British India) which are characterised by long-tailed seeds. To illustrate this type in which the epidermal cells are unusually large we have chosen R. *asperulum* Hutch. et Ward.

Leaving aside, for the present, a number of exceptions, it may be said that Rhododendrons, according to the anatomy of their leaves, fall into one of four well defined groups, which will be readily recognised by comparing the characteristics of the four representative species.

The four outstanding types of leaf structure described

1. A Uniseriate or One-Layered Epidermis

R. chloranthum Balf. f. et Forrest (Pl. I and II)

The leaves of R. *chloranthum* are approximately 280 μ in thickness.

The cuticle is smooth and thin (4 μ in depth). The upper epidermis is a single layer of thin-walled, elongated, rectangular cells 36 μ long, 18 μ broad. The palisade mesophyll consists of two layers of closely packed, moderately elongated cells (five times as long as broad), which occupy slightly less than half the total depth of the lamina. The spongy mesophyll is a highly aerated tissue, the cells tending to form anastomosing filaments which connect the palisade layer with the lower epidermis. The mesophyll surrounding the vascular bundle of the midrib consists of almost spherical cells very variable in size, up to 95 μ in diameter. The walls of the mesophyll cells between the vascular bundle and the upper epidermis are moderately thickened, a similar thickening of the cell walls may be observed in the mesophyll below the bundle in the cells immediately adjacent to the lower epidermis.

The vascular bundle of the midrib, which shows no specialised features, is of moderate size and is enclosed in a sclerosed bundle sheath.

The sclerenchyma associated with the larger lateral nerves of the lamina forms " girders " connecting the vascular bundles with the upper epidermis. Similar tissue associated with the smaller bundles forms a simple sheath round the bundle, but is not produced upwards to meet the epidermis.

Crystals of calcium oxalate are few but may be observed immediately below the vascular bundle. Sclereids are absent.

The lower epidermis is composed of small ovate cells variable in size, not above 25 μ in length.

The cuticle is thin, stomata are only slightly raised above the level of the epidermis, papillae are absent.

2. A Biseriate or Two-Layered Epidermis

R. argyrophyllum Franch. (Pl. III and IV)

The leaves of R. *argyrophyllum* are approximately 420 μ in thickness.

The cuticle is moderately thick (7 μ in thickness). The upper epidermis consists of a double layer of moderately thick-walled cells, approximately equal in size. The cells are rectangular or square in outline, from 20 to 35 μ in length and about 20 μ deep.

The palisade mesophyll consists of three rather irregular layers of cells (three times as long as broad), occupying less than one-third of the total depth of the lamina. The spongy mesophyll is highly specialised; water tissue is present between each pair of vascular bundles in the form of groups of large thin-walled colourless cells. Below each vascular bundle and connecting it with the lower epidermis are groups of vertically elongated hyaline cells with pitted walls—transfusion tissue, which is clearly shown in the illustration (Pl. III).

Two types of cells are to be found in the mesophyll surrounding the midrib, firstly chains or filaments of small oval cells with slightly thickened walls which branch and anastamose forming a network, and secondly large, thin-walled cells which fill the spaces in the network—water tissue.

The vascular bundle of the midrib is similar to that of R. *chloranthum* but is larger and shows greater development of the bundle sheath.

The lateral nerves are poorly developed, but are numerous and occur at regular intervals. They have a narrow bundle sheath which is produced upwards to meet the epidermis as a weak band of strengthening tissue.

Small compound crystals occur in the leaf especially in close proximity to the vascular bundle of the midrib.

The cells of the lower epidermis are small, rectangular, 16 μ long, 10 μ wide. The stomata are raised on subsidiary cells to as much as a 100 μ above the epidermal surface. Papillae are absent.

3. A Multiseriate or Three- to Four-Layered Epidermis

R. bullatum Franch. (Pl. V and VI)

The leaves of R. *bullatum* are approximately 235 μ in thickness.

The cuticle is smooth and thin (4 μ in depth).

The upper epidermis consists of three layers of cells, the cells of the lower layers being considerably larger than those of the upper layer. Those of the upper layer are rectangular in outline more or less elongated transversely, slightly variable in size, approximately 30 μ long by 10 μ deep. The cells of the middle layer are distinctly longer than broad while those of the lower layer are almost spherical. The cells of the middle layer, very variable in size, are, on an average, 46 μ in length and 23 μ in depth; those of the lower layer are approximately 36 μ in diameter.

The palisade mesophyll is made up of two to three moderately regular layers of typical palisade cells, 80 μ long by 10 μ wide. The cells of the

spongy mesophyll are small and spherical, 12 μ in diameter and closely packed, and, in consequence, the intercellular spaces are much more restricted than in the normal leaf. These cells contain a greater number of chloroplasts than the usual spongy mesophyll cell.

The vascular bundle of the midrib resembles that of R. *argyrophyllum*; the bundle sheath is well developed and easily distinguished from the midrib parenchyma.

The midrib parenchyma contains sclereids with very thick walls, singly or in groups of three or four. Calcium oxalate crystals occur, but are not numerous.

The sclerenchyma associated with the larger lateral nerves (not shown in the illustration) is strongly developed and produced upwards to the upper epidermis. This thickening occurs also below the bundle but never meets the lower epidermis, being always separated from it by at least a few mesophyll cells.

The lower epidermis is composed of moderately sized cells (rather larger than those of the outer layer of the upper epidermis), approximately 28 μ long and 14 μ deep. The outer walls of the cells are convex, or produced as papillae varying up to 30 μ long.

4. A Uniseriate Epidermis with the Cells Megamorphic

R. asperulum Hutch. et Ward (Pl. VII and VIII)

The leaves of R. *asperulum* are about 615 μ in thickness.

The cuticle is thick (18 μ in depth). The upper epidermis is made up of a continuous layer of very large cells which are rectangular or pyriform in outline, elongated vertically, thin-walled and somewhat variable in size, up to 140 μ deep and 57 μ wide. The lateral walls of adjoining cells are either in contact for their whole length or are separated for part of their length by the palisade parenchyma which intrudes between them to varying depths.

The palisade cells are small, never more than twice as long as broad, about 10 μ in width and 20 μ in depth; they are not arranged in regular layers.

The spongy mesophyll is a homogeneous tissue, which occupies fully two-thirds of the whole leaf thickness. This tissue is well aerated and contains more chloroplasts than are normally present in such cells, which may be accounted for by the poor development of the palisade layer.

The vascular bundle of the midrib is a simple small bundle enclosed in a narrow but strongly sclerosed bundle sheath. The bundles of the lamina differ only in that they are smaller. The bundle sheath is not produced either upwards or downwards, the bundles are therefore completely surrounded by mesophyll cells.

Sclereids, which are large, few and exceptionally strongly thickened, occur singly in close proximity to the main vascular bundle and only rarely in the mesophyll of the lamina. Crystals are few and scattered. The cells of the lower epidermis, although more variable in size than is normal, show no remarkable features. The cuticle is of similar thickness to that of the upper epidermis.

It will be noted that the first three types, illustrated by R. *chloranthum*, R. *argyrophyllum* and R. *bullatum* can be readily distinguished according to whether the epidermis is single, double or triple. The striking feature of

the fourth type, illustrated by R. *asperulum* is the upper dermal layer formed of very large cells whose main function is obviously water storage. This layer of gigantic cells may itself be discontinuous and the cells may be variable in size, although always very much larger than corresponding cells in other types.

Modifications which call for Comment

To the general statement that Rhododendrons may be classified in four distinct categories according to their leaf structure, some qualification is required, but this is in the main explanatory and limited to species of the Vireya group and to those of the Ovatum and Lepidotum Series.

Species in these three sections show certain minor modifications which call for further comment in relation to the types which have already been illustrated.

1. The Vireya Group

Although all species of the Vireya group, including species of the Vaccinioides Series, appear to fall into the fourth category, they show some diversity. The epidermis consists of a well defined single layer, but in some species a few cells may occur above the regular cell layer. These, however, when present, are never numerous. It should be noted also, that in some species of this group, the cells of the lower epidermis are of normal size, but in others they are unusually large, although not so large as the cells of the upper layer.

As to the cuticle, this is thick on both the upper and lower epidermis, but, owing to the presence of the small cells in the upper epidermal layer, the thickness cannot be indicated with reference to the depth of the first cell layer.

Certain modifications of structure to be observed in species of the Vaccinioides Series may here be noted.

In R. *quadrasianum* Vidal, the lower epidermal cells are large, approximately half the size of those of the upper dermal layer. The spongy mesophyll is highly aerated. In R. *vaccinioides* Hook. f. the lower epidermis is irregularly composed of larger and smaller cells. In R. *Vidalii* Rolfe the single layer of the upper epidermis is very irregular, composed of very large and comparatively small cells intermittently distributed.

2. The Ovatum Series

Species of the Ovatum Series, it is interesting to note, have characteristic features showing in their upper epidermal structure a certain similarity to species of the Vaccinioides Series.

The epidermis, although very definitely two-layered, has a distinctive structure which is a reliable diagnostic criterion for the group. The cells of the upper layers are small, but the lower layer is composed of large cells similar to those described in R. *asperulum*. This resemblance between species of the Ovatum Series and those of the Vaccinioides Series, though not necessarily indicative of relationship, is worthy of notice.

The leaf of R. *ovatum* Maxim. has a lower epidermal layer which is somewhat irregular, of cells of varying size, up to 32 μ wide and 64 μ deep, and these cells intrude into the mesophyll, as observed in species of the Vaccinioides series. The leaf of R. *Bachii* Lévl. is similar in structure but less irregular; some of the large epidermal cells in R. *hongkongense* Hutch.

attain the size of corresponding cells in R. *ovatum*, but they tend to be narrower. R. *Vialii* Delavay et Franch. is again like R. *ovatum* but with an incomplete layer of large cells immediately under the lower epidermal layer, a condition which recalls the leaf of R. *quadrasianum* Vidal. In R. *leptothrium* Balf. f. et Forrest, however, the cells of the upper layer are large and form an easily distinguishable continuous layer, while those of the lower layer are much smaller than in previously mentioned species (25 μ wide, 37 μ deep).

3. The Lepidotum Series

All species of the Lepidotum Series, the other series which calls for special mention, should, in our opinion, be regarded as having a single-layered epidermis, although the epidermal cells are frequently divided by a transverse septum. In the species figured R. *lepidotum* Wall. (Pl. XI) and in some others the septae lie midway between the upper and lower cell walls and the epidermis consequently appears to be 2-layered, but this regularity is infrequent, the septae are not as a rule equidistant from the cell walls. The presence of these transverse septae is a useful diagnostic criterion; although not present in all species they are of very common occurrence in the series.

Finally, as a general note, it should be remarked that when sections are examined, with regard to the number of epidermal cell layers, the examination should be made at some distance from the midrib and between the lateral veins, because of a tendency for the regularity of the layers to be disturbed in close proximity to the vascular bundles.

Leaf anatomy of the species in relation to their Classification

The second part of our investigation was a general survey of the species in their series from the point of view of their leaf anatomy. Altogether the leaves of some 587 species were examined and the main anatomical features, which we have already discussed were recorded for each species. The results, for the sake of conciseness, have been set out in tabular form and will be found as an appendix. In this table the species are listed in their series and against each the following anatomical details are recorded—(*a*) the number of dermal layers; (*b*) the relative size of the cells of each layer when there is more than one cell layer, equal or larger when those of the lower layer are larger, or much larger than those of the upper layer; (*c*) the thickness of the cuticle; (*d*) the presence or absence of water tissue; and (*e*) the presence or absence of papillae. Additional notes are added when comment seems called for upon any other anatomical feature of taxonomic interest. The leaf sections examined were cut by hand and the preparations required were made from fresh material whenever this was available. Dried material had to be used for a very small percentage of the species examined. No detailed survey was made of species in the Azalea Series where there is apparently no great variation in structure.

Taxonomic Data Summarised

In summing up the data, whereby the taxonomic value of the anatomical characters may be assessed, a distinction has been made between series which are homogeneous (the lists include series with a single species) and series which are heterogeneous.

Yet a closer scrutiny will reveal that there is more uniformity than at first appears; frequently the homogeneity is disturbed only by one or two aberrant species. We may classify the series and subseries under the various headings: (1) Number of Cell Layers; (2) Relative Size of Cells of the Different Layers; (3) Thickness of the Cuticle; (4) Presence or Absence of Water Tissue; (5) Presence or Absence of Papillae.

From the information before us in the appendix, it will be seen that series, such as the Anthopogon Series, where the species all agree in the details of their leaf anatomy are the exceptions. In the great majority of the series disparity among the species will be remarked and in some series, like the Ponticum Series, the species are notably heterogeneous.

1. Number of Cell Layers

The number of cell layers of the upper epidermis is one, two, three or rarely four. The special characteristics of species of the Vireya group and of the Vaccinioides, Ovatum and Lepidotum series have already been commented upon. According to the number of cell layers in the upper epidermis the series and subseries may be arranged in the following manner.

(*a*) Epidermis 1 layered

Homogeneous Series—Albiflorum, Azalea, Camtschaticum, Micranthum, Semibarbatum, Stamineum, Anthopogon, Carolinianum, Dauricum, Ferrugineum, Lapponicum, Lepidotum, Saluenense, Trichocladum, Vaccinioides.

Homogeneous Subseries—Oreotrephes, Yunnanense (with a few exceptions).

(*Heterogeneous Series* mainly 1 layered—Uniflorum, Heliolepis.
,, ,, almost equally 1 and 2 layered—Triflorum.
,, ,, mainly 2 layered, partly 1 layered—Arboreum, Ponticum, Glaucum.)

(*b*) Epidermis 2 layered

Homogeneous Series—Auriculatum, Irroratum, Ovatum, Camelliaeflorum, Cinnabarinum, Moupinense, Scabrifolium, Virgatum.

Homogeneous Subseries—Crinigerum, Forrestii, Neriiflorum, Sanguineum, Wasonii, Campylocarpum, Souliei, Selense, Hanceanum, Maddenii, Megacalyx.

(*Heterogeneous Series* 1–3 layered—Arboreum, Ponticum, Triflorum.
,, ,, 2–3 layered—Barbatum, Campanulatum, Falconeri, Fortunei, Grande, Lacteum, Neriiflorum, Taliense, Thomsonii, Edgeworthii.)

(*c*) Epidermis 3 layered

Homogeneous Series—none.

Homogeneous Subseries—Martinianum, Barbatum.

(*Heterogeneous Series* 2–3 and 4-layered—Maddenii, Boothii.)

Further details regarding the heterogeneous series and subseries may be given ; the figures indicate the number of species.

Series	*Subseries*	1 *layered*	2 *layered*	3 *layered*	4 *layered*
Arboreum		2	18	4	—
	Arboreum	—	2	4	—
	Argyrophyllum	2	16	—	—
Ponticum		4	10	1	—
	Caucasicum	3	8	—	—
	Ponticum	1	2	1	—
Glaucum		1	6	—	—
Heliolepis		6	3	—	—
Triflorum		24	26	2	—
	Augustinii	5	2	—	—
	Polylepis	3	1	1	—
	Triflorum	4	21	1	—
Uniflorum		5	1	1	—
Barbatum		—	17	8	—
	Barbatum	—	—	4	—
	Crinigerum	—	2	—	—
	Glischrum	—	7	3	—
	Maculiferum	—	8	1	—
Campanulatum		—	7	1	—
Falconeri		—	6	7	—
Fortunei		—	24	1	—
Fulvum		—	2	3	—
Grande		—	6	7	—
Lacteum		—	11	4	—
Neriiflorum		—	24	4	—
	Haematodes	—	5	4	—
Taliense		—	39	15	—
	Adenogynum	—	7	9	—
	Roxieanum	—	15	1	—
	Taliense	—	11	5	—
Thomsonii		—	33	6	—
	Thomsonii	—	6	4	—
Edgeworthii		—	1	4	—
Maddenii		—	34	11	2
	Ciliicalyx	—	18	11	2
Boothii		—	2	7	2

2. Relative Size of Cells of the Different Layers

As to the relative size of the cells of the different layers the following information is available.

(*a*) Cells of the different layers of equal size

Homogeneous Series—Arboreum, Auriculatum, Campanulatum, Falconeri, Fortunei, Fulvum, Grande (except R. *protistum*), Irroratum, Lacteum, Neriiflorum (except R. *catacosmum*), Ponticum (except R. *ponticum*), Taliense, Thomsonii, Cinnabarinum, Moupinense.

(*b*) Cells of the lower layer notably large

Homogeneous Series—Ovatum, Boothii, Camelliaeflorum, Edgeworthii, Maddenii, Scabrifolium, Virgatum.

(*Heterogeneous Series*—Barbatum, Glaucum, Triflorum, Uniflorum.)

3. Thickness of the Cuticle

According to the thickness of the cuticle the series and subseries fall into the following classes.

(*a*) Cuticle Thin

Homogeneous Series—Albiflorum, Azalea, Dauricum, Micranthum, Semibarbatum, Trichocladum, Vaccinioides.

(*Heterogeneous Series*, Cuticle thin—medium:—Campanulatum, Cinnabarinum, Glaucum.)

(*b*) Cuticle of Medium Thickness

Homogeneous Series—Auriculatum, Camelliaeflorum, Camtschaticum, Campylogynum, Scabrifolium, Virgatum.

(*Heterogeneous Series*, Cuticle medium—thick:—Edgeworthii, Falconeri Fulvum, Heliolepis, Lacteum, Lepidotum, Saluenense, Stamineum, Taliense.)

(*c*) Cuticle Thick

Homogeneous Series—Anthopogon, Carolinianum, Ferrugineum, Moupinense, Ovatum.

(*Heterogeneous Series*, Cuticle thin—medium—thick:—Arboreum, Barbatum, Boothii, Fortunei, Grande, Irroratum, Lapponicum, Maddenii, Neriiflorum, Ponticum, Thomsonii, Triflorum, Uniflorum.)

4. Presence or Absence of Water Tissue

(*a*) Water tissue present

Homogeneous Series—Barbatum (except R. *pseudochrysanthum*), Fortunei, Fulvum, Irroratum (except R. *irroratum*).

Homogeneous Subseries—Argyrophyllum.

(*b*) Water tissue absent

In all series not specifically mentioned water tissue is commonly absent.

Heterogeneous Series—water tissue present or absent—Arboreum, Campanulatum, Falconeri, Grande, Heliolepis, Ponticum.

5. Presence or Absence of Papillae

(*a*) Papillae present

Homogeneous Series—Anthopogon, Campanulatum, Cinnabarinum, Edgeworthii, Ferrugineum, Lepidotum, Maddenii (except R. *Maddenii*), Micranthum, Moupinense, Scabrifolium, Virgatum.

(*b*) Papillae absent

Homogeneous Series—Albiflorum, Auriculatum, Campanulatum, Campylocarpum, Dauricum, Falconeri, Fulvum, Grande, Lacteum, Ovatum, Saluenense, Semibarbatum, Stamineum, Taliense, Vaccinioides.

Homogeneous Subseries—Arboreum, Crinigerum, Maculiferum.

Heterogeneous Series—Papillae present or absent—Arboreum, Barbatum, Boothii, Carolinianum, Fortunei, Glaucum, Heliolepis, Irroratum, Lapponicum, Neriiflorum, Ponticum, Thomsonii, Trichocladum, Triflorum, Uniflorum.

Tentative Conclusions

From the information given in the preceding paragraphs and set out in detail in the Appendix, we may draw certain tentative conclusions. Furthermore, a number of observations remain to be made, and some interesting points for discussion arise concerning the currently accepted classification.

1. In the first place, it may be stated that the outstanding taxonomic criterion afforded by the leaf anatomy lies in the varying number of the upper dermal cell layers, and that the sub-division of the genus according to this character follows a new and independent line. There is, for example, no correlation between the grouping of the species according to the number of cell layers and their arrangement according to the presence or absence of scales, the broad division of the genus into lepidote and elepidote.

2. It is admitted, however, without discussion, that this sub-division (based on the number of dermal cell layers) is not a fundamental one. The investigation has shown conclusively that, leaving aside other characters, modifications of leaf anatomy do not furnish satisfactory criteria upon which to found a sound classification of the genus as a whole.

Until evidence was provided by this investigation we were unable to evaluate the extent to which the varying structure of the leaf might be regarded as a factor in the taxonomy of the genus, but now we know with certainty that the characters afforded are of secondary importance only, yet a valuable adjunct to other criteria, in part confirmatory of the accepted arrangement, in part conflicting with it.

The full significance of these new data is not, however, immediately apparent. A full appreciation of their value must await a review of the genus, when they with other criteria will be considered together.

It may be stated that the preparation of an artificial key based upon differences of the leaf structure presents no great difficulty with the information now available, but advisedly no attempt has been made to follow and extend the work of Vesque and Breitfeld because such a key would be purely artificial, incomplete and of little practical value.

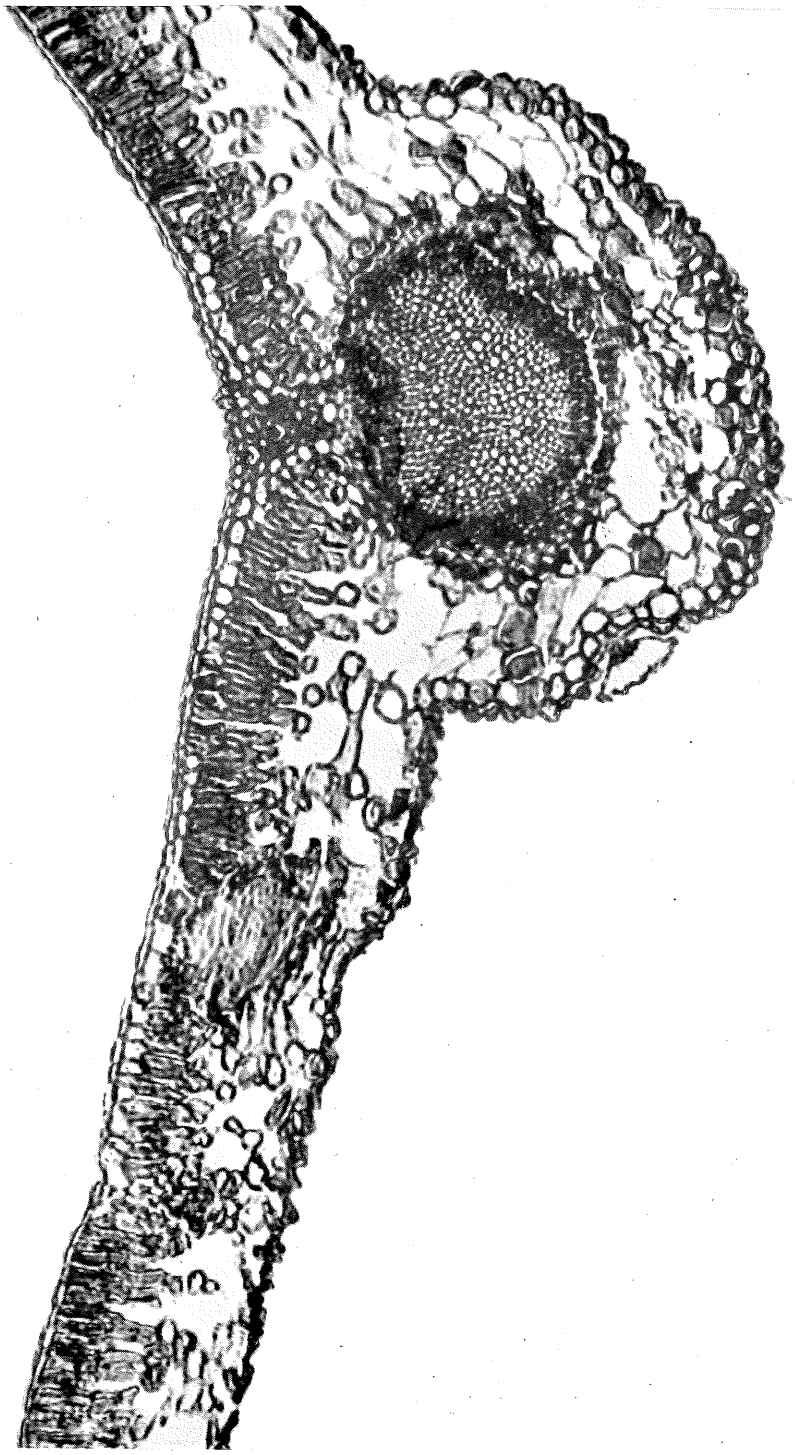
3. How far can similarity in leaf structure be regarded as indicative of relationship?

The first point to be raised in this connection is that few of the series are homogeneous as to leaf structure. (Some of those in the foregoing list, as mentioned, consist of single species only, others of only a few very closely allied species.)

However, the conformity (as regards the listed characters) of the species in such large series as Anthopogon and Fortunei suggests that similarity of leaf structure does in fact denote a close affinity.

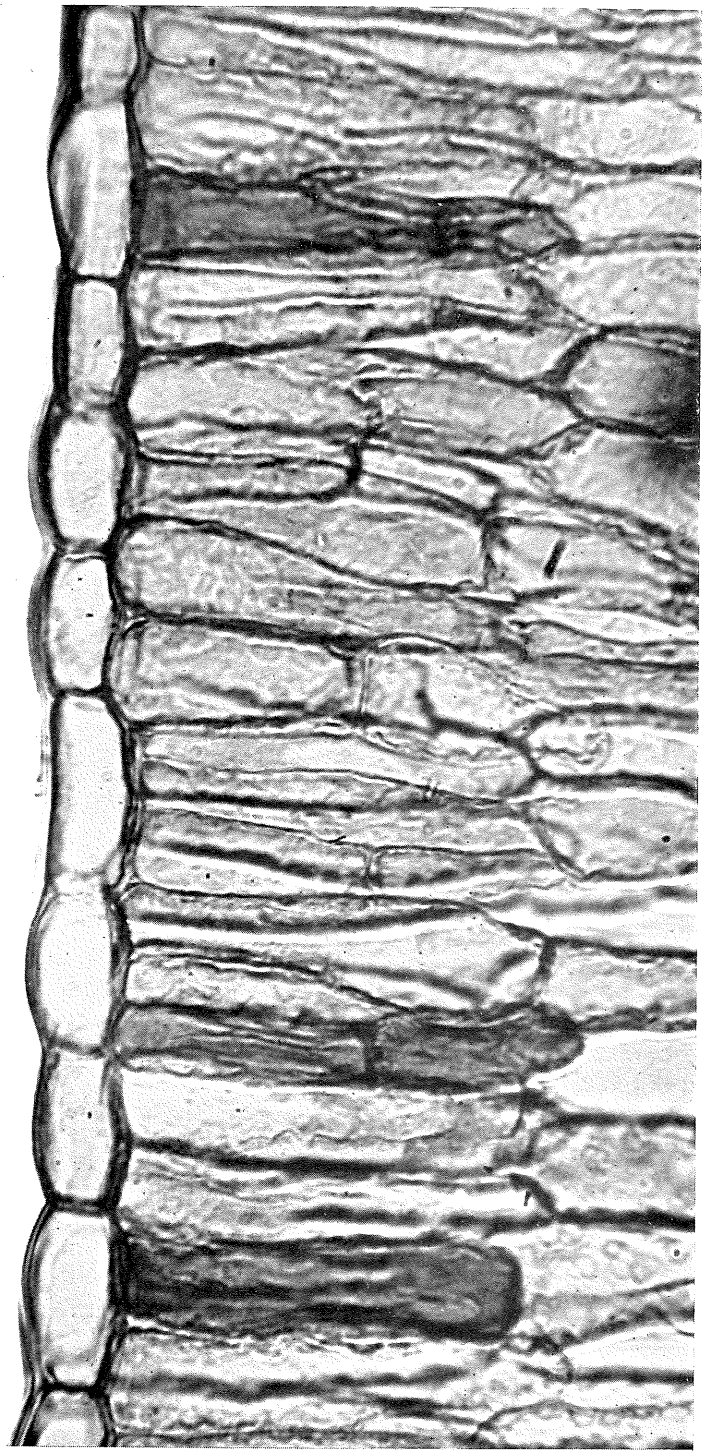
If this can be assumed, then we might expect the converse to be true, that heterogeneous series are (as some are acknowledged to be) somewhat confused and artificial assemblages. The admitted admixture in series such as Ponticum, Neriiflorum and Taliense, for example, is reflected in the heterogeneity of their leaf anatomy in detail. But, if we assume that diversity in leaf anatomy signifies an absence of kinship, then certain important divergences must be explained. For example, in the Thomsonii series, R. *Thomsonii* Hook. f. has a two-layered epidermis and R. *Meddianum* G. Forrest a three-layered epidermis, and yet these two species are most closely allied. Again, species of the Falconeri and Grande series are almost equally divided in this respect, and in other series similar discrepancies may be observed between species which are without doubt closely akin.

PLATE I



T.S. of leaf of R. chloranthum. Balf. f. et forrest, × 120

PLATE II

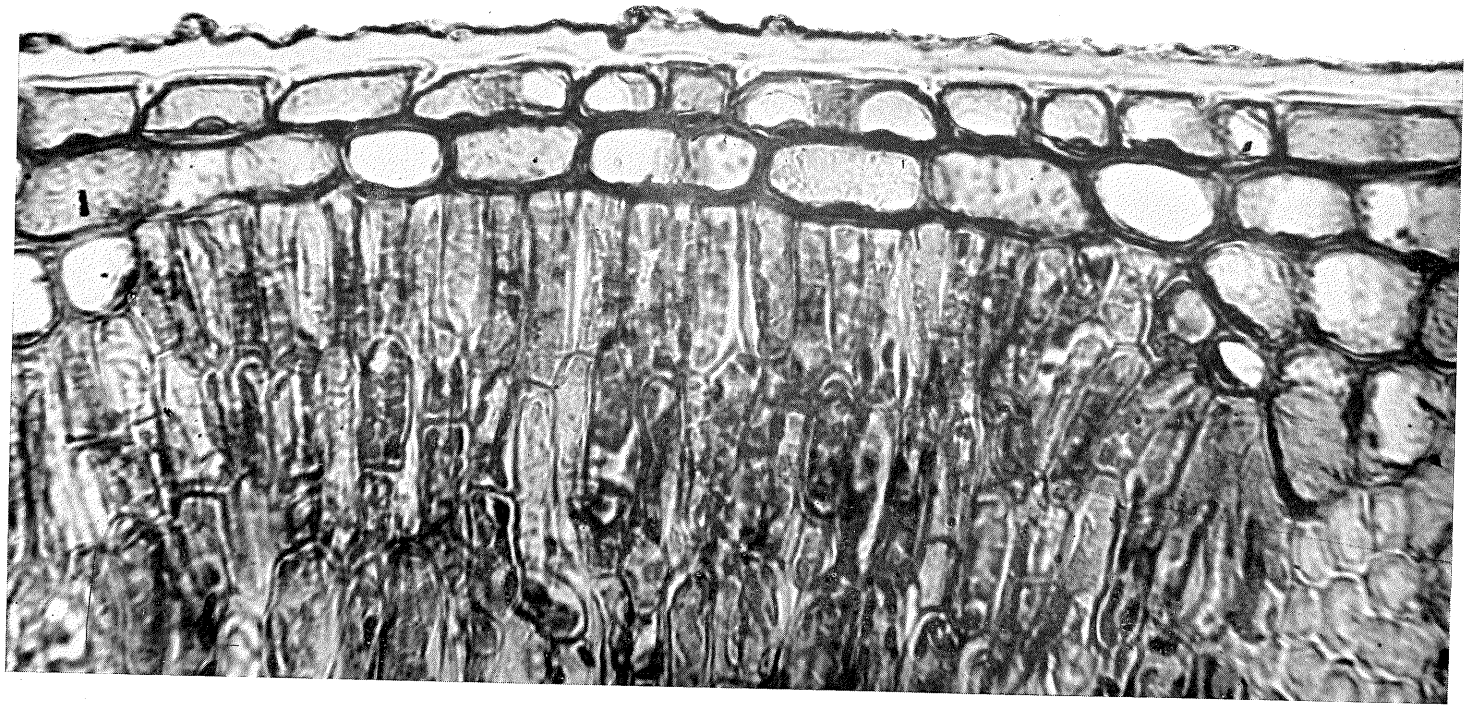


R. CHLORANTHUM. BALF. F. ET FORREST. × 750
Simple one-layered epidermis.

PLATE III



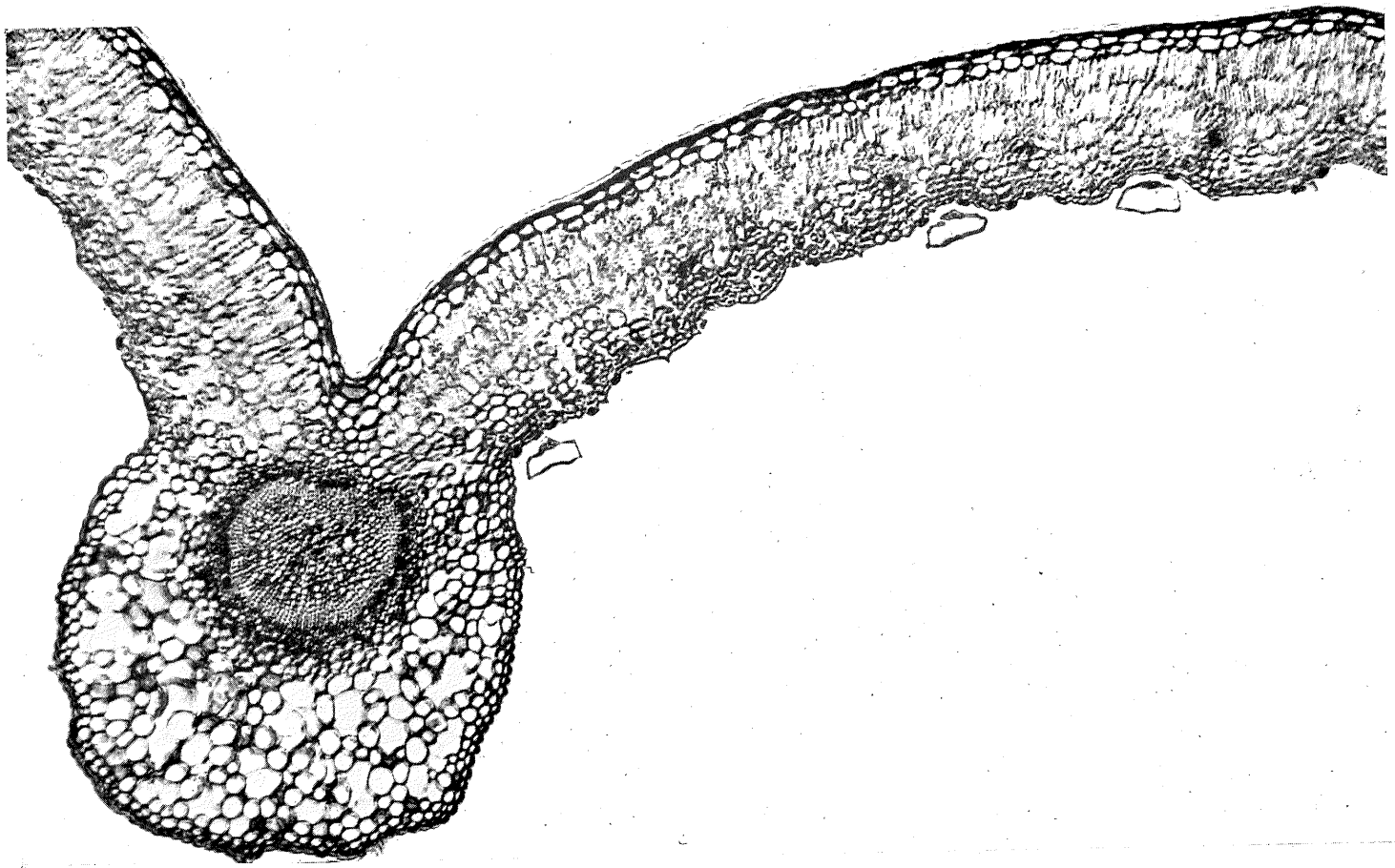
T.S. of leaf of R. argyrophyllum Franch showing transfusion tissue. × 45



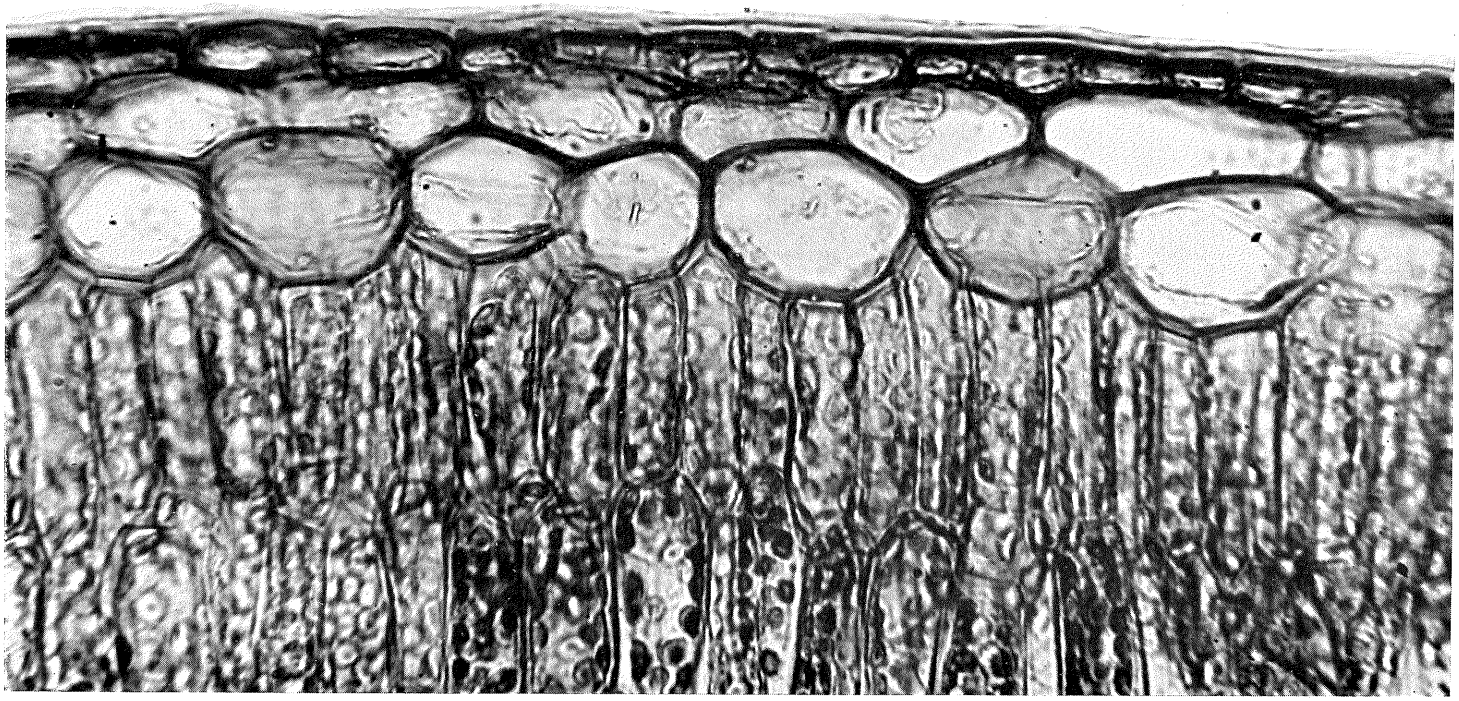
R. ARGYROPHYLLUM FRANCH. × 750

A multiple two-layered epidermis.

PLATE V



T.S. OF LEAF OF R. BULLATUM FRANCH. × 75



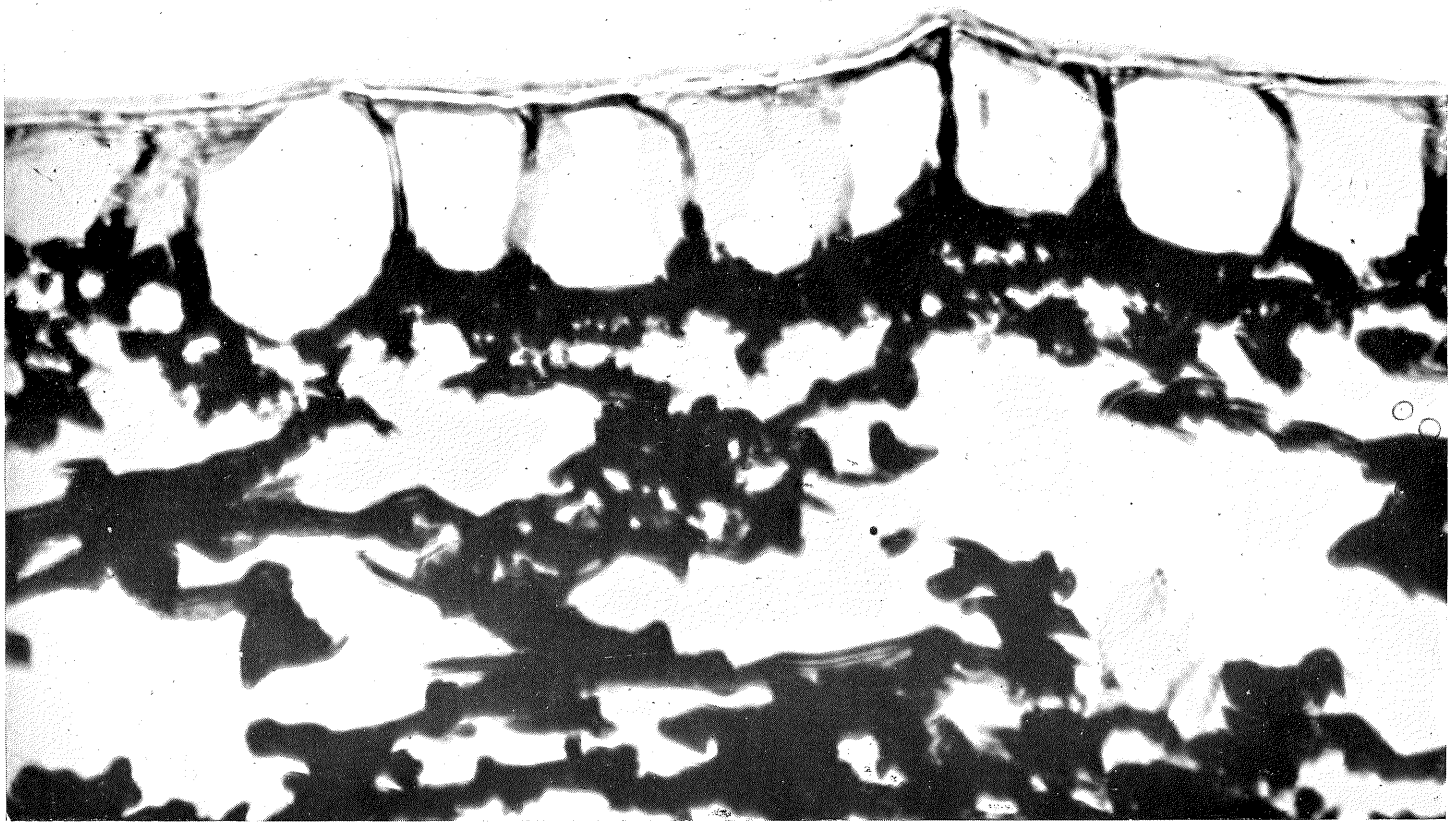
R. BULLATUM FRANCH. × 750

A multiple three-layered epidermis.

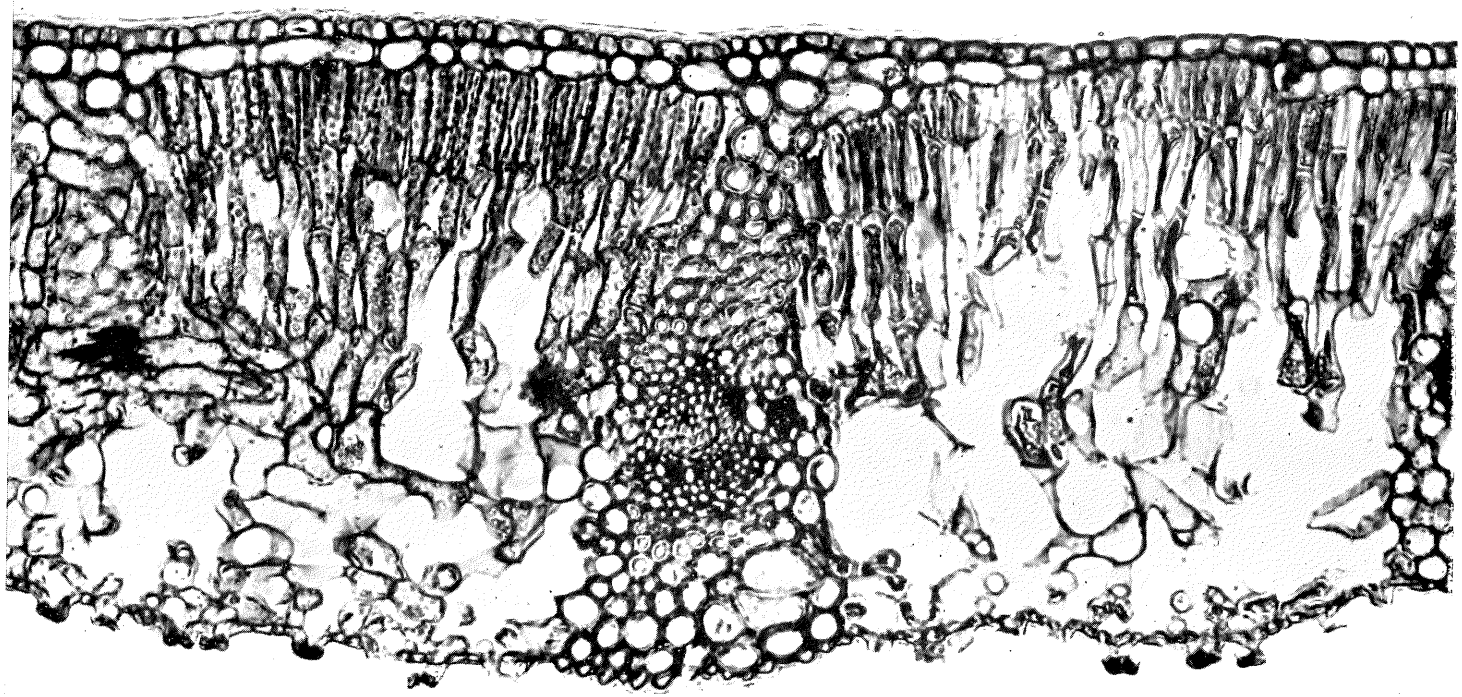
PLATE VII



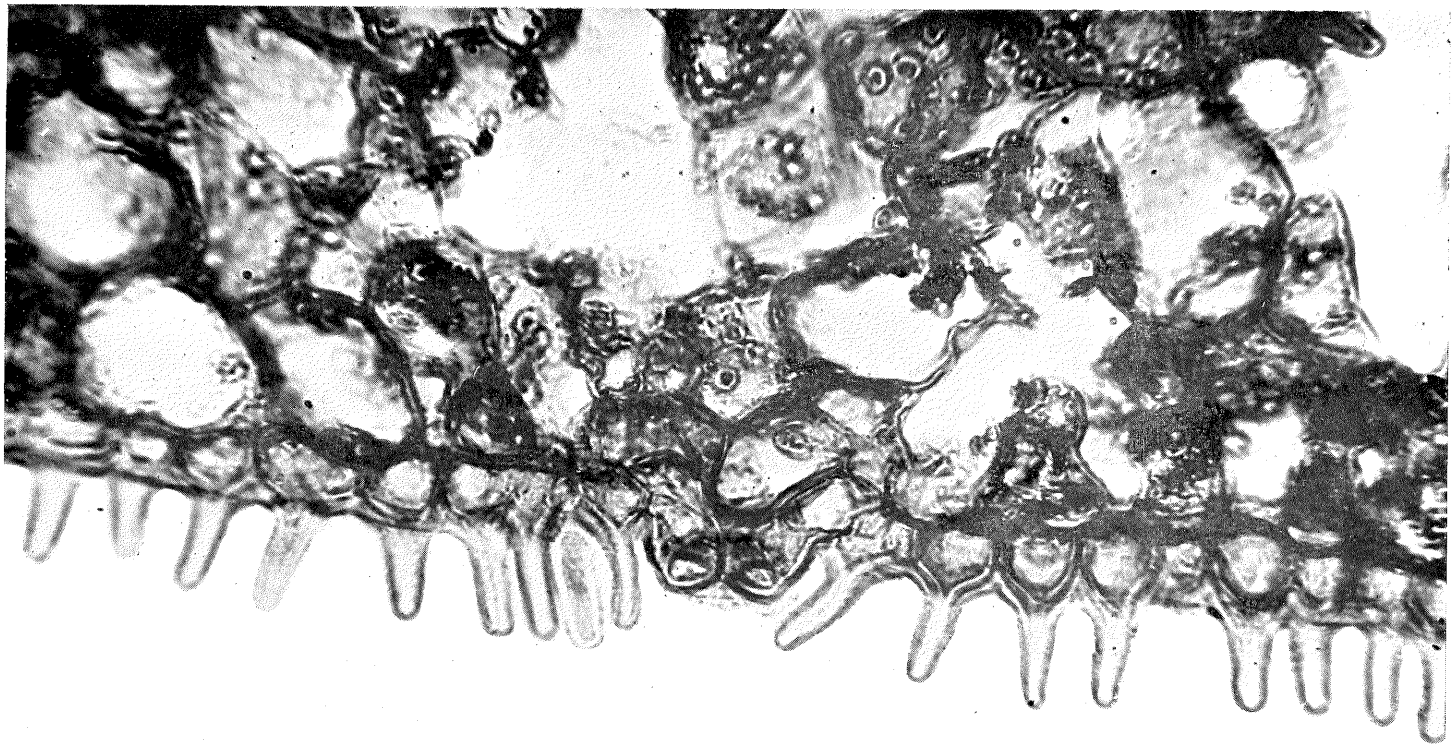
T.S. of leaf of R. asperulum Hutch. et Ward. × 75



R. ASPERULUM HUTCH. ET WARD. × 800
Showing megamorphic epidermal cells.



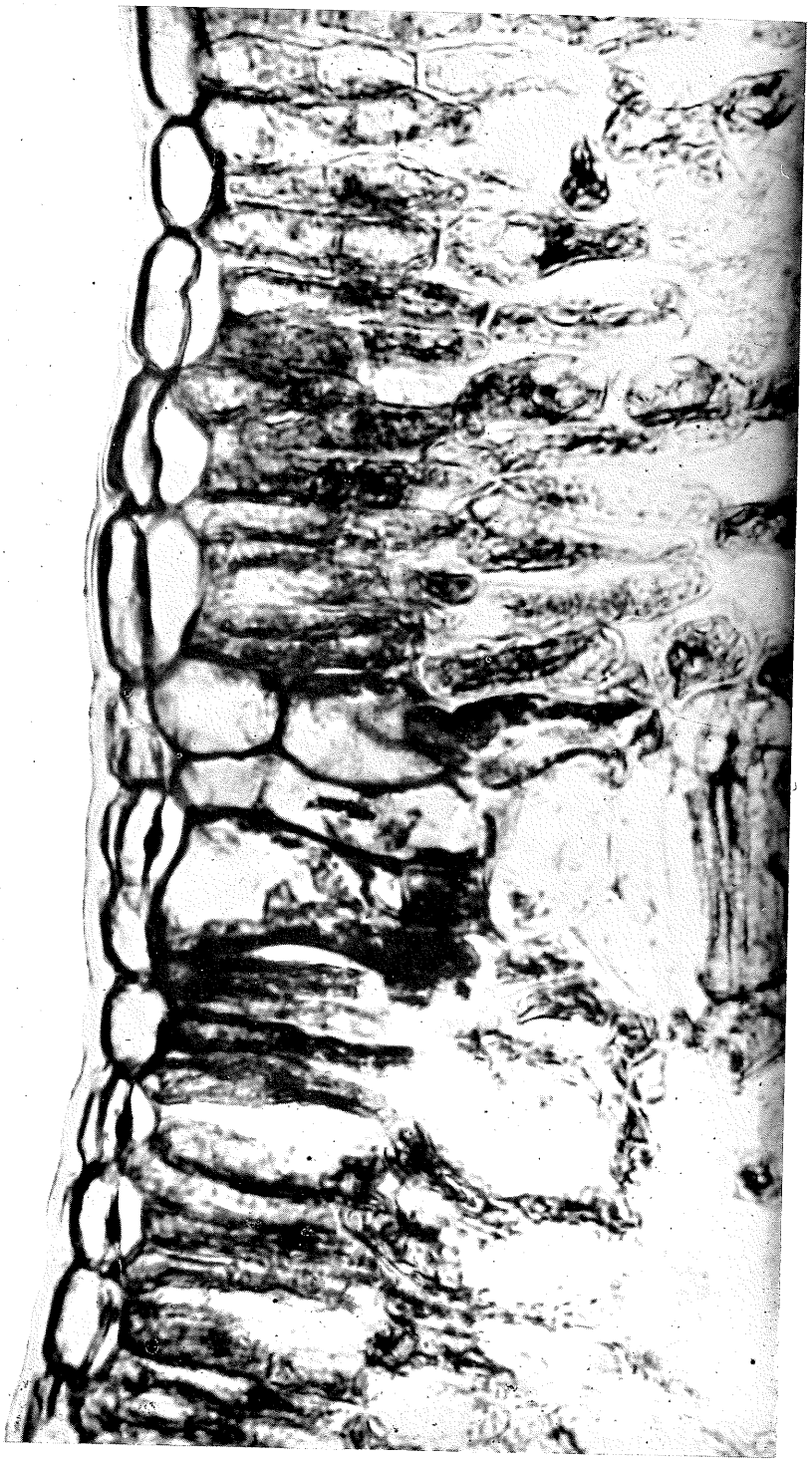
T.S. OF LEAF OF R. ARBOREUM SM. × 225
Showing a "girder system".



T.S. of leaf of R. Boothii Nutt. × 725
Showing stomata and papillae.

PLATE X

PLATE XI



R. OPIDOTUM WALL. × 725
Showing cells of a single-layered epidermis divided by transverse septae.

The conclusion we should come to is perhaps that similarity of leaf anatomy may indicate close relationship, but this cannot be asserted as an invariable fact. Divergences within a group of supposedly related species may indicate absence of affiliation suggesting the need for a revised arrangement, but other characters must be taken into consideration. It cannot be assumed forthwith that dissimilarity denies a close kinship.

4. For a primary division of the genus into subgenera the one and only taxonomic criterion which the leaf anatomy affords is, as has been stated, the varying number of the upper dermal cell layers. This offers the alternatives of arranging the species either in two or in four principal categories. In the first instance the contrast is between (*a*) species in which the epidermis is single, of one cell layer, and (*b*) species in which the epidermis is multiple, of more than one cell layer. In the second instance the four categories would be based upon the number of cell layers, whether one, two, three or four, but on account of the indecisiveness in the second and third categories and the few species in the fourth this delimitation would be an impractical one and need not be given further consideration.

Assuming that the genus is sub-divided into the two broad categories, (*a*) epidermis simple and (*b*) epidermis multiple, the distribution of the series in these two categories is noteworthy and the contrast is interesting. In the first category we find, as might be expected, all deciduous rhododendrons —the azalea series, and also the small and possibly related series Albiflorum, Camtschaticum, Micranthum and Semibarbatum. Along with these are the deciduous lepidote series Dauricum and Trichlocadum. The inclusion in this same category of the Stamineum series is of special interest from a phyletic standpoint. The above mentioned series, together with the Anthopogon and Vaccinioides series, are all somewhat apart from other rhododendrons, distinct enough in their general characteristics to have been regarded by various botanists as constituting separate subgenera or sections, excluded from Eurhododendron. To find ranged along with them the further lepidote series Carolinianum, Ferrugineum, Lapponicum, Lepidotum and Saluenense (also with a single epidermis) is unexpected. Hitherto these series have commonly been classed as typical members of the Eurhododendron group and for their alignment with Azaleas, etc., in this instance no entirely satisfactory explanation can be given. With regard to the remaining series Vaccinioides (and linked with it is the Vireya section), the unique structure already described is of special significance. The view expressed in the Flora of British India that Vireya and Pseudovireya (*R. vaccinioides*) should constitute distinct subgenera is strongly supported. It may be that the large-celled epidermal layer is a character which runs parallel to the possession of long tailed seeds, but evidence is not complete. It may be remarked also that the leaf anatomy favours the arrangement in the Flora of British India rather than that of certain later authors, who have given these subgenera (or sections) a different scope.

We may conclude that in deciding upon a primary sub-division of the genus characters other than differences of leaf anatomy will take precedence, but the number of cell layers in the epidermis may at certain points prove to be a useful subsidiary character.

5. In a secondary division of the genus, at the level of the series, subseries or section, the leaf anatomy is occasionally completely diagnostic and often provides a supplementary character for clearer demarcation.

Already the outstanding diagnostic characters associated with the Ovatum

and Lepidotum series as well as with the Vaccinioides series, have been fully described.

At series level, provided certain adjustments are made, the varying number of cell layers is a useful supplementary character, particularly in the segregating of series which have a single epidermis.

With regard to series with a multiple epidermis, although the number of cell layers in the series is often inconstant, definite tendencies may be observed. Certain series are predominantly in the two-layered category; only one subseries is entirely, and one series predominantly in the three-layered category. Discrepancies require to be carefully examined.

The relative size of the cells in the various layers is constant in the series but a few exceptions call for further investigation. This character is probably not of much taxonomic importance, although in certain instances it may furnish a useful supporting criterion. The large cells of the lower layer are a noteworthy feature of a limited number of lepidote series; that the cells are of equal size in the Moupinense series provides contrast for the segregation of species of this series from its allies of the Maddenii series.

The thickness of the cuticle is so variable that this character can be regarded as of secondary significance only, although it is one that may often be an aid to identification when only leaves are available. Species with a single epidermis for example, can readily be divided into two groups according to whether the cuticle is thin or thick. Several series, however, are markedly heterogeneous.

The pronounced development of water tissue in a limited number of series may prove to be a useful character in separating certain closely allied series and as a supporting criterion in establishing the relationships of species in series which are mixed assemblages. It will also be a character of value in connection with the alignment of various units in the course of taxonomic revision. For example, the suggestion has been made on other grounds, as to the Arboreum series, that the Arboreum and Argyrophyllum subseries are so distinct, that the latter should stand apart forming a distinct section. The marked development of water tissue in the Argyrophyllum subseries, and its absence in the Arboreum subseries, adds weight to this view. In any subsequent taxonomic reorganisation the pronounced development of water tissue in the closely allied Barbatum series should also be taken into consideration. At the same time full reliance cannot be placed on this character which in markedly homogeneous series, such as Falconeri and Grande, is inconstant.

The development of papillae, though marked in various series and absent in others, would often appear to be fortuitous and this character, therefore, which is inconstant, is merely of incidental value.

6. At the level of the species this investigation seldom offers taxonomic criteria for certain identification.

Contrary to this general rule, however, species of the Ovatum and Vaccinioides series can be identified at once by examining a section of the leaf. Again R. *hyperythrum* Hayata in the Ponticum series is readily recognisable by the curious necrotic spots on the lower epidermis, a feature in which this species is unique. In the Saluenense series R. *fragarifolium* Ward may be at once distinguished because the stomata are not raised above the epidermis; forked papillae are a noticeable feature of R. *eritimum* Balf. f. et W. W. Sm. These and the few other species which are so outstanding

that they may be recognised at a glance by their leaf anatomy are, however, quite exceptional.

Leaving aside the few instances cited, it would appear that closely allied species are not distinguishable from each other in their leaf anatomy, even indeed with a closer scrutiny of the minutiae than was possible when so large a number of species had to be methodically examined.

As far as the features which have been under comparative observation are concerned, it may be said, in general, that like species conform, but there are many exceptions as the Appendix clearly shows. These are of interest and often indicative of well recognised anomalies—R. *Genestierianum* Forrest in the Glaucum series for instance; R. *pendulum* Hook. f. in the Edgeworthii series; R. *lepidostylum* Balf. f. et Forrest in the Trichocladum series; R. *setiferum* Balf. f. et Forrest (without papillae) in the Thomsonii series; R. *platypodum* Diels in the Fortunei series; R. *catawbiense* Michaux in the Ponticum series; R. *monanthum* Balf. f. et W. W. Sm. in the Uniflorum series and many others. In drawing attention to these anomalies—some readily explainable others of a puzzling kind—the investigation will have served a useful purpose and at least provides a basis for discussion when the genus is reviewed.

7. It is interesting to note further that a study of the leaf anatomy gives full support to the amalgamation of the Anthopogon and Cephalanthum series which was recently made. The merging of the Virgatum and Scabrifolium series, which could be suggested on other grounds, would also be in accordance with the data now available.

With the recent revision of the Boothii, Glaucum and Lepidotum series the leaf anatomy is for the most part also in accord. Had the evidence of the leaf anatomy been available, however, R. *monanthum* and R. *Ludlowii* Cowan would not have been placed in the Uniflorum series. They are undoubtedly more appropriate in the Boothii series where they were.

8. In conclusion it may be said that the leaf anatomy, in the broad classification of the genus, is significant not as a major criterion (as it was never assumed to be), but as a supplementary one.

The data provided are an aid to the accurate delimitation of certain natural groups, they will assist in the unravelling of certain series as yet confused assemblages and may lead to the better understanding of the relationships of some aberrant species. It may be added, with regard to the phylogeny of the genus, that the data offer some interesting suggestions, and from a physiological point of view that it would be interesting to examine the modifications of structure here described in relation to environment.

SUMMARY

The leaves of 587 species of Rhododendron have been examined in order to ascertain whether or not the leaf anatomy will afford any criteria of significance in the taxonomy of the genus. A summary of earlier work is given.

The anatomical characters of the leaf which have a diagnostic value are found to be,

1. The number of cell layers in the dermal layer.
2. The relative cell size of a multiple epidermis.
3. The thickness of the cuticle.

4. The presence or absence of water tissue.
5. The presence or absence of epidermal papillae.

The incidence of these characters in the various series and subseries of the genus has been tabulated and the data are summarised. How the leaf anatomy may play a part in the taxonomy of the genus is fully discussed.

In a primary sub-division of the genus the arrangement in accordance with the criteria afforded by the leaf anatomy follows a new and independent line.

In a secondary sub-division the criteria are rarely alone fully significant; often they support an arrangement based on other characters, sometimes they conflict with it.

At the level of the species distinctions are seldom diagnostic.

The anatomy of the leaf, although not of fundamental significance, furnishes criteria which are clearly of value in the classification of the genus.

APPENDIX I

(Explanation of numbered columns in tables)

Col. 1. The number of cell layers in the dermal layer is indicated by numbers 1, 2, 3, 4.

Col. 2.—The letter E indicates that the cells of the various layers are equal or sub-equal, the letter L that the cells of the lower layer or layers are much larger (always more than twice the size) than those of the upper layer.

Col. 3. The thickness of the cuticle in relation to the depth of the cells of the outer epidermal cell layer is indicated by the letters a, b, c.

a. The cuticle is thin, not more than $\frac{1}{3}$ the width of the cell.

b. The cuticle is of medium width, more than $\frac{1}{3}$ the width of the cell but less than the width of the cell.

c. The cuticle is thick, equal to or greater than the width of the cell.

Col. 4. The presence or absence of water tissue is shown by the signs + and —.

Col. 5. The presence or absence of papillae is indicated by the signs + and —, ± where the papillae are extremely small.

Series S. and Subseries SS.	Species	1	2	3	4	5	Remarks
		Epidermis					
		Number of cell layers	Relative cell size	Cuticle	Water tissue	Papillae	
Albiflorum S.	albiflorum	1		a	—	—	Cells of lower epidermis similar in size to those of the upper epidermis.
Anthopogon S.	anthopogon	1		c	—	+	
	anthopogonoides	1		c	—	+	
	cephalanthum	1		c	—	+	
	Collettianum	1		c	—	+	
	hypenanthum	1		c	—	+	Homogeneous Series.
	kongboense	1		c	—	+	Sclereids few or absent.
	laudandum	1		c	—	+	
	platyphyllum	1		c	—	+	R. *radendum* not seen.
	pogonophyllum	1		c	—	+	
	primulaeflorum	1		c	—	+	
	rufescens	1		c	—	+	
	Sargentianum	1		c	—	+	
	trichostomum	1		c	—	+	
Arboreum S. Arboreum SS.	arboreum	3	E	c	—	—	Stomata raised.
	niveum	3	E	b	—	—	Sclereids in all species.
	silvaticum	3	E	a	—	—	Tendency to full
	Wattii	3	E	b	—	—	girder system. Water
	Delavayi	2	E	b	—	—	tissue confined to Ar-
	peramoenum	2	E	a	—	—	gyrophyllum subseries.

Series S. and Subseries SS.	Species	1	2	3	4	5	Remarks
		Epidermis					
		Number of cell layers	Relative cell size	Cuticle	Water tissue	Papillae	
Argyrophyllum SS.	argyrophyllum	2	E	b	+	—	
	Chienianum	2	E	b	+	—	
	Coryanum	2	E	b	+	—	
	denudatum	2	E	c	+	—	
	farinosum	2	E	c	+	—	
	floribundum	2	E	c	+	—	
	fokienense	2	E	c	+	—	
	formosanum	2	E	b	+	—	
	hypoglaucum	2	E	b	+	±	
	insigne	2	E	b	+	—	
	longipes	2	E	b	+	—	
	Pingianum	2	E	c	+	—	
	Ririei	2	E	c	+	—	
	Rockii	2	E	c	+	—	
	simiarum	2	E	b	+	—	
	Youngae	2	E	c	+	+	
	Hunnewellianum	1–2	E	b	+	±	
	Thayerianum	1–2	E	c	+	±	
Auriculatum S.	auriculatum	2	E	b	—	—	Homogeneous.
	Griersonianum	2	E	b	—	—	Sclereids occur in R. *Griersonianum*.
Barbatum S. Barbatum SS.	argipeplum	3	E	a	+	±	Sclereids in all species.
	barbatum	3	E	a	+	+	Papillae very small.
	Smithii	3	E	b	+	+	Vertically elongated
	imberbe	2–3	E	a	+	±	hyaline water transfusion cells in all species.
Crinigerum SS.	Bainbridgeanum	2	L	b	+	—	
	crinigerum	2	L	c	+	—	
Glischrum SS.	erosum	3	E	b	+	—	Vertical transfusion
	exasperatum	3	E	b	+	—	tissue only in R.
	spilotum	2–3	E	b	+	+	*erosum*, R. *exasperatum*
	diphrocalyx	2	L	c	+	+	and R. *spilotum*.
	glischroides	2	L	b	+	—	Sclereids in all species.
	glischrum	2	L	c	+	—	
	habrotrichum	2	L	b	+	—	
	hirtipes	2	E	b	+	—	
	rude	2	L	b	+	—	
	vesiculiferum	2	L	b	+	—	
Maculiferum SS.	pseudochrysanthum	2–3	E	c	—	—	Epidermis sub-equal.
	anwheiense	2	E	c	+	—	No vertical trans-
	longesquamatum	2	E	c	+	—	fusion tissue in R.
	maculiferum	2	E	b	+	—	*anwheiense*, R. *Morii*,
	monosematum	2	E	b	+	—	and R. *strigillosum*.
	Morii	2	E	c	+	—	R. *nankotaisanense* not
	ochraceum	2	E	b	+	—	seen.
	pachytrichum	2	E	b	+	—	
	strigillosum	2	E	b	+	—	
Boothii S.	chrysodoron	4	L	a	—	+	Moderately homo-
	sulfureum	4	L	a	—	+	geneous. Cells of
—	auritum	3	L	b	—	+	first epidermal layer
	Boothii	3	L	a	—	—	very small. Sclereids
	chrysolepis	3	L	b	—	+	few in all species.
	mishmiense	3	L	b	—	—	Strong development

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Boothii S. (*cont.*)	leucaspis	3	L	b	—	+	of bundle sheath in R. *chrysolepis*. Scales deeply sunk in lower epidermis. Tendency for stomata to be confined to scale containing depressions.
	tephropeplum	3	L	b	—	+	
	xanthostephanum	3	L	b	—	+	
	Dekatanum	2–3	L	b	—	+	
	megeratum	2	L	c	—	+	
Camelliaeflorum S.	camelliaeflorum	2	L	b	—	+	Sclereids present. R. *lucidum* not seen.
Campanulatum S.	aeruginosum	3	E	a	—	—	Homogeneous. Sclereids observed only in R. *campanulatum* and R. *tsariense*. Stomata raised.
	campanulatum	3	E	b	—	—	
	fulgens	3	E	b	+	—	
	lanatum	3	E	b	—	—	
	miniatum	3	E	b	+	—	
	Sherriffii	3	E	b	+	—	
	Wallichii	3	E	b	—	—	
	tsariense	2	E	a	—	—	
Campylogynum S.	charopoeum	2	L	b	+	—	Sclereids not observed.
	cremastum	2	L	b	+	—	
	campylogynum	1		b	+	—	
	myrtilloides	1		b	+	—	
Camtschaticum S.	camtschaticum	1		a	—	—	Sclereids not observed. Upper and lower epidermal cells of R. *glandulosum* large and thin-walled. R. *Redowskianum* not seen.
	glandulosum	1		a	—	—	
Carolinianum S.	carolinianum	1		c	—	±	Homogeneous. Strong cuticle both above and below. Sclereids not observed.
	Chapmanii	1		c	—	—	
	minus	1		c	—	—	
Cinnabarinum S.	cinnabarinum	2	E	b	—	+	Homogeneous. Sclereids not observed. Papillae short.
	concatenans	2	E	b	—	+	
	igneum	2	E	a	—	+	
	Keysii	2	E	a	—	+	
Dauricum S.	dauricum	1		a	—	—	Homogeneous.
	mucronulatum	1		a	—	—	
Edgeworthii S.	bullatum	3	L	c	—	+	Homogeneous. Sclereids in all species. Tendency to quadruple epidermis except in R. *pendulum*.
	Edgeworthii	3	L	c	—	+	
	pendulum	2	L	b	—	+	
	sciaphilum	3	L	c	—	+	
	seinghkuense	3	L	c	—	+	
Falconeri S.	arizelum	3	E	b	—	—	Homogeneous. Water tissue slight. Sclereids in all species.
	basilicum	3	E	c	—	—	
	Hodgsonii	3	E	b	+	—	
	lanigerum	3	E	b	—	—	
	preptum	3	E	c	+	—	
	fictolacteum	2–3	E	b	+	—	

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Falconeri S. (*cont.*)	rex	2–3	E	b	+	—	
	sino-Falconeri	2–3	E	b	+	—	
	coriaceum	2	E	c	+	—	Homogeneous. Water tissue slight. Sclereids in all species.
	decipiens	2	L	b	+	—	
	eximium	2	E	b	+	—	
	Falconeri	2	E	b	+	—	
	galactinum	2	E	b	+	—	
Ferrugineum S.	ferrugineum	1		c	—	±	Homogeneous. Papillae small. Sclereids not observed.
	hirsutum	1		c	—	±	
	Kotschyi	1		c	—	±	
Fortunei S. Calophytum SS.	calophytum	2	E	b	+	±	SS. Fortunei. R. *Hemsleyanum* not seen.
	Openshawianum	2	E	c	+	+	
Davidii SS.	Davidii	2	E	b	+	—	Homogeneous series. Vertical hyaline cells under vascular bundles. Sclereids not observed in all species. Papillae small or absent.
	Huianum	2	E	c	+	—	
	planetum	2	E	b	+	±	
	praevernum	2	E	b	+	—	
	sutchuenense	2	E	b	+	—	
Fortunei SS.	platypodum	3	E	c	+	+	
	Chengianum	2	E	b	+	±	
	decorum	2	E	c	+	+	
	diaprepes	2	E	b	+	±	
	discolor	2	E	b	+	+	
	Faithae	2	E	b	+	±	
	Fortunei	2	E	c	+	+	
	glanduliferum	2	E	b	+	+	
	Houlstonii	2	E	b	+	+	
	serotinum	2	E	b	+	±	
	vernicosum	2	E	c	+	±	
Griffithianum SS.	Griffithianum	2	E	a	+	—	
Orbiculare SS.	cardiobasis	2	E	a	+	±	
	orbiculare	2	E	b	+	+	
Oreodoxa SS.	erubescens	2	E	b	+	+	
	Fargesii	2	E	b	+	+	
	oreodoxa	2	E	b	+	+	
	praeteritum	2	E	b	+	±	
Fulvum S.	dendritrichum	3	E	c	+	—	Homogeneous in general appearance. Sclereids few. Raised stomata.
	fulvoides	3	E	c	+	—	
	fulvum	3	E	b	+	—	
	niphargum	2	E	c	+	—	
	uvarifolium	2	E	c	+	—	
Glaucum S.	brachyanthum	2	E	b	—	+	
	charitopes	2	E	a	—	+	

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Glaucum S. (*cont.*)	glaucophyllum	2	L	a	—	±	Sclereids not observed. Scales in deep pits in R. *micromeres*.
	shweliense	2	L	a	—	+	
	tsangpoense	2	E	a	—	+	
	Genestierianum	1		a	—	+	
	micromeres	2	L	a	—	+	
Grande S.	Macabeanum	3	E	b	—	—	
	praestans	3	E	b	—	—	
	pudorosum	3	E	b	—	—	
	semnoides	3	E	b	—	—	Homogeneous. Epidermis tends to be irregular. Stomata often raised. Sclereids in nearly all species.
	sidereum	3	E	c	+	—	
	Watsonii	3	E	b	—	—	
	giganteum	2–3	E	a	—	—	
	magnificum	2–3	E	b	—	—	
	peregrinum	2–3	E	b	+	—	
	coryphaeum	2	E	b	—	—	
	grande	2	E	b	—	—	
	protistum	2	L	a	—	—	
	sinogrande	2	E	b	—	—	
Heliolepis S.	desquamatum	2	L	c	+	±	
	Leclerei	2	L	b	+	±	
	rubiginosum	2	L	c	—	+	Sclereids few or absent. Species with single layered epidermis. All very similar. R. *rubiginosum* atypical.
	brevistylum	1		b	—	—	
	fumidum	1		b	—	—	
	heliolepis	1		b	—	—	
	invictum	1		b	—	—	
	oporinum	1		b	—	—	
	pholidotum	1		b	—	—	
Irroratum S. Irroratum SS.	agastum	2	E	b	+	±	
	Annae	2	E	b	+	—	
	anthosphaerum	2	E	b	+	±	
	araiophyllum	2	E	b	+	—	
	cerochitum	2	E	b	+	—	
	dimitrum	2	E	b	+	±	
	epapillatum	2	E	b	+	—	
	eritimum	2	E	c	+	+	
	Hardingii	2	E	b	+	—	
	irroratum	2	E	b	—	—	
	Kendrickii	2	E	b	+	—	
	laxiflorum	2	E	a	+	—	
	leptopeplum	2	E	c	+	—	
	lukiangense	2	E	b	+	—	
	mengtszense	2	E	a	+	—	
	ningyuenense	2	E	a	+	—	
	ombrochares	2	E	a	+	—	
	pankimense	2	E	a	+	—	
	papillatum	2	E	b	+	+	
	pennivenium	2	E	a	+	—	
	pogonostylum	2	E	b	+	—	
	Ramsdenianum	2	E	b	+	—	
	Shepherdii	2	E	b	+	±	
	spanotrichum	2	E	b	+	—	
	tanastylum	2	E	c	+	—	
Parishii SS.	agapetum	2	E	c	+	—	Homogeneous. Epidermis consistently subequal. Water tissue
	Elliottii	2	E	c	+	—	
	eriogynum	2	E	c	+	—	

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Parishii, SS. (*cont.*)	facetum	2	E	b	+	—	more strongly developed in Parishii sub-series. Sclereids in all species. Peculiar forked papillae in R. *eritimum* and also in its sub-species.
	Kyawi	2	E	c	+	—	
	Parishii	2	E	c	+	—	
	schistocalyx	2	E	b	+	±	
	venator	2	E	c	+	—	
Lacteum S.	lacteum	3	E	b	—	—	
	sigillatum	3	E	c	—	—	
	Traillianum	3	E	b	—	—	
	Wightii	3	E	b	—	—	
	aberrans	2	E	c	—	—	
	aiolopeplum	2	E	b	—	—	Homogeneous. Sclereids not observed. Epidermis treble in all species near the mid-rib.
	Beesianum	2	E	b	—	—	
	colletum	2	E	b	—	—	
	dictyotum	2	E	b	—	—	
	dignabile	2	E	b	—	—	
	dryophyllum	2	E	b	—	—	
	dumosulum	2	E	b	—	—	
	emaculatum	2	E	b	—	—	
	levistratum	2	E	c	—	—	
	nakotiltum	2	E	b	—	—	
Lapponicum S.	achroanthum	1		b	—	+	
	alpicola	1		b	—	+	
	Amundsenianum	1		b	—	+	
	blepharocalyx	1		b	—	+	
	Bulu	1		b	—	+	
	capitatum	1		b	—	+	
	chamaezelum	1		b	—	+	
	chryseum	1		b	—	+	
	compactum	1		b	—	+	
	complexum	1		b	—	+	
	cuneatum	1		c	—	+	
	dasypetalum	1		c	—	+	Homogeneous Series. Spongy mesophyll strongly aerated. Papillae commonly flattened at apex. Sclereids not observed. Upper girder system either absent or very weakly developed. R. *Tsaii* and R. *verruculosum* not seen.
	diacritum	1		b	—	—	
	drumonium	1		b	—	+	
	Edgarianum	1		b	—	+	
	fastigiatum	1		b	—	+	
	fimbriatum	1		b	—	+	
	flavidum	1		b	—	±	
	glomerulatum	1		b	—	+	
	hippophaeoides	1		b	—	+	
	idoneum	1		b	—	+	
	impeditum	1		a	—	+	
	intricatum	1		b	—	+	
	lapponicum	1		b	—	+	
	litangense	1		b	—	+	
	lysolepis	1		b	—	+	
	microleucum	1		b	—	+	
	nigropunctatum	1		b	—	+	
	nitidulum	1		b	—	+	
	nivale	1		b	—	+	
	orthocladum	1		b	—	+	
	paludosum	1		b	—	+	
	parvifolium	1		b	—	+	
	peramabile	1		b	—	+	
	polifolium	1		b	—	+	
	polycladum	1		b	—	+	

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Lapponicum, S. (*cont.*)	ramosissimum	1		b	—	+	
	ravum	1		c	—	+	
	rupicola	1		b	—	+	
	russatum	1		b	—	+	
	scintillans	1		c	—	+	
	setosum	1		c	—	—	
	spilanthum	1		a	—	+	
	stictophyllum	1		a	—	—	
	tapetiforme	1		b	—	+	
	telmateium	1		b	—	+	
	thymifolium	1		b	—	+	
	violaceum	1		b	—	+	
	Websterianum	1		b	—	+	
	yungningense	1		b	—	+	
Lepidotum S.	Baileyi	1		c	—	+	Homogeneous. Papillae short. R. *lepidotum*, R. *obovatum*, R. *salignum* and R. *elaeagnoides* all similar.
	lepidotum	1		b	—	+	
Maddenii S. Ciliicalyx SS.	dendricola	4	L	b	—	+	
	scopulorum	4	L	b	—	+	
	amandum	3	L	c	—	+	
	burmanicum	3	L	c	—	+	
	ciliipes	3	L	b	—	+	
	Cuffeanum	3	L	b	—	+	
	formosum	3	L	c	—	+	
	inaequale	3	L	b	—	+	
	Johnstoneanum	3	L	b	—	+	Sclereids observed in nearly all species. Upper epidermal cells small. Lower epidermal cell large, may be water storing hypodermis. Subseries Ciliicalyx R. *Smilesii* and Subseries Maddenii R. *excellens* not seen.
	Lyi	3	L	c	—	+	
	notatum	3	L	c	—	+	
	Parryae	3	L	b	—	+	
	taronense	3	L	a	—	+	
	carneum	2	L	b	—	+	
	ciliatum	2	L	c	—	—	
	ciliicalyx	2	L	b	—	+	
	Cubittii	2	L	b	—	+	
	iteophyllum	2	L	b	—	+	
	lasiopodum	2	L	b	—	+	
	Ludwigianum	2	L	c	—	+	
	missionarum	2	L	c	—	+	
	pachypodum	2	L	c	—	+	
	pilicalyx	2	L	c	—	+	
	pseudociliicalyx	2	L	b	—	+	
	roseatum	2	L	b	—	+	
	rufosquamosum	2	L	b	—	+	
	Scottianum	2	L	b	—	+	
	supranubium	2	L	a	—	+	
	Surasianum	2	L	b	—	+	
	Valentinianum	2	L	b	—	+	
	Veitchianum	2	L	c	—	+	
Maddenii SS.	brachysiphon	2	L	c	—	+	
	calophyllum	2	L	b	—	+	
	crassum	2	L	b	—	+	

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Maddenii SS. (*cont.*)	Maddenii	2	L	b	—	+	
	manipurense	2	L	c	—	+	
	odoriferum	2	L	b	—	+	
	polyandrum	2	L	b	—	+	
Megacalyx SS.	Dalhousiae	2	L	c	—	+	
	Headfortianum	2	L	c	—	+	
	liliiflorum	2	L	c	—	+	
	Lindleyi	2	L	b	—	+	
	megacalyx	2	L	b	—	+	
	Nuttallii	2	L	b	—	+	
	rhabdotum	2	L	b	—	+	
	sinonuttallii	2	L	b	—	+	
	Taggianum	2	L	b	—	+	
Micranthum S.	micranthum	1		a	—	±	
Moupinense S.	dendrocharis	2	E	c	—	+	Homogeneous. Approximate to full girder system. Strong cuticularisation and development of sclerenchymatous sheath. Scales arise from deep depression to which stomata tend to be confined.
	moupinense	2	E	c	—	+	
	petrocharis	2	E	c	—	+	
Neriiflorum S. Forrestii SS.	erastum	2	E	c	—	—	Epidermal cells tend to be sub-equal, and variable. Few species papillose. Tendency for lower layers to be thickened.
	Forrestii	2	E	c	—	—	
	porphyrophyllum	2	E	a	—	+	
	repens	2	E	b	—	—	
	serpens	2	E	b	—	—	
Haematodes SS.	coelicum	3	E	c	—	—	
	hemidartum	3	E	b	—	—	
	mallotum	3	E	b	—	—	
	pocophorum	3	E	b	—	—	
	Beanianum	2	E	b	—	—	
	catacosmum	2	L	b	—	—	
	chaetomallum	2	E	b	—	—	
	chionanthum	2	E	b	—	+	
	haematodes	2	E	c	—	—	
Neriiflorum SS.	Albertsenianum	2	E	b	—	±	
	euchroum	2	E	b	—	—	
	floccigerum	2	E	c	—	+	
	neriiflorum	2	E	c	—	+	
	sperabile	2	E	c	—	+	
	sperabiloides	2	E	c	—	+	
Sanguineum SS.	aperantum	2	E	b	—	+	
	citriniflorum	2	E	c	—	—	
	dichroanthum	2	E	c	—	—	
	eudoxum	2	E	b	—	—	
	fulvastrum	2	E	b	—	—	
	parmulatum	2	E	b	—	—	

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Sanguineum SS. (*cont.*)	sanguineum	2	E	b	—	—	
	temenium	2	E	b	—	—	
Ovatum S.	Bachii	2	L	c	—	—	
	hongkongense	2	L	c	—	—	
	leptothrium	2	L	c	—	—	
	ovatum	2	L	c	—	—	
	Vialii	2	L	c	—	—	
Ponticum S. Caucasicum SS.	adenopodum	2	E	c	+	+	
	brachycarpum	2	E	b	—	±	
	caucasicum	2	E	b	—	—	Heterogeneous. Sclereids few or absent. Tendency to amphiploic midrib bundle. Peculiar necrotic spots on lower epidermis of R. *hyperythrum*.
	chrysanthum	2	E	b	+	—	
	Degronianum	2	E	b	+	—	
	hyperythrum	2	E	c	+	—	
	Metternichii	2	E	c	+	—	
	Smirnowii	2	E	b	—	—	
	Ungernii	2	E	b	+	—	
	Fauriei	1		b	—	—	
	Makinoi	1		c	—	—	
	yakusimanum	1		c	+	—	
Ponticum SS.	californicum	2–3	E	a	+	—	
	maximum	2	E	b	—	—	
	ponticum	2	L	a	—	—	
	catawbiense	1		c	—	±	
Saluenense S.	calciphilum	1		b	—	—	
	calostrotum	1		c	—	—	
	chameunum	1		c	—	—	
	charidotes	1		b	—	—	Homogeneous. Stomata raised except in R. *fragariflorum*. Sclereids not observed. R. *cosmetum* not seen.
	fragariflorum	1		c	—	—	
	keleticum	1		c	—	—	
	nitens	1		c	—	—	
	prostratum	1		c	—	—	
	radicans	1		c	—	—	
	riparium	1		c	—	—	
	saluenense	1		c	—	—	
Scabrifolium S.	hemitrichotum	2	L	b	—	+	
	mollicomum	2	L	b	—	+	Homogeneous. Scales in pits. Sclereids present. Papillae variable in length and narrow.
	pubescens	2	L	b	—	+	
	scabrifolium	2	L	b	—	+	
	spiciferum	2	L	b	—	+	
	spinuliferum	2	L	b	—	+	
Semibarbatum S.	semibarbatum	1		a	—	—	
Stamineum S.	Cavaleriei	1		b	—	—	
	Championae	1		c	—	—	
	Esquirolii	1		c	—	—	Homogeneous series. The sclerenchyma associated with the lateral bundles only *rarely* produced upwards. Epidermal cells small. Sclereids few or absent.
	Feddei	1		c	—	—	
	Hancockii	1		c	—	—	
	Henryi	1		c	—	—	
	Latoucheae	1		c	—	—	
	leiopodum	1		c	—	—	
	moulmainense	1		c	—	—	
	oxyphyllum	1		c	—	—	

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Stamineum S. (*cont.*)	pectinatum	1		b	—	—	R. *leucobotrys* and R. *taiense* not seen.
	stamineum	1		c	—	—	
	stenaulum	1		c	—	—	
	Tutcherae	1		b	—	—	
	Westlandii	1		c	—	—	
	Wilsonae	1		c	—	—	
Taliense S. Adenogynum SS.	adenogynum	3	E	c	—	—	
	adenophorum	3	E	c	—	—	
	alutaceum	3	E	c	—	—	
	Balfourianum	3	E	c	—	—	
	Bureavii	3	E	c	—	—	Homogeneous series. Epidermal variation not marked. Sclereids in most species. Subseries Adenogynum R. *Faberioides* and R. *wuense*. Subseries Wasonii R. *coeloneuron* not seen.
	circinnatum	3	E	c	—	—	
	detonsum	3	E	c	—	—	
	elegantulum	3	E	c	—	—	
	mimetes	3	E	c	—	—	
	bureavioides	2	E	c	—	—	
	codonanthum	2	E	c	—	—	
	cruentum	2	E	c	—	—	
	detersile	2	E	c	—	—	
	dumicola	2	E	c	—	—	
	Faberi	2	E	c	—	—	
	Prattii	2	E	b	—	—	
Roxieanum SS.	globigerum	3	E	c	—	—	
	aischropeplum	2	E	c	—	—	
	bathyphyllum	2	E	c	—	—	
	comisteum	2	E	c	—	—	
	gymnocarpum	2	E	c	—	—	
	iodes	2	E	c	—	—	
	lampropeplum	2	E	c	—	—	
	microgynum	2	E	c	—	—	
	perulatum	2	E	c	—	—	
	pronum	2	E	c	—	—	
	proteoides	2	E	c	—	—	
	recurvoides	2	E	c	—	—	
	Roxieanum	2	E	c	—	—	
	russotinctum	2	E	c	—	—	
	triplonaevium	2	E	c	—	—	
	tritifolium	2	E	c	—	—	
Taliense SS.	Clementinae	3	E	b	—	—	
	principis	3	E	c	—	—	
	Purdomii	3	E	c	—	—	
	taliense	3	E	c	—	—	
	vellereum	3	E	c	—	—	
	aganniphum	2	E	c	—	—	
	agglutinatum	2	E	c	—	—	
	doshongense	2	E	c	—	—	
	flavorufum	2	E	b	—	—	
	glaucopeplum	2	E	c	—	—	
	lophophorum	2	E	c	—	—	
	phaeochrysum	2	E	c	—	—	
	Przewalskii	2	E	c	—	—	
	schizopeplum	2	E	c	—	—	
	sphaeroblastum	2	E	c	—	—	
	syncollum	2	E	c	—	—	

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Wasonii SS.	inopinum	2	E	c	—	—	
	paradoxum	2	E	c	—	—	
	rufum	2	E	c	—	—	
	Wasonii	2	E	c	—	—	
	Weldianum	2	E	c	—	—	
	Wiltonii	2	E	c	—	—	
Thomsonii S. Campylocarpum SS.	callimorphum	2	E	b	—	+	Sclereids few or absent. Subseries homogeneous except *R. Thomsonii*. Papillae very small in Selense and Souliei subseries. Very long papillae in *R. Lopsangianum*.
	caloxanthum	2	E	a	—	+	
	campylocarpum	2	E	b	—	+	
	cyclium	2	E	b	—	+	
	hedythamnum	2	E	b	—	+	
	myiagrum	2	E	b	—	+	
	telopeum	2	E	b	—	+	
Martinianum SS.	eurysiphon	3	E	b	—	+	
	Martinianum	3	E	a	—	+	
Selense SS.	calvescens	2	E	c	—	±	
	cymbomorphum	2	E	b	—	±	
	dasycladoides	2	E	c	—	±	
	dasycladum	2	E	b	—	±	
	erythrocalyx	2	E	b	—	±	
	esetulosum	2	E	c	—	±	
	jucundum	2	E	b	—	±	
	manopeplum	2	E	b	—	±	
	rhaibocarpum	2	E	b	—	±	
	selense	2	E	b	—	±	
	setiferum	2	E	c	—	—	
	vestitum	2	E	b	—	±	
Souliei SS.	astrocalyx	2	E	c	—	±	
	Bonvalotii	2	E	b	—	+	
	croceum	2	E	b	—	+	
	litiense	2	E	b	—	+	
	puralbum	2	E	a	—	+	
	Souliei	2	E	b	—	±	
	Wardii	2	E	b	—	±	
	Williamsianum	2	E	b	—	+	
Thomsonii SS.	Hookeri	3	E	b	—	+	
	hylaeum	3	E	b	—	+	
	Meddianum	3	E	c	—	+	
	populare	3	E	b	—	+	
	cerasinum	2	E	a	—	+	
	cyanocarpum	2	E	b	—	±	
	eclecteum	2	E	b	—	+	
	Lopsangianum	2	E	b	—	+	
	Stewartianum	2	E	b	—	+	
	Thomsonii	2	E	b	—	+	

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Trichocladum S.	lepidostylum	2	E	a	—	+	
	chloranthum	1		a	—	—	
	lithophilum	1		a	—	—	
	lophogynum	1		a	—	—	Homogeneous (except R. *lepidostylum*). Epidermal cells thin walled. Papillae very small or absent.
	mekongense	1		a	—	—	
	melinanthum	1		a	—	±	
	oulotrichum	1		a	—	±	
	rubrolineatum	1		a	—	±	
	semilunatum	1		a	—	±	
	trichocladum	1		a	—	±	
	viridescens	1		a	—	±	
Triflorum S. Augustinii SS.	bivelatum	2	L	b	—	+	
	hirsuticostatum	2	L	b	—	±	
	Augustinii	1		a	—	—	
	chasmanthoides	1		a	—	—	
	chasmanthum	1		a	—	—	
	trichophorum	1		a	—	—	
	villosum	1		a	—	—	
Hanceanum SS.	afghanicum	2	E	c	—	±	
	Hanceanum	2	E	c	—	—	
Oreotrephes SS.	apiculatum	1		b	—	±	
	artosquameum	1		b	—	±	
	bracteatum	1		b	—	—	
	exquisetum	1		b	—	±	
	oreotrephes	1		b	—	±	
	sycnanthum	1		b	—	±	
	timeteum	1		b	—	±	
Polylepis SS.	concinnoides	3	L	b	—	+	
	polylepis	2	E	b	—	±	
	Amesiae	1		b	—	±	
	concinnum	1		b	—	+	
	pseudoyanthinum	1		b	—	±	
Triflorum SS.	kasoense	3	L	b	—	+	
	bauhiniiflorum	2	E	b	—	+	
	triflorum	2	E	b	—	+	
	xanthocodon	2	E	b	—	±	
	ambiguum	1		b	—	+	
	caseium	1		b	—	+	
	Keiskei	1		b	—	±	
	lutescens	1		b	—	—	
Yunnanense SS.	Bodinieri	2	E	c	—	—	
	caeruleum	2	L	c	—	±	
	charianthum	2	E	a	—	—	
	chartophyllum	2	L	a	—	—	
	erileucum	2	L	b	—	+	Heterogeneous. Papillae small or absent; rarely long. Sclereids of rare occurrence. Tendency to double epidermis in R. *caesium* and R. *Davidsonianum*.
	hesperium	2	L	b	—	±	
	hypophaeum	2	L	b	—	±	
	leilungense	2	L	b	—	+	
	lochmium	2	E	b	—	—	
	longistylum	2	L	c	—	—	
	pleistanthum	2	L	a	—	—	
	rigidum	2	L	b	—	—	
	siderophyllum	2	E	b	—	±	

Series S. and Subseries SS.	Species	1 Epidermis: Number of cell layers	2 Epidermis: Relative cell size	3 Cuticle	4 Water tissue	5 Papillae	Remarks
Yunnanense SS. (*cont.*)	stereophyllum	2	L	b	—	—	Subseries Triflorum R. *Chenshienianum* R. *flavantherum* and R. *Wongii*. Subseries Yunnanense R. *pallescens* not seen.
	suberosum	2	L	a	—	—	
	tatsienense	2	L	b	—	—	
	yunnanense	2	L	b	—	—	
	zaleucum	2	E	a	—	+	
	aechmophyllum	1		a	—	—	
	Davidsonianum	1		b	—	—	
	hormophorum	1		a	—	—	
	Searsiae	1		a	—	+	
	Vilmorinianum	1		a	—	—	
Uniflorum S.	monanthum	3	L	b	—	+	Sclereids not observed. R. *monanthum* and R. *Ludlowii* atypical.
	Ludlowii	2	E	b	—	—	
	imperator	1		a	—	+	
	patulum	1		c	—	+	
	pemakoense	1		c	—	+	
	pumilum	1		b	—	+	
	uniflorum	1		b	—	+	
Vaccinioides S.	asperulum	1		a	—	—	This series can definitely be identified by leaf structure. Epidermal cells very large. Palisade poorly developed. Spongy mesophyll highly aerated. No upper girder system. Large isolated sclereids. R. *emarginatum* and R. *Kawakamii* not seen.
	euonymifolium	1		a	—	—	
	insculptum	1		a	—	—	
	Quadrasianum	1		a	—	—	
	rosmarinifolium	1		a	—	—	
	vaccinioides	1		a	—	—	
	Vidalii	1		a	—	—	
Virgatum S.	oleifolium	2	L	b	—	+	
	racemosum	2	L	b	—	±	
	virgatum	2	L	b	—	±	

APPENDIX II

Series	Number of Species in Series	Number of Species Examined
Albiflorum	1	1
Anthopogon	14	13
Arboreum	24	24
Auriculatum	2	2
Barbatum	26	25
Boothii	11	11
Camelliaeflorum	2	1
Campanulatum	8	8
Campylogynum	4	4
Camtschaticum	3	2
Carolinianum	3	3
Cinnabarinum	4	4
Dauricum	2	2
Edgeworthii	5	5
Falconeri	13	13
Ferrugineum	3	3
Fortunei	26	25
Fulvum	5	5
Glaucum	7	7
Grande	13	13
Heliolepis	9	9
Irroratum	33	33
Lacteum	15	15
Lapponicum	52	50
Lepidotum	2	2
Maddenii	49	47
Micranthum	1	1
Moupinense	3	3
Neriiflorum	28	28
Ovatum	5	5
Ponticum	16	16
Saluenense	12	11
Scabrifolium	6	6
Semibarbatum	1	1
Stamineum	18	16
Taliense	57	54
Thomsonii	39	39
Trichocladum	11	11
Triflorum	56	52
Uniflorum	7	7
Vaccinioides	9	7
Virgatum	3	3