5. THE ERICACEAE.

5.1. INTRODUCTION.

This chapter is devoted to a revision of the generic and tribal limits of the Rhododendroideae, Arbutoideae, and superior-ovaried Vaccinoideae. The inferior-ovaried Vaccinoideae are treated in less detail, and brief notes are given on the Pyroloideae, Monotropoideae and Ericoideae. Finally the genus Wittsteinia is placed in a new subfamily.

The nomenclature of the taxa is not treated exhaustively, although in many cases there is a short discussion on the subject. The synonymy does not pretend to be complete, and those names listed with an asterisk in front of the citation have not been checked with the original publication. Those names which have been checked agree with my concept of the taxon, although in most cases the original types (if any) have not been seen.

5.2. THE RHODODENDROIDEAE.


Shrubs or trees, leaves convolute or revolute in bud, usually entire. Indumentum diverse, well developed, often with two types of multicellular hairs on the same plant; rarely lacking. Inflorescence usually terminal, with or without bud scales, often corymbose. Bracts and basal bracteoles usually present, deciduous or persistent. Corolla gamo- or polypetalous; mouth
rarely contracted. Stamens without appendages; filaments not geniculate. Anthers smooth (except Daboecia), dehiscing by terminal pores or long introrse slits; viscin threads usually mixed with the pollen. Ovary 3-9 locular, often covered with glandular hairs, placentae often bilobed. Stigma often peltate and prominently lobed. Fruit a septicidal capsule, sometimes partially loculicidal as well. Seeds variable.

The Rhododendroideae may be distinguished from the other subfamilies by the following group of characters. None of these characters is constant throughout the subfamily, and only number six is diagnostic where it occurs.

1. Indumentum well-developed and very variable, even within the same plant.

2. Leaves convolute or revolute; elsewhere revolute leaves occur only in Agauria, Agarista (probably) and Andromeda.

3. Inflorescence nearly always terminating the growth of the main axis (except some Kalmia/spp.). Such inflorescences are rare elsewhere except in the Ericoideae and the Arbutoideae, and then they are not corymbose.

4. Corolla usually infundibular, widely campanulate or hypocrateriform. Elsewhere it is usually narrowly campanulate, tubular or urceolate. Urceolate corollas in the Rhododendroideae are known from some species of Phyllodoce and from Daboecia.
5. No trace of anther or filament appendages. Of the other subfamilies, only the Pyroloideae and the monotypic Wittsteinioideae entirely lack these stamen appendages.

6. Viscin threads intermixed with the pollen tetrads are found in most genera.

7. Placentation is axile, but usually with a prominent parietal zone at the apex of the ovary; the placentae are more or less prominently bilobed.

8. The megagametophyte has elongated synergid cells (Ganapathy and Palser, 1954).

9. The fruit is a septicidal capsule.

5.2.2. PREVIOUS TRIBAL LIMITS IN THE RHODODENDROIDAE.

De Candolle (1838) divided the Rhododendroidae (which he recognised at the tribal level) into two groups on whether or not the corolla lobes were fused. Klotzsch (1851) did not use this character. He recognised a Menziesiaceae with squamose buds and anthers dehiscing by a ± elongated slit, and a Rhodoraceae with strobiliform leaf buds and anthers dehiscing by pores, the pollen being mixed up with viscin threads. Maximowicz (1870) introduced two other characters; whether or not the testa was firm and the persistence of the bracteoles. He also used Klotzsch's characters and delimited two subtribes corresponding to the Rhodoreae and Bejarieae combined and the rest of the subfamily
respectively. This arrangement differed from Klotzsch only in the transfer of *Menziesia* from the Menziesiaceae to the Rhodoraceae. Hooker (1876) divided the Rhodoreae (= Rhododendroidese) into two groups on testa type, and each group was subdivided on whether or not the corolla was gamopetalous.

Drude (1897) emphasised the nature of the corolla and the winging of the seeds, and recognised three tribes:

1. **Ledeae** - Long-winged seeds, polypetalous corolla.
2. **Rhododendreae** - Winged seeds; gamopetalous and weakly zygomorphic corolla.
3. **Phyllodoceae** - Unwinged seeds; usually gamopetalous and actinomorphic corolla.

Copeland (1943) was especially interested in the anatomy of the lamina, and in details of embryology and floral vasculature. He made two new tribes out of the Ledeae, the Bejarieae and the Cladothammeae. The remaining genus of the old Ledeae, *Ledum* he transferred to the Rhodoreae since the stamens, seed and indumentum were all similar. His Bejarieae had a prominent endothecium and resorbtion tissue which did not break the epidermis of the anther. In addition the inflorescence was eperulate and the seeds were spindle-shaped. The Cladothammeae had a resorbtion tissue which involved the anther for the whole length of the anther. Also, its inflorescence was eperulate and
Its seeds ovoid.

Copeland's Phyllodoceae was the same as Drude's, and his Rhodoreae the same apart from the addition of Ledum. He thought that these two tribes were separable on a number of characters. The Rhodoreae had viscin threads, no resorption tissue in the anther, bud scales and a number of other differences. The Phyllodoceae lacked viscin threads, had resorption tissue in the anther, lacked bud scales and so on.

Cox (1948) based his classification of the subfamily mainly on details of the wood anatomy. He created a new tribe, the Daboecieae (nomen nudum), but apart from this his system follows that of Copeland. Schultze-Motel (1964) follows Copeland entirely; he does not maintain the Daboecieae.

Watson et al. (1967) in the course of their numerical studies, found that Beijaria was the most isolated of all the genera that they studied, and therefore put it in a monogeneric tribe. They recognised two other tribes; one corresponds to Drude's and Copeland's Phyllodoceae, the other to Copeland's Rhodoreae plus Cladothamneae.

It has been found necessary to increase the numbers of the tribes by two. This is due to the inclusion of Enigaea in the Rhododendroideae and the placing of Diplarche in a monogeneric tribe. The maintenance of these small tribes is considered to be justified because the pattern of variation in this subfamily
<table>
<thead>
<tr>
<th>Character</th>
<th>Bejarieae</th>
<th>Rhodoreae</th>
<th>Epigaeae</th>
<th>Cladothammeae</th>
<th>Phyllodoceae</th>
<th>Daboecieae</th>
<th>Diplarcheae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf in bud</td>
<td>revolute</td>
<td>revolute &amp; convolute</td>
<td>revolute</td>
<td>convolute</td>
<td>revolute &amp; convolute</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Mature leaf</td>
<td>± flat</td>
<td>± flat</td>
<td>flat</td>
<td>flat</td>
<td>flat/ Ericoid</td>
<td>± Ericoid</td>
<td>flat</td>
</tr>
<tr>
<td>Stomata</td>
<td>tetracytic</td>
<td>anomalocytic</td>
<td>tetracytic</td>
<td>anomalocytic or paracytic</td>
<td>anomalocytic</td>
<td>anomalocytic</td>
<td>anomalocytic</td>
</tr>
<tr>
<td>Indumentum</td>
<td>long-celled</td>
<td>+</td>
<td>-</td>
<td>+(rare)</td>
<td>-</td>
<td>+</td>
<td>(rare)</td>
</tr>
<tr>
<td></td>
<td>gland heads</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>branched</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bud scales</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bracteoles green</td>
<td>+</td>
<td>- (rare +)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>absen?</td>
<td></td>
</tr>
<tr>
<td>Leaves whorled</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>rare</td>
<td>tend</td>
<td></td>
</tr>
<tr>
<td>Corolla gamopetalous</td>
<td>-</td>
<td>+ (rare -)</td>
<td>-</td>
<td>+ (rare -)</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Stamens epipetalous</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Anther dehiscence tissue</td>
<td>endothecium</td>
<td>-</td>
<td>?</td>
<td>slight</td>
<td>?</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>involved</td>
<td>resorption collapse</td>
<td>?</td>
<td>resorption</td>
<td>resorption</td>
<td>?</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>shape of orifice pore</td>
<td>+ pore</td>
<td>long slit</td>
<td>long slit</td>
<td>long slit</td>
<td>long slit</td>
<td>long slit</td>
<td>long slit</td>
</tr>
<tr>
<td>Fruit loculi</td>
<td>5-7</td>
<td>(3-5)(-12)</td>
<td>5</td>
<td>3-5</td>
<td>(2-5)(-6)</td>
<td>4-6</td>
<td>5</td>
</tr>
<tr>
<td>Fruit peculiarities</td>
<td>-</td>
<td>-</td>
<td>fleshly</td>
<td>tend apical</td>
<td>knobbly wall</td>
<td>-</td>
<td>septifragal</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>thick walls</td>
<td>(Ledothamnus)</td>
<td>2-layer wall</td>
<td>2-layer wall</td>
</tr>
<tr>
<td>Testa - cell shape</td>
<td>long (v. rare short)</td>
<td>long</td>
<td>short, short</td>
<td>short, short</td>
<td>usually short, short, papillate</td>
<td>short?</td>
<td></td>
</tr>
<tr>
<td>Abaxial calyx stomata</td>
<td>+</td>
<td>usually +</td>
<td>-</td>
<td>+</td>
<td>rarely +</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

Table 3: MAIN INTER-TRIBAL VARIATION IN THE RHODODENDROIDEAE
has turned out to be very complex. If tribes are to be recognised at all, they have to be small; only then is there much within-group similarity and between-group difference. The problem has been made more acute by the discovery of anatomical approaches to the Ericoideae every bit as remarkable as that shown by *Calluna*, and which are similarly unsupported by details of flower and fruit morphology. Study of embryology; floral anatomy and the structure of the testa has provided additional evidence apparently supporting taxa separated on morphological and anatomical grounds.

Seven tribes are recognised here (see Table 3):—Bejarieae, Rhodoreae, Epigae, Cladothamneae, Phyllococeae, Daboecieae and Diplarcheae.

5.2.3. GENERA INCLUDED IN THE RHODODENDROIDEAE.

*Tripetaleia* (= *Cladothamnus*) was originally described as a genus in the Olacaceae (Siebold and Zuccarini, 1840), but has since been included in the Rhododendroideae by all recent authors. The genera here included in the Rhododendroideae are the same as those placed in this subfamily by Drude (1897), with the addition of *Epigae* (including *Orphanidesia*) from the Andromedeae. This was first suggested by Watson et al. (1967). *Diplarche* is retained in the Rhododendroideae despite its recent transference to the Diapensiaceae by Airy-Shaw (1964) — see section 4.2.3.
Epigaea and Orphanidesia  All previous workers in the Ericaceae have included Epigaea and Orphanidesia in the Andromedeae since they were supposed to have loculicidally dehiscent capsules. Watson et al. (1967), in the course of their numerical studies on the Ericaceae, transferred Epigaea to the Rhododendroideae, where it was put in the same tribe as the Phylloodoceae sensu Drude.

Epigaea and Orphanidesia were always keyed out together in the classical treatments and were easily distinguishable from the other genera of the Andromedeae. Bentham (1876) noted that they had the vegetative facies of a Gaultheria, but in this respect they are more like some of the Rhododendroideae, and this similarity becomes more apparent when the inflorescence is taken into account. It is terminal in Epigaea and Orphanidesia, axillary in most species of Gaultheria. Although some other members of the Andromedeae have terminal inflorescences, they do not have the infundibular hypocrateriform corollas of the two genera in question. Apart from these genera such a corolla is restricted to the Rhododendroideae.

The indumentum of Epigaea and Orphanidesia is a mixture of long-celled and long-stalked glandular hairs such as is to be found in a number of the Rhododendroideae, although it is also known from some species of Gaultheria. Epigaea has glandular ovary hairs; this is unknown outside the Rhododendroideae.
The anthers of *Epigaea* and *Orphanidesia* dehisc by long introrse slits which run down at least half the length of the thecae (Fig. 50). A number of genera of the Rhododendroideae have such slits, e.g. *Loiseleuria*, *Elliottia*, *Ledothamnus*, but they are not so well developed nor do they involve the fertile part of the anther in the Andromedae. Neither genus has stamen appendages; they also lack the white deposit (dissolution tissue) on the back of the anthers which is to be found in a number of the Andromedae and Gaultherieae sensu Drude. Ikuse (1954) observed the occurrence of viscin threads amongst the pollen of *Epigaea repens*. I have found these threads in all three species from the two genera. Such threads are unknown outside the Rhododendroideae.

All three species have adaxial calyx stomata; these are unaccompanied by abaxial calyx stomata or by any corolla stomata. Only *Cassione* of the Arbutoideae sensu Drude has such a stomatal distribution, and it is unknown elsewhere in the Ericaceae apart from several genera of the Rhododendroideae, e.g. *Phyllodoce*, *Loiseleuria*, *Leiophyllum*, *Kalmia* and *Rhodothamnus*.

The placentation of *Epigaea* and *Orphanidesia* is very like that of many of the Rhododendroideae (Fig. 10), with very prominently bilobed placentae and a zone of parietal placentation at the apex of the ovary. The same is true of the curved style of *Orphanidesia* and the prominently indusiate stigma/style
complex of all three species. The stigmatic lobes of *Epigaea repens* are perhaps the most prominent of the whole family (see Watson, 1965), but those of *E. asiatica* and *Orphanidesia* are more like those of the other members of the Rhododendroideae (c.f. Figs. 11 and 50). I do not know whether the odd sepal has the unusual abaxial position or not.

Palser (1952) noted that *Epigaea repens* had very elongated synergid cells. None of the other Andromedeae sensu Drude that she studied had such elongated cells; they are characteristic of the Rhododendroideae.

As mentioned above, it was the presumed dehiscence of the capsule which was responsible for the placing of the two genera in the Andromedeae, and it now appears that there was initially confusion due to plants other than *Epigaea* being included in that genus, but since then there has been a history of misobservations.

In the initial description of *Epigaea* by Linnaeus (1753) no mention is made of capsule dehiscence. De Candolle (1838) included *Epigaea* in the loculicidally dehiscent Andromedeae, possibly because he combined it with part of another genus. *Epigaea* sensu de Candolle contained two sections. One, *Euenigaea*, contained *E. repens* alone; the other, *Brossea*, contained *E. cordifolia* Swartz. This latter "Epigaea" in fact contains two species of Gaultheria, *G. coccinea* and *G. sphagnicola*. The two sections differed in corolla shape; that of the former was
hypocrateriform, that of the latter was ovate, with an erect, five-fid limb. Both were supposed to have a calyx which did not become fleshy in fruit, hence their inclusion in Epigaea. These two species of Gaultheria certainly have plentiful, loculicidally-dehiscent fruit, and it is suspected that they are the source of the subsequent reports of loculicidally dehiscent fruit in Epigaea sensu stricto. Even when these two species of Gaultheria were removed from Epigaea, the report of loculicidal capsules may have stuck to the remaining species of Epigaea. Hooker (1876) did not see fruits of Epigaea when making his description for the "Genera Plantarum".

Boissier (1875) in his description of Orphanidesia gaultherioides wrote "Capsula sphaerica membranacea loculicida valvis septiferis, 1 . .". Thus it would seem that the capsule was observed to dehisce in the same way as the other Andromedeae, but it must be borne in mind that Boissier and Balansa had but a single specimen for their original description, and, correctly recognising their plant's affinity to Epigaea, they may have become convinced that its capsules dehisced in the same way as those of Epigaea were supposed to do. Hence the inclusion of Orphanidesia, too, in the Andromedeae. Again Hooker (1876) did not see the capsule for his description; he based it on the original description of Boissier and Balansa.

The septae of these two genera are very thin and this may
have been responsible for some of the more recent erroneous reports on capsule dehiscence. Turrill (1943), describing *Orphanidesia gaultheroides*, noted that the dehiscence was loculicidal, but the rather poor drawing suggests that the line of dehiscence is along the sepal radii. Similarly Stapf (1930) described *Epigaea asiatica* as having loculicidal capsules. At Kew there is good fruiting material of this species (E. H. Wilson, 7121; cultivated the Marquis of Headfort, Kells, County Meath, Ireland), and both of these have the line of dehiscence of the capsule along the sepal radii (Fig. 51). The latter specimen is especially interesting in that it was on this plant that the faulty description of the fruit was based by Stapf (1930). Barrows' illustration of *E. repens* (1936, Fig. 2a) clearly shows that the lines of dehiscence of the fruit are along the sepal radii. Finally it may be mentioned that Small (1914) keyed out *E. repens* from the other N. American Ericaceae with loculicidal or septicidal capsules on its "marginicidal capsule", which may mean everything or nothing.

On sectioning the young ovaries of all three species involved, I have found that they all have their septa opposite the sepals (Fig. 51), the normal position in the Ericaceae. Therefore, since the lines of dehiscence are opposite the sepals as well, it follows that dehiscence must be septicidal. Unfortunately I have not seen good fresh fruit of any of the species, however, some rather
slug-eaten material of *Orphanidesia gaultheriodes* showed no evidence of loculicidal dehiscence; on the contrary, the edges of the valves of the capsule were curling inwards as would be expected if there had been septicidal dehiscence.

All the evidence presented above suggests that *Epigaea* and *Orphanidesia* were correctly placed in the Rhododendroideae by Watson et al. (1967). The most important pieces of evidence are the inflorescence type, corolla shape, stamen type, viscin threads, ovary and placentation, shape of the synergid cells, and finally the capsule dehiscence. What misled earlier workers was not so much a fault in their taxonomic philosophy as incorrect observations.

5.2.4. ARTIFICIAL KEY TO THE GENERA OF THE RHODODENDROIDEAE.

1. Inflorescence bud with large, brown perulae, bracts and bracteoles usually deciduous

2. Anthers dehiscing by ± ovate pores

3. Inflorescence axis elongated, with leaves below the flowers; bracts and bracteoles leafy, ± persistent

4. Flowers polypetalous; capsule valves separating from the bottom first

5. Flowers gamopetalous; capsule valves usually separating from the apex first

3. Therorhodon.

4. Ledum.

2. Rhododendron.
2. Anthers dehiscing by short slits
   5. Flowers densely covered by unicellular hairs; ovary
      3-locular
      5 Tsusioiphylum.
      5. Flowers without unicellular hairs, glandular hairs may be present; ovary 4-locular
      6 Menziesia.
1. Inflorescence eperulate, bracts and bracteoles persistent or lacking

6. Flowers polypetalous, or corolla tube <1 mm.

7. Leaves Ericoid
   8. Leaves scattered; anthers dehiscing by a short terminal slit
      14 Bryanthus.
   8. Leaves whorled; anthers dehiscing by a slit their entire length
      15 Ledothamnus.

7. Leaves plane
   9. Flowers 5-merous; anthers dehiscing by terminal pores
      1 Befaria.
   9. Flowers 5-merous; anthers dehiscing by long, introrse slits
      10. Leaves decussate
      16 Lelophyllum.
   10. Leaves scattered
      11. Plant deciduous; seeds ovoid
      7 Cladothamnus.
      11. Plant evergreen; seeds flattened and winged
      8 Elliottia.

6. Flowers gamopetalous
12. Anthers with slits at least half their length

13. Leaves decussate; stamens 5 17 Loiseleuria.

13. Leaves scattered; stamens 10

14. Leaves <2 cm.; antisepalous stamens 2/3 epipetalous 19 Diplarche.

14. Leaves >5 cm.; stamens not epipetalous 9 Epigaea.

12. Anthers with terminal short slits or pores

15. Corolla with ten pouches 10 Kalmia.

15. Corolla without pouches

16. Leaves plane

17. Leaves with ciliate margins, scale-like hairs absent 12 Rhodothamnus.

17. Leaves without ciliate margins, scale-like hairs present 11 Kalmiopsis.

16. Leaves with margins strongly recurved, or Ericoid

18. Leaves Ericoid; style impressed into the top of the ovary 13 Phyllococe.

18. Leaf margins merely strongly revolute; style continuous with the ovary 18 Daboecia.

5.2.5. THE BEJARIEAE


Large shrubs; leaves flat, revolute in bud, entire, evergreen. Indumentum of long-celled hairs and long-stalked glands. Inflorescence terminal, paniculate or corymbose, eperulate; bracts
and bracteoles well developed, + leafy and persistent, bracteoles variable in position; calyx not articulate with the pedicel.

Number of flower parts variable, 5-7 merous. Calyx lobes almost free, rather small, green. Corolla polypetalous, + campanulate. Filaments hairy, anthers dehiscing by terminal pores made by resorption tissue not involving the epidermis, an endothecium also present; viscin threads occur. Ovary with prominently bilobed placentae and apical parietal zone; style impressed into the tip of the ovary, stigma indusiate. Thick-walled septicidal capsule showing some tendency to split loculicidally as well. Seeds numerous, spindle-shaped; testa with long, thin-walled cells.

A monogeneric tribe.

1. **Bejaria** Mutis ex Linn., Mant. Plant. 242 (1771).

There are about thirty species in this genus, which has the characters of the tribe. Six species have been studied.

**Relationships of the Tribe.**

**Bejaria** is a very distinct and apparently isolated genus, and I have followed Copeland (1943) in considering it to be tribally separable. **Bejaria**, with its large polypetalous flowers, variable number of flower parts and unspecialised inflorescence,
has often been considered to represent a very primitive Ericaceous stock (see Abbott, 1936; Camp, 1941).

Its indumentum is unremarkable. Such a combination of hair types is common in the Rhododendroideae, and there are none of the specialised hair types found in the Rhodoreae.

Its inflorescence is very simple. The prominent bracts and bracteoles, rather extended inflorescence axis and lack of bud scales are not basically dissimilar to other Rhododendroideae, apart from the Rhodoreae; but even so the inflorescence as a whole is rather different from the other tribes.

The variability in number of flower parts is approached by the Hymenanthes group of Rhododendron, and several unrelated genera of the Rhododendroideae are polypetalous. The stamens are unremarkable in external morphology (Fig. 45); they dehisce by a terminal pore. However, Copeland (1943) found that dehiscence was by resorbtion tissue like all the tribes apart from the Rhodoreae; but unlike these tribes the dissolution tissue did not involve the epidermis. Furthermore, all the species examined have a prominent endothecium (Fig. 33).

The robust capsule showing a mixture of the two types of dehiscence (but with septicidal predominating, Fig. 11) is not very remarkable, but the seeds have very elongated testa cells. Such cells are found elsewhere only in the Rhodoreae, and in a few species of Kalmia of the Phyllodoceae.
Anatomically there are some rather interesting characters. The leaf stomata are tetracytic, and in at least some species they are orientated transversely to the long axis of the leaf. All the S. American species have a "mucilaginous epidermis" and a midrib bundle which shows an approach to the Oxydendrum-type. In these species three-trace, one-gap nodes are best developed (Fig. 23; see below). Cox (1948a) noted that in details of wood anatomy Bejaria was not particularly primitive. The details of wood anatomy that he gives do not support his statement that Bejaria "seems to have evolved along characteristically different lines from the other tribes, as indicated by conditions of perforation plate structure, vessel side wall and wood parenchyma pitting and medullary ray type." Only in the last-mentioned character does it differ from all the other Rhododendroideae that he studied; the same type of medullary ray that is found in Bejaria is also to be found in the Arbuteae sensu Drude.

Although Bejaria is like the Epigaeae in a number of characters (stomatal type, rather similar midrib bundles, stem and leaf indumentum) they differ in pith and nodal types, floral indumentum, floral stomatal distribution and many details of the stamens and the fruit. The general appearance of the genus is like a polypetalous Rhododendron, hence it has been given the name "Andenrose" by German explorers who compared it with Rhododendron ferrugineum, the "Alpenrose" (see Copeland, 1943).
FIG. 45: BEJARIA AND RHODODENDRON.

1. *Bejaria racemosa* - a = x5, b = x10, from the side; 2. *B. racemosa*, x50 - midrib;
Fedtschenko and Basilevskaja (1920) also compared it with some of the Rhodoreae and Phyllodoceae. Although *Bejaria* lacks the deciduous bud scales and perulae of the Rhodoreae and has a very different type of anther, the Bejarieae and the Rhodoreae both have long, thin-walled testa cells.

**Nomenclature of Bejaria.**

There has been considerable discussion as to how to spell the name of the genus (see Sprague, 1928). His decision is followed here. The type species of *Bejaria* itself is *B. aestuans*. Of the two generic synonyms one, *Jurgensenia*, apparently represents *B. discolor* and was originally published as a genus of the Zygophyllaceae. *Acunna* was distinguished from *Bejaria*, to which it was acknowledged to be close, solely because it was 7-merous; there seems to be no other difference between the two. There is considerable variation in the number of flower parts in this genus.

**Infrageneric Classification of Bejaria.**

Mansfeld and Sleumer (1934) divided *Bejaria* into two sections. Section *Racemosae* included the N. American *B. racemosa* alone, section *Glaucæ* contained all the other species from Mexico southwards to S. America, and the Antilles. This separation was mainly on anatomical grounds:— epidermal features, the presence of an "hypodermis" and the raising of the veins above the surface of the leaf. The two sections may be distinguished as follows:-
Racemosae
Anticlinal epidermal walls sinuous.
Stomata on both sides of the leaf.
Ordinary epidermis.
Veins raised on both surfaces.
Pieris-type midrib bundle.

Glaucae
These walls straight.
Present abaxially only.
"Mucilaginous epidermis".
Veins raised abaxially only.
Near Oxydendrum-type bundle.

Copeland (1943) studied only B. racemosa, so he could not confirm this division. However, he failed to note the occurrence of stomata on both sides of the leaf in B. racemosa. It should be noted that there are quite a number of configurations in all species which are not strictly tetracytic (Fig. 26). Some of the species have very striate cuticles, and the striae may be so well developed that they obscure the cell walls in surface view. B. racemosa and B. laevis both have rather smoother cuticles than the other species studied.

Mansfeld and Sleumer (1934) failed to note that the difference in the prominence of the bundles on the two sides of the leaf was reflected in the anatomy of the midrib bundle. The Racemosae have a Pieris-type bundle, whilst all members of the Glaucae studied have a near Oxydendrum-type bundle (Fig. 45). Also, what they recorded as an hypodermis is not like the hypodermis of several other Ericaceae, but is of the type here called a "mucilaginous epidermis" (Fig. 28). It also appears that there may be an incipient difference in nodal anatomy. Species from
section **Glaucae** all have a three-trace, one-gap node, or if the node itself has not been seen three bundles have been found in the base of the petiole. *B. racemosa* seems to be tending towards the simple unilacunar node, since Bozeman 10457 and Curtiss 4922 both showed the two nodal types on the same plant; in addition the former specimen also had a leaf supplied by a two trace one gap node.

I have found abaxial corolla stomata on two species, *B. mathewsi* and *B. laevis*. I could not find them in *B. racemosa*, but the significance of this variation awaits further studies on better material.

5.2.6. **RHODOREAE** D. Don, Edin. New Phil. Journ. 17: 152 (1834)

Small to large shrubs, rarely trees. Leaves usually at least of medium size, ± entire, evergreen or deciduous, convolute or revolute in bud. Indumentum very variable indeed. Inflorescence terminal, rarely axillary, corymbose or umbellate, perulate. Bracts and paired basal bracteoles usually brown and fugaceous. Flower often slightly zygomorphic; the median sepal always (?) abaxial. Calyx variably developed, often very reduced. Corolla gamo- or polypetalous, 4-9 lobed; shape variable, but very rarely urceolate or tubular. Stamens 5-15; anthers dehiscing by means of collapse tissue only, forming pores or short slits; viscin threads usually present. Ovary 4-12 locular, often covered with glandular hairs;
placentation with a prominent parietal zone at the apex of the ovary; placentae often very bifid; the style impressed or not; the stigma often prominently indusiate. Fruit a many-seeded septicidal capsule; the seeds variably shaped and winged, the cells of the testa are nearly always elongated.

Genera recognised:— Rhododendron, Therorhodon, Ledum, Tsusiophyllum and Menziesia.

Klotzsch's (1851) separation of two ordines (= families), the Menziesiaceae and Rhodoraceae, on the grounds of anther dehiscence, bud perulae, etc. cannot be maintained, not least because Menziesia does not have the characters of its family.

Eichler's (1875) separation of the Rhodoraceae from the Ericaceae sensu restricto on the grounds that the former alone possessed the Lobelia-type floral diagram is also unsupportable (see p. 34). The character is more variable than Eichler thought.

My concept of the Rhodoreae is the same as that of Copeland (1943); he separated the Rhodoreae from the Phyllodoceae (sensu Drude, but excluding Daboecia) and other tribes on the following grounds:—

1). Large and often thin leaves.

2). Winter buds protected by specialised perulae.

3). The orientation of the flowers.

4). The lack of resorbtion tissue in the anthers.

5). Viscin threads present.
1). The Rhodoreae are rather large-leaved on the whole, although several species have small leaves. Apart from Bejaria and some species of Kalmia, the other Rhododendroideae are small leaved. There is no obvious difference in thickness of the leaf in the various groups.

2). This is a character not found outside the Rhodoreae in the Rhododendroideae. Even anomalous genera like Therorhodion have perulae at the base of its inflorescence.

3). The problem of floral orientation has been dealt with above. Copeland (1943) claimed that all genera of the Rhodoreae had zygomorphic flowers with the lobelia-type floral diagram (Fig. 6). It appears that neither the zygomorphy of the flower nor its anomalous orientation is so common elsewhere.

4) Lack of resorbtion tissue in the anther is confined to the Rhodoreae so far as is known at present; again the situation is unknown in several genera, e.g. Dinlarche, Ledothamnus, Epigaea.

5). Viscin threads do not separate the Rhodoreae from the Phyllodoceae. Ikuse (1954) first found such threads in a number of the Phyllodoceae, and these observations have been confirmed and extended by Watson et al. (1967) and myself.

There are four additional characters which may be used to separate the Rhodoreae from other tribes, especially the Phyllodoceae.
1). Nearly all the Rhodoreae I have examined have the cells of the testa very elongated. Often the seed itself is ± spindle shaped, but it may be ovoid. Even in the latter case the cells are usually elongated, e.g. *Rhododendron campylophorum*, which has ovoid seeds with the testa cells over seven times as long as broad. These long testa cells occur in some species of *Kalmia* (but not in *K. ericoides* and *K. hirsuta*, Fig. 51) and in *Bejaria*. *R. occidentale* has ± isodiametric cells in its testa, but this is the only member of the Rhodoreae which I have found to have such cells; they may yet be discovered in some other members of the Azalea group of *Rhododendron*. Other genera of the Rhododendroideae seen have the testa cells much shorter and often with rather thick cell walls.

This character has been mostly overlooked by previous authors, although Drude (1897) and Schultze-Motel (1964) noted this difference in the rather less specific terms of seed, and not cell, shape. It also correlated fairly well with Maximowicz's (1870) and Hooker's (1876) division of the seeds of the Rhododendroideae into those genera with a firm testa, and those with a loose or sawdust-like testa.

2). Maximowicz (1870) separated his subtribe Phyllodoceae from the subtribe Eurhododendreae partly because the former had green, persistent, bracts and paired basal bracteoles. This is a useful difference, since in nearly all the Rhodoreae the bracts
and bracteoles are brown and deciduous like the perulae; indeed they fall off almost as soon as the bud opens. The only exception I have come across is in the genus Therorhodion, where the bracts and bracteoles are green and leafy (Fig. 47). This character serves to separate the Rhodoreae even against the Bejarieae, although Maximowicz included Bejaria in the Eurhododendreeae.

3). There is no absolute difference in indumentum types, but again the Rhodoreae are partially distinguishable from the other tribes. Only here are glandular, lepidote scales, branched hairs and compound hairs apparently formed from the fusion of several hairs (Figs. 19, 21 and 48) to be found. The Rhodoreae with a mixture of ordinary long-celled hairs and long-stalked glandular hairs are indistinguishable from other genera of the Rhododendroideae with a similar indumentum, e.g. Diplarche, Epigaea, Bejaria.

4). There may be a difference in the distribution of floral stomata, although it must be emphasised that the large genus Rhododendron is still almost unsampled as regards this character. In the Phyllodoceae the stomata are usually adaxial on the calyx and of variable occurrence on the corolla. In the Rhodoreae they are present abaxially (and sometimes adaxially as well) on the calyx, again they are of variable distribution on the corolla. In some species of Rhododendron they are lacking from the abaxial surface of the calyx, but this may be due to the very reduced size of the calyx in these species. The Bejarieae, Diplarcheae
and Cladothamneae also have stomata on the abaxial surface of calyx and corolla, or only on the former.

Anatomically I have been unable to separate the Rhodoreae from the other tribes, and this is the same conclusion as Breitfeld (1888) reached. Again Kalmia is very heterogenous in details of its anatomy, and as Breitfeld noted, is rather similar to some species of Rhododendron in lamina anatomy. The Rhodoreae are very variable in their anatomy and encompass most of the variations which are more common outside the tribe.

From what has been written, it can be seen that the Rhodoreae can be separated from all other tribes of the Rhododendroideae by a number of characters. There is some similarity to several tribes, notably the Phyllodoceae (especially Kalmia) and the Bejarieae. Kalmia is intermediate in leaf type and anatomy, seed type and in floral stomatal distribution. However, it lacks the large perulae and deciduous bracts and bracteoles of the Rhodoreae, and it also has a different type of anther dehiscence mechanism and apparently a different orientation of the flower, hence it is better retained in the Phyllodoceae.

Such chromosome numbers as are known support the separation of the Phyllodoceae and Rhodoreae. All the counts from the Rhodoreae, with the exception of Therorhodion, are based on $x = 13$. Therorhodion, the Phyllodoceae (including Kalmia) and Daboecieae have $x = 12$, whilst there is a report of $x = 11$ from
<table>
<thead>
<tr>
<th>Character</th>
<th>Bejaria</th>
<th>Rhododendron</th>
<th>Therorhodion</th>
<th>Tausiophyllum</th>
<th>Ledum</th>
<th>Menziesia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves evergreen</td>
<td>+</td>
<td>+ and -</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Leaf vernation</td>
<td>revolute</td>
<td>revolute &amp; convolute</td>
<td>convolute</td>
<td>revolute</td>
<td>revolute</td>
<td>convolute</td>
</tr>
<tr>
<td>Bud scales</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Indumentum</td>
<td>long-celled</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>gland head</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>branched</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bracteoles</td>
<td>small, green</td>
<td>scarious</td>
<td>large, green</td>
<td>scarious</td>
<td>scarious</td>
<td>scarious</td>
</tr>
<tr>
<td>Corolla gamopetalous</td>
<td>-</td>
<td>+ (rare -)</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Calyx stomata</td>
<td>- +</td>
<td>+, - +, - +, - +</td>
<td>+ +</td>
<td>-  +</td>
<td>- (2) + (5) +</td>
<td></td>
</tr>
<tr>
<td>Stamen number</td>
<td>8-25</td>
<td>5-20</td>
<td>10</td>
<td>5</td>
<td>10</td>
<td>5, (8), 10</td>
</tr>
<tr>
<td>Anther endothecium collapse tissue</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Viscilin threads</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>not seen</td>
<td>-</td>
</tr>
<tr>
<td>Capsule open at apex</td>
<td>+, rare -</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Multicellular ovary hairs</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Ovary loculi</td>
<td>5-7</td>
<td>5-12</td>
<td>5</td>
<td>3</td>
<td>5(usually) 4 or 5</td>
<td></td>
</tr>
<tr>
<td>Leaf stomata</td>
<td>++ or ↔</td>
<td>++ or ↔</td>
<td>tetracytic</td>
<td>anomocytic</td>
<td>anomocytic</td>
<td>anomocytic</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>anomocytic</td>
<td>anomocytic</td>
</tr>
<tr>
<td>Hypodermis</td>
<td>-, &quot;mucilaginous&quot;</td>
<td>- , + , &quot;mucilaginous&quot;</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Midrib bundle</td>
<td>Pieris, c.f. various</td>
<td>Pieris</td>
<td>Pieris</td>
<td>Lyochia</td>
<td>Pieris</td>
<td></td>
</tr>
<tr>
<td>Pith</td>
<td>+ homogenous</td>
<td>homo- or heterogenous</td>
<td>homogenous</td>
<td>homogenous</td>
<td>heterogenous</td>
<td>homogenous</td>
</tr>
</tbody>
</table>

Table 4: VARIATIONS OF SOME TAXA AMONGST THE PTERIDACEAE AND RHODODENDRONEAE
Elliottia racemosa of the Cladothamineae.

I do not agree with Watson et al. (1967) who included Elliottia and Cladothamnus with the other Rhodoreae. These two genera differ in indumentum, flower, stamen and seed type, as well as in embryology from the Rhodoreae and should be placed in a separate tribe (see section 5.2.7).


   *Tsutsusi* Adans., Fam. 2: 164 (1763).

   *Hochenwartia* Crantz, Inst. Rei Herb. 2: 468 (1766).

   *Vireya* Blume, Bijd. Fl. 2: 854 (1826).

   *Hymenanthes* Blume, Bijd. Fl. 2: 862 (1826).

   *Osmothamnus* DC., Prod. 7 (2): 715 (1838).

   *Theis* Salisb ex DC., Prodr. 7 (2): 715 (1838).


   *Anthocoma* Koch, Hort. Dendrol. 338 (1853).


   *Biltia* Small, Fl. S. E. U. S. 884 (1903).


Trees to small shrubs. Leaves alternate, scattered to pseudoverticillate; entire, evergreen or deciduous; convolute or revolute in bud. Indumentum variable: glandular scales and long-celled hairs or glandular scales alone or long-celled hairs and long-stalked glands or long stalked glands and branched hairs; unicellular hairs on all (?) species. Inflorescence terminal or, less commonly, axillary, perulate; umbellate or corymbose; pedicels not articulated with the calyx; bracts and basal bracteoles brown and deciduous. Flowers 4-8-merous, often rather zygomorphic, odd sepal posterior. Calyx very variable in size, the lobes free. Corolla 4-8-lobed, the lobes variable in size, tubular to hypocrateriform in shape. Stamens 5-16; filaments hairy or glabrous; anthers dehiscing by an ovate terminal pore created by collapse tissue. Ovary (4-)5(-12)-locular; placentae often deeply bifid; the usually long style impressed at the apex, or ovary narrowed into style, stigma + indusiate. Capsule nearly always apically septicidal; seeds numerous, often winged or tailed; testa nearly always with long cells.

There are ca. 1000 species in this genus, of which only fourteen have been studied intensively; many more have been looked at in less detail.

I have not done nearly enough work on this genus to be able to make a detailed criticism of the various segregates proposed.
above. Both Hooker (1876) and Drude (1897) took a very broad view of the genus, even including Therorhodion in it. On the other hand, Small (1914) recognised six genera from N. America alone (Biltia, Rhododendron, Rhodora, Azalea, Azaleastrum, Therorhodion); this was probably due to the fact that he considered the N. American species in isolation from the other members of the genus.

Copeland's (1943) work will be used as a starting point for the following discussion, in which an attempt is made to correlate the work on several different aspects of Rhododendron by authors who have been unaware of the full literature available. The data are summarised in Table 5.

Copeland (1943) recognised five genera:

<table>
<thead>
<tr>
<th>Terminal or lateral inflorescence.</th>
<th>Indumentum peculiarities.</th>
<th>Leafy Peduncular bracts.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Azalea</td>
<td>T.</td>
<td>Flattened bristles.</td>
</tr>
<tr>
<td>Azaleastrum</td>
<td>L.</td>
<td></td>
</tr>
<tr>
<td>Hymenanthes</td>
<td>T.</td>
<td></td>
</tr>
<tr>
<td>Rhododendron</td>
<td>T.</td>
<td>Glandular scales.</td>
</tr>
<tr>
<td>Therorhodion</td>
<td>T.</td>
<td></td>
</tr>
</tbody>
</table>

These are the only differences which one can glean from his account. Other differences, such as the deciduous habit which predominates in Azalea, stamen number, etc., were found to be variable.
<table>
<thead>
<tr>
<th>Taxa</th>
<th>Leaf in Bud</th>
<th>Indumentum</th>
<th>Node</th>
<th>Midrib Bundle</th>
<th>Hypodermis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhododendron group</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhododendron (subgenus)</td>
<td>convolute,</td>
<td>glandular scales</td>
<td>simple</td>
<td>Pieris or</td>
<td>present in 128/261 app.; 81.3% of these have hypodermal cells much larger than epidermal, sometimes poorly developed &quot;mucilaginous&quot; epidermis</td>
</tr>
<tr>
<td>Pseudazalea</td>
<td>except</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhodorastrum</td>
<td>section</td>
<td>long-celled</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudorhodorastrum</td>
<td>Edgeworthii</td>
<td>hairs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;Section&quot; Vireya</td>
<td></td>
<td>glandular scales only</td>
<td></td>
<td>unilacunar</td>
<td>Lyonia types very well-developed &quot;mucilaginous&quot; epidermis</td>
</tr>
<tr>
<td>Azalea group</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Azalea</td>
<td></td>
<td>long-celled</td>
<td>simple, unilacunar</td>
<td>Pieris type</td>
<td>only section</td>
</tr>
<tr>
<td>Tsutsia</td>
<td>revolute</td>
<td>hairs +</td>
<td></td>
<td></td>
<td>Azaleastrum (5 spp.) has an hypodermis</td>
</tr>
<tr>
<td>Azaleastrum</td>
<td></td>
<td>long-stalked glands</td>
<td></td>
<td>intermediate</td>
<td>Lyonia type</td>
</tr>
<tr>
<td>&quot;Section&quot; Choniastrum</td>
<td></td>
<td>long-stalked glands</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hymenanthes group</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hymenanthes</td>
<td>revolute</td>
<td>long-stalked glands + branched hairs</td>
<td>complex</td>
<td>Lyonia type (always?)</td>
<td>present in 265/289 app.; 3.8% of these have hypodermal cells much larger than epidermal</td>
</tr>
</tbody>
</table>

**Table 5** Correlation of some characters with the main infragenetic groups of *Rhododendron*  
(see text for references)
Copeland seems to have been unacquainted with Sinclair's (1937) work on the aestivation of the leaf in bud. Sinclair found that there were two groups within *Rhododendron* sensu lato. One had convolute leaves and scale hairs, i.e. was lepidote, and might or might not have "hairs". He included the *Edgeworthii* group here, even though it had revolute leaves, because it was lepidote. The other group was elepidote and had leaves revolute in bud. (*Therorhodon* will be excluded from the discussion for the present.) Again he divided this group on whether or not it had "hairs". As Seithe (1960) noted, one cannot be sure what he meant by his term "hairs", neither did he record what species were studied, so further exceptions may come to light. The lepidote group corresponded to *Rhododendron* sensu Copeland, the elepidote group to the other genera.

Hutchinson (1946) divided the genus into three main groups. One corresponds to *Azalea* + *Azaleastrum*, another to the lepidote *Rhododendron* group; the third was elepidote and may be called the *Hymenanthes* group, since it corresponds to that genus. Although he did not specify exactly what characters he used to separate the groups, he must have used hair type and leaf aestivation. He thought that the *Hymenanthes* group was the most primitive, mainly on the grounds of meristic variability. Members of this group often have flowers which are more than five-merous (Fig. 45).
Hayes et al. (1951) studied the lamina anatomy from 567 species from all groups. The characters which they found to be of greatest use were those of the number of cell layers in the upper dermis and the relative size of these layers, and the thickness of the cuticle (to a rather lesser extent). It is with the first two that I shall be concerned. These characters they found to be of use at the sectional level, but were not necessarily indicative of relationship. It is found that they do correlate well with the three main groups (Table 5), and so would seem to be fairly good indicators of relationship.

Seithe (1960) dealt with the indumentum types within Rhododendron; her work in part supersedes that of Cowan (1950). Although Seithe's work involved fewer species (only 265 species), than that of Cowan, she did study members of the Malaysian Vireya group which Cowan did not. She was able to establish three basic combinations of hair types which she thought showed little intergradation in the species living today. They are (1), scales plus long-celled hairs (subtype, scales alone) (2), long-celled hairs plus long-stalked glands and (3), branched hairs plus long-stalked glands. These groups correlated with Hutchinson's three groups established using rather different criteria, and with the leaf aestivation data of Sinclair (1937). She gave these three groups the rank of "chori subgenera", but here they will be referred to simply as "groups".
Finally Philipson and Philipson (1968) studied the nodal anatomy of 264 species of the genus. The Rhododendron and Azalea groups had simple, unilacunar nodes, although the single trace sometimes divided in the petiole. Section Choniastrum of Azalea was the only exception; it had intermediate nodes with up to five traces leaving from one or more gaps; those species with simpler nodal structure were close to others with a more complex arrangement. They correlated their work with that of Sinclair (1937) and recognised the same three groups as Seithe (1960) and Hutchinson (1946). Unfortunately they seem to have been unaware of Seithe's work, and mention that of Hayes et al. (1951) only in passing, making no attempt to correlate it with theirs.

My work is much more fragmentary as yet, but the following points are relevant. Pith type is now known from over forty species (Watson, 1965; and personal data). The Rhododendron group has both heterogenous and homogenous pith types, but all six (of the total of nine) sections of the Azalea group examined have homogenous pith. In the Hymenanthes group all the species examined (from six sections) had a rather distinctive type of heterogenous pith with very thick-walled cells enclosing small islands of thin-walled cells not very different in size and containing druses. Also there seem to be ± asteroid-shaped sclereids in the stem cortex of species of the Hymenanthes group.
These have also been found in the petiole of *R. intranervatum* (section Vireya, Rhododendron group); but the character seems worth further study.

Referring to Table 5, it is seen that on the whole the variation mentioned is correlated with the three main groups, with the partial exceptions of sections Vireya and Choniastrum, which will be dealt with in more detail below. Even so, these three main groups show overlap in most of the characters, and other characters are even more variable. Thus species with five stamens and those with the deciduous habit are not absolutely correlated. Seeds with cells differentiated from the others, becoming swollen, and forming wings are to be found in all three of the groups. If any genera are to be segregated at all they will have to be based on single character differences, as are those of Copeland (1943). His genera are delimited on characters which commonly vary within genera, e.g. Gaultheria, Vaccinium, and even the small genus Kalmia. Davis' (1962) criticisms of this attitude are justified in this case; one cannot split a large genus just because it happens to be large, especially when the segregates (as in this case) overlap in all other characters apart from the one chosen and are part of an otherwise coherent entity (see section 3.3.2.). Hence it is thought that Rhododendron sensu lato (but excluding Therorhodion for the time being) should be maintained as a genus which holds together on a
basic similarity of indumentum, habit, inflorescence, stamen and seed, no one group being easily distinguishable from all others. For a comparison of Rhododendron with the other members of the Rhodoreae, see Table 4.

**Remarks on future lines of investigation within the genus.**

Although hypodermal type has been extensively studied, there still remains much work to be done on leaf anatomy. All three species of series Lapponicum studied had the same leaf anatomy (Fig. 31), with very small adaxial xylem cells and the spongy mesophyll arranged in a curtain (Plate 4). The same anatomy occurs in R. anthopogonoides, of section Pogonanthum, but not in any other species examined. Further work is needed to see if this is indicative of relationship. R. zoelleri is notable for its branched sclereids which are modified palisade cells; this is another character whose distribution is unknown. Little attention has been paid to the type of the midrib bundle; see Fig. 45 for some variations.

The three species of section Choniastrum examined all had rather large, flat leaves on which the stomata were transversely orientated. No other species of Rhododendron had this stomatal orientation, although often the indumentum is so dense that any orientation might be expected to be disturbed (see p. 110). R. tashiroi, R. mindaense and R. crassifolium all have at most a sparse indumentum, yet even so their stomata were unorientated.
R. ericoideas and R. quadrasianum, which were examined because their leaves are superficially rather Ericoid in appearance, have their stomata orientated parallel to the leaf. Further work is needed on this character, but the stomatal orientation of section Choniastrum, coupled with its odd nodal type and Lyonia-type midrib bundle (according to Hayes et al., 1951, the normal condition for the Azalea group is the Pieris-type), together support the suggestion of Philipson and Philipson (1968) that subgeneric rank may be needed for this section.

Another character which needs much more study in Rhododendron is the seed type. Sleumer (1949) divided the seed appendages of Rhododendron into three groups:- (1) small tails at one end, (2) small tails at both ends, and (3), long tails at both ends. The tails of section Vireya are multicellular protrusions of elongated, unspecialised cells similar to the smaller tails of Ledum, Menziesia and some species of Rhododendron. The lateral wings of species like R. nematocalyx are also multicellular projections, but here the cells of the wings are different in shape from the other cells of the testa. R. canadense has tails at both ends of the seed which are no more than the combined swellings of several adjacent cells, the other testa cells are much elongated. In R. occidentale the wings are multicellular plates of cells; the whole testa is made up of cells which are not elongated (Fig. 46).
FIG. 46: RHODODENDRON SEEDS

Sleumer (1949) suggested that section *Vireya* from Malaysia might best be raised to subgeneric rank, since it differed from all other groups in seed, fruit and corolla. In this large group the only multicellular hairs known are glandular scales (Seithe, 1960). Mucilaginous epidermes (Hayes et al., 1951) are far better developed here than in any other group of *Rhododendron*, although epidermes divided by a single periclinal wall are known from some species of the *Rhododendron* group. According to Sleumer (1949) there are some corolla shapes to be found in this section which are not to be found in any other members of the genus. The seeds have very long tails at both ends, such well developed, comparable tails are not known elsewhere. I have been unable to establish whether or not the capsules dehisce differently to those of other members of the genus, (they seem to be unremarkable in this respect) but the evidence already at hand suggests a re-examination of the rank of section *Vireya*.

3. **THERORHODION** Small, N. Am. Fl. 29 (1): 45 (1914).

Low-growing shrubs with deciduous, ± entire leaves revolute in bud. Indumentum of long-stalked glands and long-celled hairs. Inflorescence terminal, few flowered, perulate; floral axis elongated with leaves lower down; bracts and bracteoles leafy; long pedicels not articulated with the calyx. Flowers rather zygomorphic, especially in the lobing of the corolla, odd sepal posterior. Calyx well developed, leafy. Corolla subrotate,
deeply lobed. Stamens ten, the upper smaller than the lower; filaments glabrous; anthers dehiscing by two terminal pores, viscin threads present. Ovary five-lobed, covered with glandular hairs; placentae bifid; style curved, ± impressed, stigma indusiate, five-lobed. Fruit and seed not seen.

There are two-three species in the genus, two have been studied. The type species of the genus is *T. clematicum*.

*Thororhodion* has been accepted as a genus by a number of recent authors, e.g. Hutchinson (1921, 1946), Sleumer (1949), Seithe (1960), or considered to be on the border lines of generic distinction, e.g. Philipson and Philipson (1928).

In its facies it seems at first sight rather unlike a *Rhododendron*. Although the flower in winter is surrounded by bud scales, the 1-4-flowered inflorescence has an axis of 4-6 cm. bearing leaves lower down, and leafy bracts above. In the rest of the Rhodoreae such leaves are lacking and the bracts are deciduous; the inflorescence is never so elongated unless there are numerous flowers. It seems that the whole inflorescence completely dies down in winter; the leaves on its lower part do not have buds producing shoots in their axils. Thus the inflorescence, although superficially so different, behaves similarly to those of the other Rhodoreae. In this respect Hutchinson's (1921) comments are incorrect; the flower buds are specialised and it is perhaps misleading to say that the flowers
are borne on young leafy shoots. Both Small, in his original
description of the genus, and Sleumer (1949) were incorrect in
stating that there was a terminal flower. Sleumer based his
statement on an illustration (Bot. Mag., T. 3210) in which it is
impossible to see the exact nature of the inflorescence. The
topmost flower is not terminal, since there is usually a portion
of the axis with a bud and reduced bract beyond the point of
departure of the uppermost pedicel (Fig. 47). Some of the
confusion may have arisen because the pedicel and inflorescence
axis are undiverged for a short distance above the bract.

Both Small and Hutchinson (1921) emphasise the fact that the
corolla is split more deeply on its abaxial side. This is
apparently better developed in T. redowskianum than in T.
camschaticum, although it can be seen in this latter species
(Fig. 6). In many species of Rhododendron the corolla is slightly
zygomorphic, and in R. canadense the two lower lobes are almost
free, the three upper ones fused (Stevenson, 1947). As in some
species of the Azalea group the upper stamens are shorter than
the lower ones. The stamens seem to be very similar to those of
Rhododendron and Ledum.

In general leaf and stem anatomy, etc. Therorhodon shows
many similarities to Rhododendron subgenus Azalea. The
indumentum is of the type found in Azalea and the deciduous leaves
are apparently revolute in bud (Hara, 1958). The pith is
FIG. 47: RHODOEAE - GENERAL (1).

1. Therorhodion camtschaticum, x1 - flowering shoot; 2. Menziesia glabella;
3. Rhododendron lapponicum; 4. Ledum palustre (capsules, all x6); 5. T. camtschaticum, x100 - midrib bundle; 6. L. columbianum, x5; 7. M. ciliicalyx, x66;
8. M. pentandra, x50; 9. Tsusiophyllum tanakae, x100 (e = epidermis).
homogenous, the midrib bundle of the Pieris-type and there is no hypodermis (Fig. 47), all characters of the Azalea group. However, Philipson and Philipson (1968) found that although the vegetative leaves had a simple unilacunar node, the single trace dividing into three in the stem cortex, there were three traces from a single gap supplying the leaves on the peduncle. I have confirmed this in T. camschaticum, and the three-trace one gap nodes were also found on the peduncle of T. glandulosum.

There are stomata on both sides of the calyx and corolla, but whether or not this is similar to the Azalea group is at present unknown.

Therorhodion is doubtfully generically distinct from Rhododendron. Its inflorescence and nodal anatomy are distinctive, and it is interesting to note that T. camschaticum has a basic chromosome number of $x = 12$, the only member of the Rhodoreae known with this. If not maintained as a genus, Therorhodion is best included as a subgenus in the Azalea group of subgenera.


**Dulia** Adans., Fam. 2: 165 (1763).

Small to medium-sized evergreen shrubs. Leaves entire, revolute in bud and often when mature. Indumentum of long-celled hairs and glandular scales; papillae and/or unicellular hairs often present. Inflorescence many-flowered, corymbose, paniculate
or not, perulate; bracts and bracteoles deciduous; pedicel not articulate with the calyx. Calyx small, lobes free. Corolla polypetalous, rotate, five(-seven) petals. Stamens usually ten; filaments hairy; anthers dehiscing by paired, terminal pores; viscin threads present. Ovary five-locular, covered with scales; placentae bifid; style ± impressed, stigma hardly expanded. Pendulous septicidal capsule, valves separating from the base upwards; seeds numerous, long spindle-shaped, unwinged; cells of the testa elongated.

There are ca. ten species in the genus, of which six have been studied. The type of the genus is *L. palustris*.

*Ledum* may be easily distinguished from *Rhododendron* on three characters:

1. All members of *Ledum* are polypetalous, with an essentially rotate corolla. Although *R. micranthum* and similar species have deeply lobed corollas, a very definite corolla tube is also present.

2. The flower is held erect, but after the petals fall it becomes deflexed and remains this way until the seed is ripe. Then the capsule valves separate from the central placental column at the anatomical base of the fruit first (Fig. 47). This is very rare in *Rhododendron*, although *R. nematocalyx* dehisces in this way (Fig. 11). Other members of section *Nematocalyx* have capsules dehiscing normally with the valves separating from the apex of the fruit first. The seeds of *Ledum* are unremarkable (Fig. 48).
FIG. 48: RHODORAE - GENERAL (2).

3). All species of *Ledum* examined have lysigenous spaces in the spongy mesophyll (Fig. 47). These have not been found in *Rhododendron*.

*Ledum*, with its indumentum of long-celled hairs (which may be reduced to an uniseriate hair; see Fig. 21) and glandular scales (Fig. 19) is very close to the *Rhododendron* group of *Rhododendron*. Copeland (1943) noted the similarity of the scale types, and thought that *R. micranthum* was close to *Ledum*, although they are similar in general facies, they differ in all three characters mentioned above. He also thought that *Ledum* lacked viscin threads; both Ikuse (1954) and I have found them here. *Rhododendron* subsection *Edgeworthia* is the only member of the above-mentioned group with revolute leaves like those of *Ledum*, but it has an hypodermis which is absent in all species of *Ledum* and it also lacks the spaces in the mesophyll.

There is one putative hybrid between *Rhododendron* and *Ledum*. This is *R. vanhoefanii* (= *R. lapponicum* X *L. palustris* var. *decumbens*). This was studied in detail by Abromeit (1899), who considered that in view of the fused corolla the plant should be described as a *Rhododendron* until the situation was clarified. It has never been seen since, but I have been able to reinvestigate the leaf anatomy from a leaf of the original specimen. Details are given in Table 6, from which it can be seen that the putative hybrid is rather closer to *Ledum* than to
<table>
<thead>
<tr>
<th>Character</th>
<th>\textit{Rhododendron lapponicum}</th>
<th>\textit{Rhodo. vanhoefii}</th>
<th>\textit{Ledum palustre}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Long-celled hairs: type and distribution</td>
<td>with small branches, leaf margin</td>
<td>not seen</td>
<td>unbranched, over leaf surface (abaxial)</td>
</tr>
<tr>
<td>Scales with margins</td>
<td>+</td>
<td>- (+) Fig. 48</td>
<td>-</td>
</tr>
<tr>
<td>Papillae and unicellular hairs</td>
<td>dense, 20(\mu) - 50(\mu)</td>
<td>moderate, 3(\mu) - 65(\mu)</td>
<td>sparse, ca 60(\mu) - 70(\mu)</td>
</tr>
<tr>
<td>&quot;Mucilaginous&quot; epidermis</td>
<td>+</td>
<td>-</td>
<td>ca. 50(\mu)</td>
</tr>
<tr>
<td>Height of palisade tissue</td>
<td>ca. 100(\mu)</td>
<td>ca. 65(\mu)</td>
<td>-</td>
</tr>
<tr>
<td>Spongy mesophyll in curtains</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Lysigenous spaces in the leaf</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Lignification associated with midrib bundle</td>
<td>none</td>
<td>poor, bast and libriform</td>
<td>prominent, also thick walled &quot;pith&quot; cells</td>
</tr>
<tr>
<td>Very small adaxial xylem cells</td>
<td>well developed</td>
<td>-</td>
<td>poorly developed</td>
</tr>
</tbody>
</table>

\textbf{Table 6} Comparison of leaf anatomy of \textit{Rhododendron/Ledum} hybrid with putative parents.
Rhododendron (c.f. the scale structure: Figs. 19 and 49). However, the material was getting rather old, and some of the details were rather unclear. From the original illustration it can be seen that the corolla is slightly, but definitely fused, and that there are traces of capsules on the plant. It might still be possible to ascertain which way the capsules are held, and it would also be very interesting to find out the aestivation of the leaves in bud. The specimen should still be retained in Rhododendron until further studies are made, but it is quite possible that the specimen is a hybrid, or even a teratological form of Ledum.


Small deciduous shrub, leaves entire, revolute in bud. Indumentum dense, adpressed, flattened, long-celled hairs. Inflorescence terminal, perulate, a 1–4-flowered umbel; bracts and bracteoles deciduous; short pedicel not articulate with the calyx. Calyx small. Corolla hypocenteriform with five rather small lobes, densely covered on both surfaces by flattened, long-celled hairs. Stamens five, antisepalous; filaments hairy; anthers rather elongated and dehiscing by two rather elongated slits; viscin threads present. Ovary 3-locular, densely covered with long-celled hairs; placentae slightly bifid; style ± impressed,
stigma expanded. Capsule septicidal, with many, unwinged seeds, seeds spindle-shaped; testa cells elongated.

The genus is montypic. The sole species, *T. tanakae*, has been studied.

*Tsusiophyllum* has been kept generically distinct by all authors. Although its bud scales were originally described as breaking away from the base in a rather curious way, they did not seem to be behaving abnormally in the plant in cultivation in the garden at Edinburgh. It may be distinguished from *Rhododendron* by its three-locular ovary (unique in the Rhodoreae) and its five, antisepalous stamens which have rather long anther thecae dehiscing by a slit (Fig. 42). In this last character it approaches *Menziesia*. The anther slits do not extend down more than one-fourth the length of the thecae in the material that has been seen (but c.f. Copeland, 1943). However, the slits easily become extended by the tearing of the fragile theca wall.

In its vegetative features it approaches *Rhododendron* subgenus *Tsutsia*, as Maximowicz noted in his original description. Like this group, it has a stem with an homogenous pith and unilacunar nodes, a leaf lacking an hypodermis and with a *Pieris*-type midrib bundle (Fig. 48). Its hairs (Fig. 48) are "fransenzotte" (see Seithe, 1960), such as are to be found in subgenus *Tsutsia*. The leaves revolute in bud, capsule type,
and unwinged seeds with long cells in the testa are all characters common in Rhododendron. There are stomata on the abaxial surface of the calyx and corolla (but c.f. Watson, 1965); this is like many of the Rhodoreae.


   Deciduous shrubs; leaves entire, revolute in bud.

   Indumentum of long-stalked glands and long-celled hairs, the latter often fused into scale-like structures on the abaxial midrib of the leaf. Inflorescence terminal, few-flowered, umbellate, perulate; bracts and bracteoles deciduous; calyx not, or hardly, articulate with the pedicel. Flowers four- or five-merous; slightly zygomorphic. Calyx lobes free, prominent or reduced. Corolla tubular-urceolate with relatively short lobes. Stamens five, eight or ten; filaments large and fleshy, hairy or not; anthers rather long, dehiscing by short, terminal slits. Ovary four-five-locular, glandular hairy or not; placentae bilobed; a small hummock around the base of the impressed style, stigma little expanded. Septicidal capsule with numerous, spindle-shaped, unwinged seeds; testa with elongated cells.

   Ca. seven species in the genus; all have been studied. The type species of the genus is *M. ferruginea*.

   Menziesia is also close to Rhododendron. Its corolla shape, tubular or urceolate, is rare in Rhododendron, and in the numbers
of its floral organs it shows some similarity to the *Azalea* group but is also not the normal condition for the Rhodoreae. The American species are 4-merous, the Japanese are 5-merous and also have larger calyx lobes. The stamens differ from those of *Rhododendron* and *Ledum*, but are similar to those of *Tsusiophyllum* (Fig. 48). The rather oddly shaped ovary (Fig. 9) is also rather uncommon in *Rhododendron*, and I know of no species of *Rhododendron* with the fused long-celled hairs on the abaxial midrib (Fig. 21). Otherwise its indumentum is unremarkable (Fig. 48).

In anatomy, too, there is very little difference from the *Azalea* group of *Rhododendron*. The pith is homogenous and the nodes are unilacunar, although in *M. ferruginea* at least, there is a tendency for the bundle to divide in the lower part of the petiole. There is often a zone of weak lignification at the point of junction of the petiole and the stem (Fig. 23), this lignified tissue may persist for a little way up the petiole. The pericyclic sheath of fibres in the stem has rather large lumens. The leaves have no hypodermis and there is a *Pieris*-type midrib bundle. There seem to be tanniniferous cells associated with the midrib bundle. When in fruit *Menziesia* looks rather like *R. semibarbatum*, having a similarly shaped ovary covered with glandular hairs. However, florally and in indumentum they are quite different, and their inflorescences are also borne in different positions.

I have been unable to detect viscin threads in this genus.
This may be due to an oversight, or it may be a real absence correlated with the shape of the corolla (p. 54). Fedtschenko and Basilevskaja (1928) likewise could not find them, although according to Copeland (1943) they are present.

5.2.7. THE CLADOTHAMNEAE.


Deciduous or evergreen shrubs with thin, entire leaves convolute in bud. Indumentum of unicellular hairs alone, sometimes none. Inflorescence terminal on a shoot of the same or the preceding season, racemose/cymose, paniculate or not, eperulate; bracts and paired bracteoles green, leafy or not, pedicel not articulate with the calyx. Flowers three-five-merous. Calyx lobes large or small, free or fused; the odd sepal abaxial (always?). Corolla polypetalous, rotate. Stamens six-ten; filaments flattened, glabrous; anthers with resorbtion tissue which forms long slits; pollen with viscin threads. Ovary three-five-locular, stipitate or not; style impressed in the apex of the ovary, curved; stigma indusiate. Capsule septicidal with few to many seeds; seeds small and ovoid or large, flattened or winged; testa with ± isodiametric cells.

There are two genera in this tribe, Cladothamnus (including Tripetaleia) and Elliottia.

The Cladothamneae have a very distinctive facies because of
their thin leaves which are entirely devoid of multicellular hairs, their terminal eperulate inflorescence and their choripetalous flowers whose stamens have flattened filaments and anthers dehiscing by long, introrse slits (Fig. 49). There seem to be truely terminal flowers in this tribe (Fig. 5), and in two species of Cladothamnus the terminal flower of the small inflorescence is the first to open.

As Copeland (1943) noted, the Cladothamneae have a characteristic method of pollen discharge. He considered that the anthers dehisced in the pendant bud stage of the flower, the pollen being pushed into the spathulate tips of the petals by the action of the as yet unreceptive stigma. Visiting insects removed the pollen from the tips of the petals.

Observations on Cladothamnus pyroliflorus and Tripetaleia bracteata (Drude's classification, see below) growing in the Edinburgh Botanic Garden have enabled the exact mechanism to be established. As Copeland (1943) said, dehiscence of the anthers occurs in bud and the pollen accumulates above the stigma. However, when the flower opens the pollen remains attached to the unreceptive (?) but sticky stigma (Fig. 49), and is not found on the petals. At this stage the flower is held erect and the petals and the reflexed stamens with their broad filaments form a landing stage for the visiting insects. The stigma faces the landing stage due to the ± 180° curvature of the top of the style,
and as the insects walk around the ovary taking nectar which is exuded copiously from the nectary at the base of the ovary; masses of pollen entangled in the viscin threads become attached to the hairs on the dorsal parts of their bodies. One Bombus individual was seen trying (unsuccessfully) to remove an especially large mass of pollen from the middle of the dorsal part of its thorax. On flying to a flower in which the receptive pollen slits on the stigma have been exposed pollen may get attached, and so pollination occurs. Thus the flowers of the Cladothamneae are nototribe (pollen deposited on the insects' dorsal surface), as distinct from those of the Rhodoreae which are sternotribe (pollen deposited on the insects' ventral surfaces). Despite this elaborate mechanism for ensuring cross pollination the plants are self-fertile, since both species set fertile seed in the garden (both are only single bushes). The main visitors to the flowers were species of Bombus and Apis; one Vespa paid a fleeting visit. Bees, or hairy insects of a similar size, are the most likely pollinating agents in these species' native habitats. Elliottia racemosa, growing under glass, had the same basic arrangement of the flower parts as these two species, although the petals were not quite so reflexed. From photographs which I have seen, they seem to reflex more out of doors in America. According to Santamour (1967), this species may be self-sterile with bees visiting the plant and probably effecting pollination, although even in the wild seed set
FIG. 49: CLADOHAMNEAE = FLOWER AND FRUIT.

is very poor. *Tripetaleia paniculata* seems to behave the same as the other three species, as far as can be seen from herbarium specimens.

Copeland (1943) found that the two species which he studied (*C. pyroliflorus* and *E. racemosa*) were embryologically distinct from the other Rhododendroideae, since they both lacked an endothelium and the chalazal haustorium was very poorly developed. There is also no chalazal haustorium in *T. bracteata* (Fig. 33). Ganapathy and Palser (1946) did not notice these peculiarities in the members of the Phyllodoceae which they studied. All four species have thin-walled testa cells with large plasmodesmata (Fig. 49).

If these genera were to be included in the Ledeeae sensu Drude, the resultant tribe would have three different types of anther dehiscence, different types of seed, bud scales or not, etc. Watson et al. (1967) included these genera in the Rhodoreae; the resultant group is variable in the characters just mentioned, although the members are basically similar in floral stomatal distribution (stomata occurring predominantly on the abaxial side of the calyx and the corolla). It is thought that Copeland (1943) was correct in proposing that these genera should be recognised as a tribe.

**Generic Limits in the Cladothammeae.**

The four species in this tribe are all very distinct and
have been differently classified as follows -

<table>
<thead>
<tr>
<th>racemosa</th>
<th>paniculata</th>
<th>bracteata</th>
<th>pyroliflorus</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Elliottia</em></td>
<td><em>Elliottia</em></td>
<td><em>Elliottia</em></td>
<td><em>Cladothamnus</em></td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td><em>Botryostege</em></td>
<td>&quot;</td>
</tr>
<tr>
<td>&quot;</td>
<td><em>Tripetaleia</em></td>
<td><em>Tripetaleia</em></td>
<td>&quot;</td>
</tr>
</tbody>
</table>

In all previous classifications of this group the number of the parts of the flower has been much used, Hooker also used an incorrect observation on the type of inflorescence and Drude a misobservation on the number of the ovules. Copeland used leaf shape as an additional character in his classification. Even using several new characters from anatomy, testa and fruit it has proved very difficult to separate genera in the Cladothamneae. The variation of several of the characters is summarised in Table 7.

Although the only five-merous species, *C. pyroliflorus* (using Drude's nomenclature), is apparently very distinct from the others, there are very few characters separating it from *T. bracteata*. There is an overlapping difference in inflorescence size, the bracts, bracteoles and calyx in *Cladothamnus* are larger (although they are foliaceous in both species), and the leaves of *T. bracteata* are petiolate (there is no basic difference in shape, as suggested by Copeland, 1943). There is also the difference in the number of flower parts, but in details of fruit, flower, seed and anatomy there is very good agreement between the two.
<table>
<thead>
<tr>
<th>Character</th>
<th>C. pyroliflorus</th>
<th>C. bracteata</th>
<th>C. paniculata</th>
<th>Elliottia racemosa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves deciduous</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Leaves borne</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
<td>pseudo-verticillate</td>
</tr>
<tr>
<td>Leaves petiolate</td>
<td>-</td>
<td>+</td>
<td>convolute</td>
<td>convolute</td>
</tr>
<tr>
<td>Leaves in bud</td>
<td>convolute</td>
<td>convolute</td>
<td>convolute</td>
<td>unicellular</td>
</tr>
<tr>
<td>Leaf indumentum</td>
<td>-</td>
<td>-</td>
<td>unicellular</td>
<td>sub-paniculate</td>
</tr>
<tr>
<td>Inflorescence type</td>
<td>1 - 4 fl., &quot;racemose&quot;</td>
<td>3 - 7 fl., &quot;racemose&quot;</td>
<td>paniculate</td>
<td>term. on preceding year's growth</td>
</tr>
<tr>
<td>Infl. position</td>
<td>Terminal, on the end of this year's shoot</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bracteoles (mm.)</td>
<td>10.5</td>
<td>2.5</td>
<td>2.0</td>
<td>0.6</td>
</tr>
<tr>
<td>Bracts (mm.)</td>
<td>30.0</td>
<td>11.0</td>
<td>3.5</td>
<td>2.6</td>
</tr>
<tr>
<td>Calyx size (mm.)</td>
<td>15.0</td>
<td>5.0</td>
<td>1.2</td>
<td>1.1</td>
</tr>
<tr>
<td>Corolla shape</td>
<td>rotate</td>
<td>rotate</td>
<td>rotate</td>
<td>rotate</td>
</tr>
<tr>
<td>Petals fused</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Calyx stomata</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Corolla stomata</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Stamen number</td>
<td>10</td>
<td>6</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>Stamen appendages</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Anther dehiscence</td>
<td>By a slit almost the length of the thecae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Viscin threads</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Stigma and style</td>
<td>Curved, impressed style expanded at the apex, bearing a lobed stigma</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>C. pyroliforus</td>
<td>C. bracteatus</td>
<td>C. paniculatus</td>
<td>Elliottia racemosa</td>
</tr>
<tr>
<td>-------------------------</td>
<td>----------------</td>
<td>---------------</td>
<td>----------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>Multicellular ovary</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>hairs</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ovary stipitate</td>
<td>-</td>
<td>-(slight?)</td>
<td>+, thin stipe</td>
<td>+, stout stipe</td>
</tr>
<tr>
<td>Capsule dehiscence</td>
<td>septicidal</td>
<td>septicidal</td>
<td>septicidal</td>
<td>septicidal</td>
</tr>
<tr>
<td>Capsule walls</td>
<td>thin</td>
<td>thin</td>
<td>thin</td>
<td>thick</td>
</tr>
<tr>
<td>Seeds</td>
<td>many, ovoid</td>
<td>many, ovoid</td>
<td>rather few, ovoid</td>
<td>few, flattened</td>
</tr>
<tr>
<td>Testa</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cells of the testa</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>are slightly thickened</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>and ± hexagonal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epidermis type</td>
<td>1</td>
<td>1 - 2</td>
<td>1 - 2</td>
<td>1 - 2</td>
</tr>
<tr>
<td>Stomatal distribution</td>
<td>abaxial only</td>
<td>abaxial</td>
<td>abaxial</td>
<td>abaxial</td>
</tr>
<tr>
<td>Stomatal type</td>
<td>anomocytic</td>
<td>anomocytic</td>
<td>paracytic</td>
<td></td>
</tr>
<tr>
<td>Abaxial cuticle</td>
<td>finely striate</td>
<td>fine striate</td>
<td>finely striate</td>
<td></td>
</tr>
<tr>
<td>&quot;Mucilaginous&quot;</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>epidermis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hypodermis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Midrib bundle</td>
<td>Pieris</td>
<td>Pieris</td>
<td>Pieris</td>
<td>Lyonia</td>
</tr>
<tr>
<td>Petiole bundle</td>
<td>arcuate</td>
<td>arcuate</td>
<td>arcuate</td>
<td>closed</td>
</tr>
<tr>
<td>Pith</td>
<td>heterogenous</td>
<td>Heterogenous,</td>
<td>Heterogenous,</td>
<td>thick-walled,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+ Calluna type</td>
<td></td>
<td>heterogenous</td>
</tr>
<tr>
<td>Cortex</td>
<td>heterogenous</td>
<td>heterogenous</td>
<td>heterogenous</td>
<td>heterogenous</td>
</tr>
<tr>
<td>Node</td>
<td>unilacunar</td>
<td>unilacunar</td>
<td>unilacunar</td>
<td>unilacunar</td>
</tr>
<tr>
<td>Accessory petiole</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>bundles</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**TABLE 7B** SOME CHARACTERS OF THE MEMBERS OF THE CLADOOTHAMNEAE
The two species placed in *Tripetaleia*, although having the same number of flower parts, differ in several characters. The stomatal type is different, and the inflorescence, bracts and bracteoles and calyx are all far more different in these two species than the corresponding differences between *C. pyroliflorus* and *T. bracteata*. Also the ovary in *T. paniculata* is stipitate, it is not so in *T. bracteata*.

*E. racemosa* is by far the most distinct species of the group. It differs from all other species in its anatomy (Fig. 50), capsule (Fig. 49) and seed, and it is the only species whose inflorescence is produced the season after the growth of the shoot on which it is borne. It is linked on to the other species of the tribe by *T. paniculata*. The two species both have paracytic stomata (although the cuticle surfaces are very different), the same inflorescence (that of *E. racemosa* is often paniculate, despite its specific epithet), a stipitate ovary (although the stipe in *Eliottia* is slender and that of *T. paniculata* is stout) and also small calyces (although differing in the degree of fusion). *C. paniculata* is intermediate between *Eliottia* and the two other species in seed number, but in anatomy, seed and fruit it agrees with the latter very well.

It is thought best to maintain *Eliottia* as a monotypic genus distinct from the three other species, which are all placed in *Cladothamnus*. The new combinations this necessitates are found
in Appendix 1. C. paniculata, although intermediate in some respects, is thought to be closer to the two other species than to Elliottia, although it would perhaps be defensible to include C. paniculata in Elliottia and to retain the two remaining species in Cladothamnus. If Botryostege is maintained as a monotypic genus (separated from C._pyroliflorus by its three-merous flowers, more flowers per inflorescence and less leafy bracts) then there is no reason why all four species should not be placed in monotypic genera; it is felt that this is desirable neither from the practical point of view nor as an expression of the relationships of the species involved.

KL. 3 (3): 731 (1843).
Botryostege Stapf, Kew Bull. 191 (1934).

Small, much-branched deciduous shrubs with thin, entire leaves convolute in bud. Leaves with unicellular hairs alone, or none. Inflorescence terminal on the growth of the current season, one to many flowered, racemose, cymose or paniculate, eperulate; bracts and bracteoles large to small; green and persistent; pedicel not articulate with the calyx. Flowers 3- to 5-merous. Calyx lobes small to large and foliaceous, free or fused. Corolla rotate, polypetalous; petals 3 or 5. Stamens
six or ten; filaments rather flattened, glabrous; anthers dehiscing by an introrse slit traversing almost their entire length; viscin threads present. Ovary three or five-locular; glabrous, stipitate or not; placentae bifid; style curved, impressed, expanded at the apex, stigma lobed. Septicidal capsule thin-walled; initially dehiscing by terminal pores later becoming slits; seeds numerous–few, small, ovoid; testa with ± isodiametric cells.

Three species in the genus, all have been studied. *C. pyroliflorus* is the type species.

Both *C. pyroliflorus* and *C. bracteata* seem to have some specimens which are entirely glabrous. All three species have abaxial corolla stomata as well as abaxial calyx stomata; c.f. Watson (1965), who failed to record the former.

8. **ELLIOTTIA** Muhlenberg in Elliott, Bot. S. Carol. & Georgia 1: 448 (1817).

An evergreen shrub with rather thin, entire leaves convolute in bud. Indumentum of unicellular hairs alone. Inflorescence terminal on the previous season's growth, racemose-paniculate, eperulate; bracts and paired bracteoles small; calyx not articulate with the pedicel. Calyx lobes four, small, free. Corolla polypetalous, rotate; petals four/five. Stamens eight; filaments flattened, glabrous; anthers dehiscing by introrse
slits for almost their entire length; viscin threads present. Ovary stoutly stipitate, four-locular, glabrous; placentae bifid. Capsule thick-walled, septicidal; fertile seeds few, large and flattened; cells of the testa isodiametric.

The single species of the genus, *E. racemosa*, was studied.

The specimen in the gardens had a number of flowers with five petals, but all the other parts were in multiples of four.

5.2.8. THE EPICEAE.


Procumbent shrublets with rather large, entire leaves revolute in bud. Indumentum of long-stalked glandular and long-celled hairs, also unicellular hairs. Inflorescence terminal, shortly spicate or racemose, eperulate; bracts and paired basal bracteoles prominent, green; calyx articulate with the pedicel. Flowers five-merous, hermaphrodite or dioecious. Calyx lobes large, free, green. Corolla hypocrateriform to widely campanulate, lobes prominent. Stamens ten; filaments and the inside of the corolla with uniseriate hairs; anthers dehiscing by introrse slits at least half the length of the thecae; viscin threads present. Ovary five-locular, with glandular hairs or not; placentae deeply divided; style impressed, slightly curved or straight, stigma indusiate. Fruit a many-seeded, thin-walled septicidal capsule with fleshy placentae;
seeds ovoid; cells of the testa hexagonal, ± thick-walled.

There is a single genus, *Epigaea* (including *Orphanidesia*) in this tribe.

The *Epigaea* was separated from the other tribes of the Ericaceae, the Rhododendreae, Andromedeae, Gaultherieae and Arbuteae (excluding the Vaccineae; there were no subfamilies), by its salveriform corolla, long-dehiscent anthers and prostrate habit. Since it was published in a flora dealing only with the flora of N. America, only *E. repens* was mentioned. The name was dropped in the later editions of the "Illustrated Flora of North America", and does not seem to have been used elsewhere. Watson (in Airy Shaw, 1966) placed *Epigaea* in a monotypic subfamily, although this has never been legitimately published. Later (Watson et al., 1967) he included *Epigaea* in a group of genera corresponding to Drude's Phyllodoceae. Tribal separation is thought to be desirable for the following reasons:-

1). Tetracytic stomata are found in all three species included in this tribe; elsewhere they have been found only in *Beiaria* (5.2.5.). Some species of *Rhododendron*, e.g. *R. zoelleri*, also tend to have tetracytic stomata.

2). Such a deeply hooked *Oxydendrum*-type petiole and lamina bundle (Fig. 29) has not been seen in any other species of the Rhododendroideae.
3). The green, prominent bracts, bracteoles and calyx are very well developed here, although they are perhaps not basically dissimilar to those of the Bejarieae and the Phyllodoceae.

4). The uniseriate hairs on the corolla and stamens (Figs. 17 and 50) are also unique amongst the Ericaceae studied.

5). All three species have very large placentae which apparently remain fleshy in fruit. In Orphanidesia (= Epigaea) gaultherioideae some of the seeds remain embedded in the placenta, and in E. repens Wood (1961) reported that the seeds were presumably dispersed by ants which had been observed attacking the fleshy placentae. The seeds of the three species have rather thick-walled cells (Fig. 51); these are also to be found in some of the Phyllodoceae and the Daboecieae. No other members of the Ericaceae are reported as having fleshy placentae combined with a thin, dry, capsule wall.

6). Palser (1951 and 1952) found a number of embryological and floral anatomical peculiarities in E. repens, which was the only species of the tribe that she studied. The bracteole vascular supply was very prominent, with a number of separate traces going to each bracteole. The indistinct nectariferous zone was innervated by bundles from the carpellary supply; the ventral carpellary bundles arose in the plane of the septae and not, as is usual in the Ericaceae, in the plane of the loculi. There were also small, pointed "ears" on the megagametophyte (see
FIG. 51: EPIGAEAE AND PHYLLODOCEAE - FRUIT AND SEED.

section 2.3.3.). These latter are known elsewhere only in Enkianthus, which has a different type of stamen, corolla, seed, anatomy, etc.

7). If one considers the details of wood anatomy given by Cox (1948a and 1948b), Epigaea seems to have quite considerable differences when compared to the other Phyllodoceae. Figures for the Phyllodoceae are given first:

<table>
<thead>
<tr>
<th>Percentage scalariform vessel plates</th>
<th>&gt;9 bars</th>
<th>79</th>
<th>18</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;8 bars</td>
<td>21</td>
<td>68</td>
</tr>
<tr>
<td>Percentage of entirely porous plates</td>
<td></td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>Average number bars per scalariform plate</td>
<td></td>
<td>13.1</td>
<td>7.2</td>
</tr>
</tbody>
</table>

These differences are suggestive.

The Epigaea are closest in a number of respects to the Phyllodoceae, although they are very different in general facies and look more like a large-leaved, procumbent Rhododendron. Although their anthers are superficially like those of some of the Phyllodoceae (c.f. Figs. 50 and 51), it is not known if the actual mechanism of dehiscence is the same. Inflorescence, seed type, floral stomatal distribution agree with those of the Phyllodoceae, but they differ in fruit and in anatomy; and from all the tribes of the Rhododendroideae in floral indumentum, floral anatomy and embryology. (see Table 3).

Generic Limits in the Epigaea.


The genus has three species: its characters are those of the tribe. The type species is *E. repens*.

Boissier (1875) considered that the monotypic genus *Orphanidesia* differed from *Epigaea* in having anthers which dehisced throughout their length, whereas in the latter they dehisced via apical pores. Another possible difference, he thought, was in the nature of the fruit. One of the species of *Epigaea*, *E. repens*, has slits extending the length of the anther (Fig. 50), although in the other, *E. asiatica*, they are not so extensive; there does not seem to be any basic difference in the fruit.

Hooker (1876) gave descriptions of the two genera in which the only difference that can be found is that *Epigaea* has three bracteoles, and *Orphanidesia* two. In fact both genera have one bract and two bracteoles.

Drude (1897) keys out the two genera as follows:-

"Antheren mit länglichen gipfel poren aufspringend . . *Orphanidesia*.

Antheren mit vorn liegenden längrissen aufspringend . . *Epigaea*.

" As mentioned above, it is impossible to separate two genera on this character; the only other differentiae obtainable from his
<table>
<thead>
<tr>
<th>Characteristics</th>
<th>E. gaultherioides</th>
<th>E. asiatica</th>
<th>E. repens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves borne</td>
<td>scattered, evergreen</td>
<td>scattered, evergreen</td>
<td>scattered, evergreen</td>
</tr>
<tr>
<td>Leaves in bud</td>
<td>revolute</td>
<td>revolute</td>
<td>revolute</td>
</tr>
<tr>
<td>Long-celled hairs</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Long-stalked glands</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Perulae</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Inflorescence position</td>
<td>terminal</td>
<td>terminal</td>
<td>terminal</td>
</tr>
<tr>
<td>Inflorescence type</td>
<td>small, spicate</td>
<td>small, racemose</td>
<td>small, subspicate</td>
</tr>
<tr>
<td>Bracteoles</td>
<td>paired, green</td>
<td>paired, green, basal</td>
<td>paired, green, basal</td>
</tr>
<tr>
<td>Calyx size (mm.)</td>
<td>15</td>
<td>7</td>
<td>5.5</td>
</tr>
<tr>
<td>Calyx articulation</td>
<td>?</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Calyx stomata</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Corolla shape</td>
<td>± infundibular</td>
<td>hypocra teriform</td>
<td>hypocra teriform</td>
</tr>
<tr>
<td>Corolla lobes fused</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Corolla stomata</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Corolla indumentum</td>
<td>uniseriate</td>
<td>uniseriate</td>
<td>uniseriate</td>
</tr>
<tr>
<td>Stamen number</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Stamen appendages</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Anther dehiscence</td>
<td>slit length anther</td>
<td>slit $\frac{1}{2}$ length anther</td>
<td>slit length anther</td>
</tr>
</tbody>
</table>

**TABLE 8A VARIATION OF THE MEMBERS OF THE EPIGAEAE**
<table>
<thead>
<tr>
<th>Character</th>
<th>E. gaultherioides</th>
<th>E. asiatica</th>
<th>E. repens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Viscin threads</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Stigma</td>
<td>lobed</td>
<td>well lobed</td>
<td>5 radiating arms</td>
</tr>
<tr>
<td>Style</td>
<td>impressed, ± curved</td>
<td>impressed, ± straight</td>
<td>impressed, ± straight</td>
</tr>
<tr>
<td>Multicellular ovary hairs</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Fruit type</td>
<td></td>
<td>All species have a thin-walled, loculicidal capsule</td>
<td></td>
</tr>
<tr>
<td>Placentae fleshy</td>
<td>+</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Seed type</td>
<td></td>
<td>All species have ovoid seeds, with small, thick-walled cells</td>
<td></td>
</tr>
<tr>
<td>Dioecy</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Epidermis type</td>
<td>i</td>
<td>i</td>
<td>i</td>
</tr>
<tr>
<td>Stomatal distribution</td>
<td>abaxial</td>
<td>both surfaces</td>
<td>both surfaces</td>
</tr>
<tr>
<td>Stomatal type</td>
<td>tetracytic</td>
<td>tetracytic</td>
<td>tetracytic</td>
</tr>
<tr>
<td>&quot;Mucilaginous&quot; epidermis</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Hypodermis</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Midrib bundle</td>
<td>Oxydendrum</td>
<td>Oxydendrum</td>
<td>Oxydendrum</td>
</tr>
<tr>
<td>Pith</td>
<td>heterogenous</td>
<td>heterogenous</td>
<td>heterogenous</td>
</tr>
<tr>
<td>Cortex</td>
<td>heterogenous</td>
<td>heterogenous</td>
<td>heterogenous</td>
</tr>
<tr>
<td>Node</td>
<td>unilacunar</td>
<td>unilacunar</td>
<td>unilacunar</td>
</tr>
<tr>
<td>Pericyclic lignification</td>
<td></td>
<td>Well developed, with thick-walled cells</td>
<td></td>
</tr>
</tbody>
</table>

**TABLE 8B VARIATION OF THE MEMBERS OF THE EPICARAX**
description is reference to dioecy in *Epigaea*.

Turrill (1948) thought that if generic rank were to be maintained it would have to be on the grounds of corolla shape. In *Orphanidesia* the corolla is + infundibular, in *Epigaea* it is salveriform/hypocrateriform. Also *Orphanidesia* lacks glandular hairs on the ovary and has stomata on only one side of the leaf. *Epigaea* has stomata on both sides of the leaf, but c.f. Watson, (1965).

Stevens (1911) finally established that *E. repens* was dioecious; also its stigma is very prominently lobed. However, the stigma of *E. asiatica* is less prominently lobed and *O. gaultherioideae* has a simply peltate stigma/style complex (Fig. 50). *E. asiatica* seems to be hermaphrodite, but it too differs considerably from the other two species in that its anthers dehisce by slits only one half their length, its flowers are distinctly pedicillate, and its uniseriate pubescence is less well developed (see Table 8 for details).

If *Orphanidesia* is maintained as a genus there is no reason why another genus should not be created to accommodate *E. asiatica*, but in view of the overall similarity in facies, anatomy, indumentum, flower and fruit it is thought that the three species are best placed in a single genus. It is of interest to note that Mulligan (1939) was able to cross *E. repens* (as the female parent) with *E. asiatica*. An attempt should be made to
make the other crosses in the genus.

Takhtajan and Yatsenko-Khmelevski (1946) were the first to suggest that *Orchanidesia* should be reduced to *Epigaea*. They reached this conclusion as a result of a detailed study of the plants, including a comparison of the fine structure of the wood. Lems (1964) noted that both genera had very sharply pointed veinlet endings, and thought that they were probably congeneric because of this and similarities in habit, anatomy and floral characteristics. Unfortunately the distribution of these finely pointed veinlet endings is unknown in the Rhododendroideae.

5.2.9. THE PHYLLODOCACEAE.


Usually erect evergreen shrubs; leaves variously borne, entire or slightly serrulate, usually small; convolute or revolute in bud, or Ericoid. Indumentum of short-or long-stalked glandular hairs, long-celled hairs, unicellular hairs and sometimes papillae. Inflorescence terminal, rarely axillary, eperulate, bracts and two basal bracteoles usually present, green and persistent; calyx articulate with the pedicel or not. Calyx usually small, lobes free. Corolla gamo- or polypetalous, rotate to urceolate, actinomorphic. Stamens five-ten; dehiscing by slits or terminal pores made by resorbion tissue involving the epidermis; viscin threads usually present. Ovary
two-six-locular, glandular hairy or not; placentae bilobed;
style impressed or not; stigma variable. Fruit a septicidal
capsule, sometimes partially loculicidal as well; seeds numerous,
small, usually ovoid; cells of the testa usually not elongated,
thin- or thick-walled.

Eight genera are included in this tribe: - Kalmia,
Kalmiopsis, Rhodothamnus, Phyllodoce, Bryanthus,
Ledothonnus, Leiophyllum, Loiseleuria.

The above genera were all included in Drude's Phyllodoceae,
with the exception of Kalmiopsis, which had not yet been
discovered. Dinclarche and Daboecia, which he also included in
the Phyllodoceae, are put in monotypic tribes; for the characters
separating these tribes from the Phyllodoceae, see sections
5.2.10. and 5.2.11. Watson (in Airy Shaw, 1966) included
Daboecia and Andromeda in the Phyllodoceae, later (Watson et al.,
1967) he included Daboecia and Epigaea in this tribe, but removed
Andromeda to the Vaccinioidaeae where it properly belongs.

Breitfeld (1888) claimed to be able to recognise two groups
within the subtribe Phyllodoceae of Maximowicz. The genera he
studied all belong to the Phyllodoceae as here recognised, except
Daboecia.

Group 1.
Single-layered epidermis.
Small, thick-walled epidermal cells.

Group 2.
Single-layered epidermis.
Variously shaped cells.
Group 1.
Cuticle thick both ad- and abaxially.
No scale hairs.

Group 2.
Abaxial cuticle thin.
Abaxially long, unicellular hairs and capitate glands ("scale hairs").

In group 1 were Rhodothamnus, Leiophyllum and Kalmia angustifolia, in group 2 Loiseleuria, Phyllodoce, Daboecia and Kalmia glauca (= K. polifolia var. glauca). K. hirsuta and K. latifolia were unplaced.

Breitfeld failed to note that the epidermis in Loiseleuria and Daboecia was of the "mucilaginous" type. The other genera seem to have a simple epidermis. Copeland (1943) reported an hypodermis from near the main vein and at the leaf margin of Loiseleuria, but I could not see it.

The adaxial epidermal cells of Leiophyllum and Rhodothamnus sessilifolius are not small nor, as Copeland (1954) noted, are those of R. chamaecistus. The range of adaxial epidermal cell size for species from the first group is 27μ - 70μ X 2μ - 4μ thick cell walls. Comparable data from the second group:
27μ - 60μ X 2μ - 4μ thick cell walls. Thus this distinction of Breitfeld's breaks down. If one compares the thickness of the inner periclinal epidermal walls, then Rhodothamnus has much thinner walls than Phyllodoce (Fig. 55).

The indumentum difference is only one of degree. The second
group all have an abaxial leaf indumentum of long papillae/unicellular hairs amongst which are usually to be found some small gland-headed hairs. However, in Phyllocladua brevifolia of the second group the unicellular hairs are less dense than in Leiophyllum, and this latter genus has the same type of glandular hairs as are to be found in several species of the second group (Fig. 53). *Rhodothamnus sessilifolius*, a recently discovered species, also has unicellular hairs on the abaxial side of its leaf.

The only difference which does seem to hold for the species concerned is the difference in the abaxial cuticle thickness. In the first group the cuticle is from $3\mu - 7\mu$ thick and the cells are little smaller than those on the adaxial side. In the second group the cuticle is barely $2\mu$ in thickness, and the cells are rather smaller than in the previous group. This difference, and the partial difference in indumentum density, are probably connected with the tendency of species from the second group to have ± Ericoid leaves. The margins of the leaf are revolute, and the protection afforded to the underside of the leaf by the leaf margins and the dense indumentum make a thick cuticle rather superfluous.

The genera *Ledothamnus* and *Bryanthrus*, which Breitfeld (1888) was unable to study, are extreme members of the second group, although *Ledothamnus* does not have unicellular hairs on the
abaxial side of the leaf, but a dense covering of papillae.

Kalophasis has but a moderately thick abaxial cuticle and very large-headed glandular hairs and does not really belong to either group.

These two leaf types do not correlate well with groups formed using other characters. Both Leiophyllum and Loiseleuria have two- or three-locular ovaries, anthers dehiscing by slits, decussate leaves, etc., yet they are put in different groups. Homogenous and heterogenous pith types occur in both groups.

Anatomical studies have led to the discovery of other characters, notably stomatal orientation, the occurrence of small xylem cells above the lamina bundle, expanded flanges of lignified tissue in the petiole, etcetera. Floral characters are also very variable. As might be expected from the foregoing discussion, the genera in this tribe are rather isolated; there are few problems in the delimitation of genera. Much of the relevant data is tabulated in Table 9.


Kalmiella Small, Fl. N. Am. 29 (1): 54 (1914).

Evergreen shrubs; leaves scattered, decussate, or three-whorled, large to small, entire, revolute in bud and sometimes in the mature leaf. Indumentum of gland-headed hairs with long or short stalks, long-celled hairs and unicellular hairs. Inflorescence terminal or axillary, corymbose, eperulate; bracts and paired,
<table>
<thead>
<tr>
<th>Character</th>
<th>Kalmia</th>
<th>Kalmopsis</th>
<th>Rhodothamnus</th>
<th>Phyllodoce</th>
<th>Bryantus</th>
<th>Loethamnus</th>
<th>Loiseleuria</th>
<th>Leiophyllum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf type</td>
<td>flat</td>
<td>flat</td>
<td>flat</td>
<td>Ericoid</td>
<td>Ericoid</td>
<td>Ericoid</td>
<td>revolute</td>
<td>flat</td>
</tr>
<tr>
<td>Leaves borne</td>
<td>variable</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
<td>whorled</td>
<td>decussate</td>
<td>decussate</td>
<td></td>
</tr>
<tr>
<td>Leaves in bud</td>
<td>revolute</td>
<td>convolute</td>
<td>convolute</td>
<td>not really applicable</td>
<td>revolute</td>
<td>convolute</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hair types</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>glands</td>
<td>long stalked +</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>short stalked +</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>long-celled +</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inflorescence type</td>
<td>various</td>
<td>corymb</td>
<td>corymb</td>
<td>corymb</td>
<td>raceme</td>
<td>single fl. corymb</td>
<td>small corymb</td>
<td></td>
</tr>
<tr>
<td>Bracteoles</td>
<td>basal</td>
<td>basal</td>
<td>basal</td>
<td>basal</td>
<td>basal</td>
<td>not seen</td>
<td>basal</td>
<td>basal</td>
</tr>
<tr>
<td>Corolla shape</td>
<td>campanulate</td>
<td>campanulate</td>
<td>rotate (usu.) urceolate</td>
<td>rotate</td>
<td>rotate</td>
<td>rotate</td>
<td>rotate</td>
<td></td>
</tr>
<tr>
<td>Corolla lobes</td>
<td>$\frac{1}{3}$ - $\frac{1}{5}$</td>
<td>$\frac{1}{3}$ - $\frac{2}{3}$</td>
<td>$\frac{1}{5}$</td>
<td>$\frac{11}{12}$</td>
<td>$\frac{1}{1}$</td>
<td>$\frac{1}{1}$</td>
<td>$\frac{1}{1}$</td>
<td>$\frac{1}{1}$</td>
</tr>
<tr>
<td>Corolla pouches</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Stamen number</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>8</td>
<td>5 - 7</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>Anther dehiscence</td>
<td>short slit</td>
<td>short slit</td>
<td>short slit</td>
<td>short slit</td>
<td>short slit long slit</td>
<td>long slit</td>
<td>long slit</td>
<td></td>
</tr>
</tbody>
</table>

**TABLE 2A** VARIATION OF SOME CHARACTERS IN THE PHYLLOCOECEAE
<table>
<thead>
<tr>
<th></th>
<th>Kalmia</th>
<th>Kalmiopsis</th>
<th>Rhodothamnus</th>
<th>Phyllodoce</th>
<th>Bryanthus</th>
<th>Ledothenmus</th>
<th>Loiseleuria</th>
<th>Leiophyllum</th>
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<tr>
<td>Style impressed</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Ovary loculus number</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>4</td>
<td>5 - 7</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Multicellular ovary hairs</td>
<td>+ (usually)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Fruit type</td>
<td>septicidal</td>
<td>septicidal</td>
<td>septicidal</td>
<td>septicidal</td>
<td>septicidal</td>
<td>septicidal, knobbly</td>
<td>septicidal, long, thin</td>
<td>septicidal, short, thin</td>
</tr>
<tr>
<td>Testa cell type</td>
<td>+ elongated, thin walls</td>
<td>+ long, thin walls</td>
<td>short, thin walls</td>
<td>short, thin walls</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Calyx stomata</td>
<td>+ +, + - , - - - -</td>
<td>+ -</td>
<td>+ -</td>
<td>+ +</td>
<td>+ +</td>
<td>+ +</td>
<td>+ -</td>
<td>+ -</td>
</tr>
<tr>
<td>Corolla stomata</td>
<td>+ - , - -</td>
<td>- -</td>
<td>- -</td>
<td>- + , + -</td>
<td>- +</td>
<td>+ +</td>
<td>+ +</td>
<td>+ +</td>
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<td>Leaf stomatal orientation</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>right angles</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Midrib bundle</td>
<td>various</td>
<td>Pieris</td>
<td>Pieris</td>
<td>Pieris</td>
<td>Pieris</td>
<td>Pieris</td>
<td>Pieris</td>
<td>modified Lyonia type</td>
</tr>
<tr>
<td>Libriform tissue</td>
<td>poor, or none</td>
<td>poor</td>
<td>poor</td>
<td>none</td>
<td>none</td>
<td>poor</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>Bundle transcurrent</td>
<td>+ or -</td>
<td>?</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pith type</td>
<td>homogenous and heterogeneous</td>
<td>heterogenous</td>
<td>heterogenous</td>
<td>heterogenous</td>
<td>heterogenous</td>
<td>heterogenous</td>
<td>homogenous</td>
<td>homogenous</td>
</tr>
</tbody>
</table>

**TABLE 9B VARIATION OF SOME CHARACTERS IN THE PHYLLODOCEAE**
basal bracteoles green; long, slender pedicels articulate with the calyx. Flowers five-merous, actinomorphic. Calyx small-medium sized, lobes free. Corolla campanulate, rather shortly five-lobed, with ten pouches half way up the corolla tube. Stamens ten; filaments curved, hairy; anthers smooth, dehiscing by a pair of short, terminal slits produced by resorbtion tissue, with a reduced endothecium; viscin threads present or not. Ovary five-locular, with glandular hairs or not; placentae bifid; style impressed, stigma slightly capitate. Capsule globular, dehiscing septicidally, rarely shorter loculicidal slits as well; seeds numerous, ovoid to spindle shaped; cells of the testa oblong-much elongated, thin-walled.

There are ca. 8-11 species in this genus, of which six have been studied. The type species is K. latifolia.

This genus is instantly recognisable when in flower by its pouched corolla. When an insect lands on the flower its weight flattens the corolla, forcing the corolla lobes outwards, and the bent filaments are released from their pouches and flick over to the centre of the flower (Plate 1; Fig. 54). The pollen is discharged during this process, and in the case of K. latifolia the contents of each half anther remain held together by the viscin threads and may be thrown for as much as 5-6 cms. This pollination mechanism is not found in any other member of the Ericaceae.
Relationships.

*Kalmia, Kalmiopsis, Rhodothamnus* and *Phyllocladus* all have the same type of anther dehiscence, (Copeland, 1943, 1954). Resorbtion tissue forms slits which become broadened above by a contraction of the epidermis of the anther in which the rudimentary endothecium is involved. At least some members of all four genera have heterogenous pith; all have a rather poorly lignified pericyclic sheath in the stem. Apart from *Kalmiopsis* they have adaxial calyx stomata. *Bryantus* too has a superficially similar stamen (Fig. 54), but in several other respects it is different.

Nomenclature.

*Kalmiella* (*K. hirsuta* and *K. ericoides* were studied) was separated from *Kalmia* because of its small leaves, large green calyx and its long-celled hairs. This study also shows that it alone has both ad- and abaxial calyx stomata and small vessels on the adaxial side of the midrib bundle. Ganapathy and Palser (1964) found that *K. hirsuta* had a 3-4-layered integument, whilst the other three species of *Kalmia* sensu restricto all had a 4-5-layered integument.

These differences are not considered enough for generic separation. The two groups have the remarkable pollination mechanism in common, and although *Kalmia* sensu restricto does not have the long-celled hairs of *Kalmiella*, both groups have similar gland-headed hairs on the leaf and the ovary (Fig. 53).
In inflorescence too they are basically similar (Fig. 53). Within Kalmia sensu restricto there is enough anatomical (Fig. 55) and floral stomatal variation to enable one to delimit other groups of the same, or greater, distinctness as Kalmiella, there is also variation in the way the leaves are borne.

In recent work by Jaynes (1968) fertile seed was obtained in three out of four crosses between Kalmia hirsuta and other members of the genus. The successful crosses were with K. latifolia, K. angustifolia and K. cuneata; crossing failed with K. polifolia, perhaps because that species is tetraploid (Jaynes, 1969).

Notes on the infrageneric variation of Kalmia.

Viscin threads have been found only in K. latifolia (see also Ikuse, 1954) and K. hirsuta, but they probably occur elsewhere. Copeland (1943) was mistaken in saying that some species of Kalmia lack multicellular hairs on their leaves; they occur on all the species studied, although some individuals of K. polifolia may lack them. There is an interesting range of variation in inflorescence types (Fig. 53); however, terminal corymbs would seem to be an unusual condition for K. latifolia (see Copeland, 1943).

Anatomically this genus is very interesting and variable, as noticed by Breitfeld (1888) and Copeland (1943). All species have a "mucilaginous" epidermis most prominent in the Kalmiella group and in K. cuneata, this was not noticed by the earlier
workers, nor was the presence of the small xylem cells above an otherwise Pieris-type bundle in the Kalmiella group. The combination of these two characters makes K. hirsuta unlike any member of the Azalea group of Rhododendron known to me (c.f. Breitfeld, 1888). Copeland assumed that K. angustifolia would not have a transcurrent midrib bundle; this is incorrect (Fig. 55).

A key is given to the species of Kalmia which I have studied using vegetative (mostly anatomical) characters.

1. Midrib bundle circular; pith homogenous latifolia.
1. Midrib bundle unifacial; pith various 2
2. Midrib bundle with small fibres above it; pith homogenous 3
3. Margins of the leaf slightly revolute hirsuta.
3. Margins of the leaf very revolute ericoides.
2. Midrib bundles with no such fibres; pith heterogenous 4
4. No lignification associated with the lamina bundle; petiole with abaxial hippocrepiformly lignified cells lower down polifolia.
4. At least some lignification associated with the midrib bundle; no hippocrepiform cells in the petiole 5
5. "Mucilaginous" epidermis up to 45\(\mu\) tall; bast fibres poorly lignified cuneata.
5. "Mucilaginous" epidermis up to 30\(\mu\) tall; bast fibres are well lignified angustifolia.

Small evergreen shrub; leaves scattered, small, entire, thick, convolute in bud. Leaf indumentum of short-stalked glands with very large heads and unicellular hairs, elsewhere the heads of the glands smaller and the stalks rather longer. Inflorescence a few-flowered, terminal corymb, eperulate; green persistent bracts and small, paired, basal bracteoles; pedicels articulate with the calyx. Flowers 5-merous, actinomorphic. Calyx medium-sized (ca. 4 mm.), lobes free. Corolla widely campanulate, lobes large. Stamens 10; filaments hairy; anthers dehiscing by a pair of short, apical, flaring slits produced by resorbtion tissue; viscin threads present. Ovary 5-locular, glandular hairy; placentae bilobed; style impressed, stigma slightly capitate. Fruit a globular, septicidal capsule, sometimes with small, loculicidal slits; seeds numerous, ovoid; cells of the testa not much elongated, thin-walled.

The genus has but a single species, *K. leachiana*, which has been examined.

Copeland (1943 and 1954) considered that *Kalmiopsis* should be included in *Rhodothamnus*. Davis (1962) disagreed with this because on Copeland's own criteria for separating genera within the *Rhododendron* group, the merging of the two genera was unsupportable. Davis thought that the differences in facies,
FIG. 52: PHYLLODOCEAE - FRUIT AND SEED.

1. Kalmia latifolia, x5; 2. K. hirsuta, x6; 3. Rhodothamnus chamaecistus, x3;
4. the same, from above; 5. Kalmiopsis leachiana, x6; 6. R. chamaecistus, x50 - seed;
7. Phyllodoce nipponica, x6; 8. P. aleutica, x50 - seed; 9. P. glanduliflora,
x6 - L.S. young ovary, loculi filled with hairs; 10. P. aleutica, x6 - old capsule;
11. Loiseleuria procumbens - a = testa, b = capsule from side, x7.5, c = the same
from above, x5; 12. Leiophyllum buxifolium, x6; 13. Ledothamnus guyanensis, x6 -
b = apical placentae.
FIG. 53: PHYLLODOCEAE - INFLORESCENCE AND INDUMENTUM.

FIG. 54: PHYLLODOCEAE AND DABOECEAE - FLOWER.

1. Kalmia polifolia, x5 - flower; 2. K. polifolia - stamen; 3. K. hirsuta;
4. Kalmiopsis leachiana; 5. Rhodothamnus chamaecistus, x5; 6. Phyllodoce coerules;
10. Daboecia cantabica - slightly granular thecae; 11. Ledothamnus guyanensis;
12. L. sessiliflorus (all x10 unless otherwise mentioned).
FIG. 55: PHYLLODOCEAE - LAMINA ANATOMY.

1. Kalmia angustifolia, x50; 2. K. hirsuta, x100; 3. K. latifolia, x50;
4. Kalmiopsis leachiana, x50; 5. & 6. Rhodothamnus chamaecistus, 5. leaf, x100;
6. epidermis, x300; 7. Phyllodoce empetriformis, x300 - epidermis; 8. P. nipponica, x40;
9. P. aleutica, x40; 10. Bryanthus gmelinii, x50; 11. Kalmia ericoides, x50;
12. Ledothamnus sessiliflorus, x50 (x = very small xylem cells, e = epidermis, me = "mucilaginous" epidermis).
indumentum and corolla were sufficient to maintain the two as genera, even though they were so small. I agree with Davis (1962) for the following reasons.

1) *Kalmiopsis* has much thicker leaves than *Rhodothamnus* due to the presence of about four layers of palisade cells, as against two in *Rhodothamnus*.

2) *Kalmiopsis* has characteristic stout, glandular hairs which are especially prominent on the leaf (Fig. 19). There are no long-celled or long-stalked capitate hairs giving the marginal leaf ciliation found in the two species of *Rhodothamnus*, and which also occur on other parts of the plant. The stalked glandular hairs on the leaf of *R. sessilifolius* are unlike those of *Kalmiopsis*.

3) *Kalmiopsis* lacks adaxial calyx stomata; these are present in *Rhodothamnus*.

4) The corolla of *Kalmiopsis* is $1/3 - 1/4$ lobed; the lobes of *Rhodothamnus* are about $2/3$ the length of the corolla.

5) The cells of the testa are rather shorter in *Rhodothamnus* than in *Kalmiopsis*, although this difference is not very significant (Figs. 51 and 52).

The differences are not very great, but in view of the absence of intermediates it is thought that generic separation is desirable.

Small, evergreen shrubs with small, + entire, scattered leaves convolute in bud. Indumentum of long-stalked glands, long-celled hairs and unicellular hairs. Inflorescence few-flowered, terminal, eperulate, corymbose; green, persistent bracts and paired, basal bracteoles; pedicel articulate with the calyx, rather slender. Flowers 5-merous, actinomorphic. Calyx lobes rather large (ca. 5 mm.), free. Corolla almost rotate, lobes ca. 2/3 the length of the corolla. Stamens 10; filaments hairy; anthers dehiscing by terminal, gaping short slits or pores produced by resorption tissue; viscin threads present. Ovary 5-locular, glandular hairy; placentae bifid; style impressed, stigma capitate. Capsule septicidal, often slightly loculicidal as well; seeds many, ovoid; cells of the testa not elongated, little thickened.

There are now two species in this genus; both have been studied. The type species is \( \textbf{R. chamaecistus} \).

**Relationships.**

\( \textbf{Rhodothamnus} \), apart from its similarity in some respects to \( \textbf{Kalmiaopsis} \), also shows some similarity to \( \textbf{Phyllocladus} \). The two may be distinguished by their very different habits, indumentum (none of the multicellular hairs of \( \textbf{Phyllocladus} \) are more than about 70 µ tall) and the more deeply lobed corolla of \( \textbf{Rhodothamnus} \). In this latter respect it is approached by \( \textbf{P. breweri} \), whose corolla lobes are about \( \frac{1}{2} \) the total length of the corolla. The
other species of \textit{Phyllodoce} are not more than \(1/3\) lobed.

There is a putative hybrid between the two genera, \(X\ \textit{Phyllothamnus erectus}\). This was supposed to have originated in a Scottish nursery in the middle of the 19th century, probably from \textit{P. empetrifomis X R. chamaecistus}. In general appearance, leaf shape, corolla lobing, etc., it does seem to be intermediate between its supposed parents. This impression is borne out by its leaf anatomy, except for one particular. The hybrid has an intermediate amount of libriform tissue when compared to its parents, but what is unexpected is the presence of a very prominent "mucilaginous" epidermis which is not to be found in either parent. However, \textit{P. empetrifomis} has what appears to be a thickened periclinal/traversing the epidermal cell; as in all other species of \textit{Phyllodoce} all the walls of the epidermal cells are rather thick (Fig. 55). This periclinal wall may be a modified "mucilaginous" epidermis. In \textit{Rhodothamnus} the walls of the epidermal cells are thin (apart from the outer periclinal wall) and there is no trace of a "mucilaginous" epidermis (Fig. 55). It is possible that the hybrid develops its prominent mucilaginous epidermis by combining the ability to produce such an epidermis with the thin walls enabling it to become prominent.

The hybrid is also interesting since it involves a species with Ericoid leaves and a species with plane leaves convolute in bud. Hagerup's suggestion (1956) that these two leaves are
basically different is rendered very improbable.

Infrageneric Variation.

As Davis (1962) noticed, *R. sessilifolius* has stomata on both sides of its leaf, and in this differs from *R. chamaecistus*. Possibly connected with this is the fact that the adaxial cuticle in the former species is thinner (3 μ against some 7-16 μ).

There are no other anatomical differences between the two, except that the palisade in *R. sessilifolius* is somewhat less well developed and the midrib bundle and associated lignification not so prominent.


More or less erect, evergreen shrublets with spirally arranged, linear, Ericoid leaves whose abaxial channel is open at the base. Indumentum shortly stalked, gland-headed hairs and unicellular hairs best developed in the abaxial channel.

Terminal inflorescence (elongated) corymbose, eperulate; bracts ± reduced leaves; paired, basal bracteoles green and persistent; pedicels rather slender, articulate with the calyx. Flowers 5-merous, actinomorphic. Corolla urceolate-campanulate, lobes usually less than 1/3 the length of corolla. Stamens 10; filaments glabrous or hairy; anthers dehiscing by short, terminal, gaping slits produced by resorbtion tissue; viscin threads present in at least some species. Ovary 5-locular, with
glandular hairs; placentae bilobed; style impressed, stigma subcapitate. Thin-walled septicidal capsule; seeds numerous, small; cells of the testa at most slightly elongated, thin walled.

There are ca. 7 species in the genus; 7 have been studied. The type species is P. coerulea.

This is a distinctive genus, recognisable by its combination of scattered Ericoid leaves, septicidal capsule and deciduous, gamopetalous corolla.

Anatomically it is rather uniform. All species lack well-developed pericyclic tissue in both the leaf and the stem, although there is sometimes very slight lignification above the midrib bundle. There is bast lignification in both the petiole and the lamina, but it does not form the lignified flange of tissue such as is to be found in the Ericoideae, nor are the stomata transversely orientated. Hence the approach to the Ericoid type of leaf is only superficial in this case.

Some notes on the infrageneric variation.

There is some variation in the distribution of stomata on the corolla, and my results disagree with those of Watson (1965) for both P. breueri and P. caerulea.

Viscin threads were found only in P. breueri and P. nipponica, but not in the other campanulate-flowered species, P. empetriformis. Not surprisingly perhaps, they were undetectable in the species with urceolate corollas.
The ovary loculi in an infertile specimen of *P. glanduliflora* were filled with unicellular hairs (Fig. 52); Ganapathy and Palser (1964) noted a similar phenomenon in *P. empetriflora*.

The next two genera agree with the last in having heterogenous pith, but they differ in a number of other respects. *Bryanthus* is rather similar to *Phyllococe* in leaf type, arrangement and anatomy, and its anthers are also not dissimilar, but it differs in floral stomatal distribution, inflorescence, corolla, etc. *Ledothammus* is rather more different, e.g. in leaf and stem anatomy, anther type, etc., and does not seem to be really close to any of the other Phyllodoceae. However, in corolla, leaf type and floral stomatal distribution it agrees with *Bryanthus*. The mechanism of anther dehiscence is unknown in either genus, and I have not seen their seeds.


Small ± prostrate shrub with small, evergreen,Ericoid leaves with the abaxial channel open at the base. Indumentum of shortly stalked glandular hairs on the leaf "margin" and inflorescence especially, a dense felt of unicellular hairs on the abaxial side of the leaf. Inflorescence an erect, terminal, few-flowered, eperulate raceme; bracts and paired basal bracteoles green; calyx obscurely articulate with the slender pedicel. Flower 4(-5)-merous, apparently actinomorphic.
Calyx lobes small, free. Corolla lobes (almost) free, rotate. Stamens 3; filaments glabrous; anthers dehiscing by a short terminal slit; no viscin threads seen. Ovary 5-locular, glabrous, a small swelling around the base of the continuous style; placentae only slightly bilobed. Capsule septicidal; seeds not seen.

There is only a single species, *B. gmelinii*, which has been studied.

*Bryanthus* is immediately distinguishable from all other genera of the Ericaceae by its combination of polypetalous flowers in a raceme and scattered, Ericoid leaves.

It is usually considered to be a gamopetalous genus, but the actual extent of fusion of the petals is at most slight. It appears to be polypetalous, but the material which I have seen was inadequate to decide this point. Copeland (1943) included *Bryanthus* in a group of genera in which anther dehiscence was by slits which extended the length of the thecae. This is very definitely not so; the slits are restricted to the top part of the anther alone (Fig. 54).

*Bryanthus* seems to be similar to *Phyllodoce* vegetatively and in its anatomy. I did not see flaring masses of lignified tissue in the petiole, nor did the stomata seem to be orientated. The ovary has the same shape as that of *Menziesia* and *Leiophyllum*. *Bryanthus* is perhaps closest to the four preceding genera of the Phyllodoceae.
15. **LEDOTHAMNUS** Meissner in Martius, F. Brazil. 7: 172 (1863).

Small Ericoid shrubs, leaves in whorls of 3; Ericoid, their abaxial channel open at the base. Indumentum of papillae densely covering the abaxial surface of the leaf and stout, long-celled hairs on the leaf "margins", stem and pedicel; on the last-named there may also be irregularly uniseriate hairs. Inflorescence terminal, eperulate; either single flowers in the axils of the topmost leaves or a solitary, truely (?) terminal flower; bracts leaf-like, bracteoles not seen; pedicels variable in length and stoutness, not articulate with the calyx. Flowers 5-7-merous, actinomorphic. Calyx lobes variable in size, free. Corolla rotate, polypetalous; petals sometimes fringed. Stamens the same number as the petals, antisepalous; filaments glabrous; anthers dehiscing by slits the length of the thecae; viscin threads present. Ovary 5-7-locular, verrucose; placentae bilobed; style impressed, short, stigma capitiate and lobed. Fruit a verrucose, septicidal capsule; seeds not seen.

There are about 5 species in this genus; only 2 have been studied. The type species is *L. guyanensis*.

*Ledothamnus* is an unmistakable genus with its polypetalous flowers, verrucose ovary and whorled, Ericoid leaves.

It combines in a remarkable way the characters of the polypetalous Rhododendroideae and the Ericoideae (Table 10).
Although its heterogenous pith, floral stomatal distribution and all other details of the flower are very much like other Rhododendroideae, in its stomatal orientation on the leaf, lignified flange of tissue in the petiole and general leaf anatomy (Figs. 55 and 56) it is very close to the Ericoideae (see also section 5.2.10.). In view of its remarkable mixture of characters, some of which are unknown elsewhere in the Rhododendroideae, it may eventually have to be placed in a monotypic tribe; this must await further work, especially on the anther, seed, inflorescence and indumentum.

*L. guvanensis* is one of the few members of the Ericaceae with fringed petals.

The last two genera considered to be members of the Phyllodoceae are also rather separate from the others. *Loiseleuria* and *Leiophyllum* both have rather small, decussate leaves, homogenous pith/2- or 3-locular ovary. Their anthers dehisce by resorbtion tissue which involves the whole length of the thecae. The long slits so produced (Figs. 9 and 54) are broadened by the action of the epidermis which acts as an exothecium (Artopezu, 1903; Copeland, 1943). *Leiophyllum* is also supposed to have a rudimentary endothecium. Both genera also have the cells of the testa considerably thickened. In
common with many of the Phyllodoceae they have adaxial calyx stomata alone.

In most systems they are placed rather far apart from one another because of the over-weighting of the polypetalous condition, but in view of their many similarities they are best considered to be fairly close (c.f. also Ledum and Rhododendron). It is interesting to note that in Watson et al.'s (1967) dendrogram they come out in the same group, although I cannot see that they have and affinities to the Ericoideae.

   **Ameryrsine** Pursh, Fl. Am. Sept. 1: 301 (1814).

Small erect shrub with small, decussate, entire leaves, convolute in bud. Indumentum of sparse unicalcular hairs and small capitate glands on the abaxial surface of the leaf and elsewhere. Inflorescence a terminal, eperulate, 5-15-flowered corymb; bracts and paired, basal bracteoles green and persistent; pedicel articulate with the calyx. Flowers basically 5-merous, actinomorphic. Calyx small, green, lobes free. Corolla rotate, polypetalous. Stamens 10; filaments glabrous; anthers dehiscing by an introrse slit the length of the thecae; viscin threads not seen. Ovary 3-locular, glandular hairy; placentae bilobed; style continuous with the swollen apex of the ovary,
stigma subcapitate. Fruit a septicidal capsule, not showing signs of loculicidal dehiscence; seeds numerous, ovoid; cells of the testa not elongated and with rather thick walls.

There is probably only a single species in the genus: \textit{L. buxifolium}. It has been examined.

\textit{Leiophyllum} is easily distinguishable from \textit{Loiseleuria} because it has 10 stamens (only 5 in \textit{Loiseleuria}), polypetalous corolla (gamopetalous) and leaves convolute in bud (revolute). Apart from the other similarities mentioned above, they are rather similar anatomically, in that both genera have small xylem cells above the midrib bundle (Fig. 30). I have not seen the well-developed "mucilaginous" epidermis of \textit{Loiseleuria} in \textit{Leiophyllum}.

I have been unable to find viscin threads in this genus.


Subprostrate evergreen shrub; leaves decussate, small, entire, revolute in bud and also in the mature leaf. Indumentum of dense unicellular hairs and short-stalked glands on the abaxial surface of the leaf. Inflorescence an eperulate, few-flowered, terminal corymb; bracts and paired basal bracteoles green and persistent; calyx articulate with the pedicel.
Flower basically 5-merous, actinomorphic. Calyx small and green, lobes free. Corolla gamopetalous, campanulate, 1/3 lobed. Stamens 5, antisepalous; filaments glabrous; anthers dehiscing by slits the length of the thecae; viscin threads present. Ovary 2-3-locular, glabrous; placentae bilobed; style continuous with the ovary, stigma + capitata. Fruit a septicidally dehiscent capsule with the valves often prominently loculicidally bifid at the apex; seeds numerous, ovoid; cells of the testa not elongated, thick-walled.

The single species of the genus, L. procumbens, has been studied.

Nomenclature.

In the International Code of Botanical Nomenclature (1935) Loiseleuria Desv. was proposed as a nomen genericum conservandum, an earlier name being Chamaecistus Oeder (Flora Danica p.4, l: T. 9). Chamaecistus is not properly published here, being referred to in the synonymy of Azalea (=Loiseleuria) procumbens as "Chamaecistus VII. Clus. Hist. 75. Ei anonymos pann. 57. Chamaecistus serpyllifolia floribus carneis. C. B. P. 466. Chamaerhododendros ferruginea......" etc.

Thus it was not necessary to conserve Loiseleuria. Some authorities consider that A. procumbens L. is the type species of Azalea (see Rehder, 1921; Dandy, 1967), and if this is so, then Azalea would be a synonym of Loiseleuria (which is also based
on *A. procumbens*. Apart from the mention of 5-locular fruit in the description of *Azalea* (Gen. Plant, 1754) this description agrees very well with *A. procumbens*, so it would seem that this typification is correct. However, Copeland (1943) accepts *A. indica* as the type species of *Azalea*. I have not gone into the matter of typification fully, and so *Azalea*, for the time being, is retained as a synonym of *Rhododendron*, which is the usual position.

**Notes on *L. procumbens***.

The leaves are very thick for their small size, and are very similar to the young leaves in the bud stage of some *Rhododendroideae*. *Loiseleuria* may have paedomorphic leaves. Both Ikuse (1954) and I have found viscin threads in this genus.

5.2.10. THE DABOECIEAE.

**DABOECIEAE Tribus Nova.**

*Daboecieae* Cox, Am. Mid. Nat. 39: 238 (1948) _anglica._

Small shrubs with decussate or scattered evergreen leaves, leaves entire, revolute in bud and when mature. Indumentum of stalked capitate glands, the abaxial leaf covered with a dense felt of unicellular hairs. Inflorescence terminal, racemose, eperulate; bracts rather large and leafy, bracteoles not seen; calyx articulate with the pedicel. Flowers 4-5(-6)-merous,
actinomorphic. Calyx medium-sized, lobes free. Corolla gamopetalous, urceolate, 1/5 lobed. Stamens usually 8; filaments glabrous; anthers granular, dehiscing by a short, terminal slit produced by the action of resorption tissue; viscin threads not seen. Ovary 3-5(-6)-locular, with glandular hairs; placentae bilobed; ovary attenuate into the style; stigma ± truncate. Rather thin-walled, septicidal capsule; seeds several, ovoid; cells of the testa thick-walled, papillate, not elongated.

There is only a single genus in the tribe. For a Latin description of the tribe, see Appendix 1.

The tribe has the facies of a rather vigorous Bryanthus, but when in flower it looks just like the Ericaideae. It differs from the Rhododendroideae on a number of counts; the situation parallels that of Ledothamnus, although here anatomical agreement with the Ericaideae is not quite so good, but the floral similarities rather more marked (see Table 10).

Its leaves are superficially very like those of some of the Ericaideae, e.g. Erica taxifolia, E. oatesii (Fig. 2). Anatomically they agree in having a "mucilaginous" epidermis and a flange of lignified tissue in the petiole. However, its midrib bundle tends to be transcurrent (Fig. 56) and its foliar stomata are apparently unorientated. The pith is very heterogenous, and is almost Calluna-type, since there is a sheath of thick-walled cells surrounding the inner cells which are all
<table>
<thead>
<tr>
<th>Character</th>
<th>Rhododendroideae (most)</th>
<th>Ledothamnus</th>
<th>Daboecia</th>
<th>Erica (most)</th>
<th>Calluna</th>
<th>Cassiope</th>
<th>Andromedae (most)</th>
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<tr>
<td>Leaves whorled</td>
<td>- (+)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>decussate</td>
<td>decussate</td>
<td>- (+)</td>
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<td>Leaves Ericoid</td>
<td>- (+)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
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<tr>
<td>Leaves Calluna-type</td>
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<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Bracteoles</td>
<td>+ (-)</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+ (-)</td>
</tr>
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<td>Calyx stomatal distribution</td>
<td>+,+,-,+,-,++</td>
<td>++</td>
<td>+,-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+,-,+,-,++</td>
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<td>-</td>
<td>+</td>
<td>+</td>
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<td>-</td>
<td>+ (-)</td>
<td>+ (-)</td>
<td>+</td>
<td>-</td>
<td>- (+)</td>
</tr>
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<td>Stamen appendages (flattened)</td>
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<td>-</td>
<td>-</td>
<td>+ (fl.)</td>
<td>- + (fl.)</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Viscin threads</td>
<td>+ (-)</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
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<td>Capsule dehiscence</td>
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<td>Vesya cell walls thick</td>
<td>- (+)</td>
<td>?</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+ (-)</td>
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<tr>
<td>Epidermis &quot;mucilaginous&quot;</td>
<td>- , +</td>
<td>+</td>
<td>+ (-)</td>
<td>+ (-)</td>
<td>+</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Stomata transversely orientated</td>
<td>+ (+)</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
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<td>+ (-)</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+</td>
</tr>
<tr>
<td>Petiole with lignified flanges</td>
<td>-</td>
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<td>-</td>
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<tr>
<td>Vessel type</td>
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<td>v. hetero.</td>
<td>homo.</td>
<td>Calluna</td>
<td>Calluna</td>
<td>various</td>
</tr>
</tbody>
</table>

homo. = homogenous; hetero. = heterogenous

**TABLE 10** COMPARISON OF THE ERICOIDAE, RHODODENDROIDEAE, ANDROMEDA,
FIG. 56: LEDOTHAMNUS, DABOECIEAE AND DIPLARCHIEAE.

1. Ledothamnus sessiliflorus, x33 - stem, T.S. node; 2. L. parviflorus - a = T.S. leaf, x50, b = T.S. petiole, x125; 3. Daboecia cantabrica, x50; 4. D. azorica, x75; 5. & 6. D. cantabrica; 5. T.S. petiole, x50, 6. stem hair; 7. & 8. D. azorica, 7. T.S. ovary, x20, 8. fruit, x5; 9-11. Diplarche multiflora, 9. fruit, x6 - v = outer wall of valve, w = inner wall, 10. T.S. leaf, x100, 11. leaves, x10 - a & b, foliage leaves; c, a bract (me = "mucilaginous" epidermis).
rather thin-walled and only slightly heterogenous in size.

Its inflorescence is the same as that of *Bryanthus*, but this type is otherwise rare in the Rhododendroideae. It apparently lacks bracteoles. Its flowers are 4-5-merous and in this approach the Ericoideae, although 4-merous species are quite common throughout the family. It is also odd in having stomata on both sides of the calyx, but none on the corolla. This type floral stomatal distribution is unusual in the Ericaceae, although it is also to be found in some species of *Pieris*.

Its anthers dehisce by resorbtion tissue as do those of many of the Rhododendroideae, but it is peculiar amongst these in that this tissue is restricted to the apex of the anther and does not extend the length of the thecae. (Copeland, 1943). Alone amongst the Rhododendroideae the thecae are granular (the papillae are ca. 15μ), rather elongated and saggitate (Fig. 54; see also Copeland, 1943). There is a dorsal prolongation of the vascular hook which has not been found in any other genera of the Ericaceae (Fig. 33; see Matthews & Knox, 1926). I have been unable to find viscin threads in this tribe.

It differs from other members of the Rhododendroideae in several embryological details (for sources, see Petrosilot, 1904a; Copeland, 1943; Ganapathy & Palser, 1964). The ovule, alone amongst the Ericaceae studied, has an hypostase, and the integument is very thick, with 7-9 layers of cells. All these
layers get absorbed during the development of the seed, except for the tanniniferous second layer which persists in the seed of *D. cantabrica*. In my material of *D. azorica* this second layer was little in evidence (Fig. 15). The cells of the outer layer are ± isodiametric, very thick-walled on their inner periclinal surface, but forming thin-walled papillae on the outer surface. My observations on *D. azorica* agree with those of the earlier authors who studied *D. cantabrica*, apart from the one particular mentioned above.

It is thought that tribal recognition is needed for this curious genus. This was first suggested by Cox (1948a) as a result of his investigations on wood anatomy. *Daboecia* (*D. polifolia*) was unique in that it had thick and uneven thickening of the vessel walls and was the only genus in the Rhododendroideae which had porous vessel perforations alone, no scalariform plates being present. Cox thought that it was paralleled to some extent only by *Bryanthus*.

The Daboecieae do seem rather close in several respects to the Phyllodoceae, notably to *Bryanthus*, although *Bryanthus* and *Daboecia* are rather different florally. The Daboecieae also form a notable approach in several respects to the Ericoideae.


[Borella Neck, Elem. Bot. 1: 212 (1790)]
The characters of the genus are of those of the tribe. Both
the species in the genus have been studied; *D. cantabrica*, the
type species, and *D. azorica*.

5.2.11. THE DIPLARCHEAE.


Erect shrublets with small, serrulate leaves. Indumentum
of gland-headed hairs of various sizes, long-celled hairs and
unicellular hairs. Inflorescence terminal, capitulate, eperulate;
bracts and paired bracteoles present, leafy; calyx articulate with
the pedicel. Flower 5-merous, actinomorphic. Calyx medium-sized,
lobes free. Corolla hypocrateriform, with the antisepalous stamens
weakly epipetalous for much of their length, the antipetalous
stamens less so. Stamens 10; anthers dehiscing by slits the length
of the thecae; viscin threads present. Ovary 5-locular, glabrous,
bifid placentae attached near the top of the loculi; style
impressed, stigma indusiate. Capsule septifragal, the outer walls
separating into two layers periclinally; seeds not seen, apparently
reticulate.

There is but a single genus in this tribe.

*Diplarche* is best placed in a monogeneric tribe for the
following reasons:

1.) Its serrate leaves. As already mentioned some of the
Rhododendroideae do have serrulate leaves. The leaves nearer
the inflorescence are broader than those elsewhere (Fig. 56).
2.) Capitulate inflorescence. The individual flowers have very short pedicels and, as Watson (1965) noted, this gives the inflorescence rather a distinctive appearance. However, it is only a more extreme form of the normal inflorescence of the Rhododendroideae; similarly short pedicels are to be found in some species of Epigaea and Rhododendron of the Rhododendroideae, and also some of the Vaccinioideae.

3.) There are abaxial calyx stomata. Although this is not a rare character in the Rhododendroideae such a floral stomatal distribution is not found in the Phyllodoceae and Daboecieae, with which Diplarche otherwise shows some similarity.

4.) The pronounced epipetalal of the stamens, unique in the Ericaceae (Fig. 37).

5.) The remarkable septifragal dehiscence of the capsule (Fig. 56). The only other genus of the Ericaceae known to dehisc septifragally is Calluna; on all other grounds Calluna is not close to the Diplarcheae. In Diplarche the thin, scarious septa remain attached to the central placental column and the five valves themselves split into two layers, the outer spreading and the inner incurved.

The relationships of this tribe are more towards the Phyllodoceae than elsewhere, as Hooker and Thompson (1854) noted. The stamens are similar to those of Leiophyllum and Loisaleuria in general appearance, and the habit of the plant
with rather small leaves, eperulate inflorescence and small, apparently actinomorphic flowers in general agreement with the Phyllodoceae. *Rhodothammus* is especially similar in habit. There are no members of the Phyllodoceae in the Himalayas.

19. **DIPLARCHE** Hooker fil. & Thompson, J. of Bot. & Kew Misc. 6: 380 (1854).

The genus has the characters of the tribe. There are two species in the genus. The type species, *D. multiflora*, has been studied.

5.3. **THE ERICOIDEAE**

This is a very distinctive subfamily in general facies. Nearly all its members have whorled leaves which are either Ericoid or strongly revolute (Fig. 2), and the nearly always 4-merous corolla is marcescent, i.e. it does not fall from the plant after flowering, but persists. Loculicidal capsule dehiscence is common in this group.

Although anatomical studies in this group have been limited to 20 species, a few points are worth recording. All species (apart from *Calluna*, see section 5.5.4.) from both the Ericaceae and the Salaxidae are anatomically very similar. They often have a "mucilaginous epidermis" but never have an hypodermis, their stomata are restricted to the abaxial side of the leaf or the abaxial channel and are transversely orientated, and their
petiole bundle has a flange of lignified tissue on either side (Fig. 25). Bast fibres are always found in the leaf, libriform fibres often; in the stem the whole of the phloem apart from the flaring phloem parenchyma rays becomes prominently lignified with age.

Corolla stomata have not been seen (see also Watson, 1965), abaxial calyx stomata may or may not be present. Stamen appendages, when present, are flattened (Fig. 8, see Falser & Murty, 1967). The anthers dehisce by pores, or slits which have very definite limits.

5.4. THE ARBUTOIDEAE

5.4.1. CHARACTERS OF THE SUBFAMILY.


Usually evergreen trees or shrubs; leaves usually thick, scattered or rarely whorled, entire or serrate, convolute in bud. Indumentum of uni- or bicellular hairs, stalked glands and sometimes long-celled hairs. Inflorescence terminal, racemose or paniculate, usually eperulate; bracts and paired basal bracteoles usually present, sometimes becoming indurated and persistent; pedicel not articulate with the calyx. Flowers usually 5-merous. Calyx small and green, lobes free. Corolla gamopetalous, urceolate, lobes short; unicellular hairs on the inside. Stamens 8-10; filaments usually swollen at the base, hairy or not; anthers almost smooth with paired, apical, granular spurs, dehiscing by terminal pores/short slits; no viscin
threads. Ovary 4-10-locular, fleshy, papillate or not, a well-marked disc around the base; placentae apical, small, with 1-10 ovules; style continuous with the ovary, stigma truncate. Fruit usually baccate or drupaceous; 1-10 large seeds per loculus; cells of the testa moderately elongated, easily separating or not, thick walled; embryo variable in shape.

It is thought that the Arbuteae sensu Drude should be placed in a sub-family by itself for the following reasons:

1). All genera have anthers inverting only just before anthesis, and the filament is attached to the tip of the anther (Arctopoeus, 1903; Palser, 1954). This is an uncommon character in other Ericaceae.

2). There are fewer than 10 ovules per loculus; the fruit is fleshy or very rarely secondarily schizocarpic (Arctostaphylos - Schizococcus group).

3). All members examined (12 species from 4 genera) contained ellagic acid. There are no reports of this from other members of the Ericaceae. Also there are a number of other phenolic compounds apparently restricted to this group making it instantly recognisable on a chromatogram.

4). There is very poor development of the libriform, bast and stem pericyclic lignification, even though the leaves are otherwise coriaceous and xeromorphic. Most species have a Lyonia-type midrib bundle.
5). The inflorescence is terminal and the flowers are urceolate; elsewhere this combination is found only in *Oxydendrum* which is otherwise very different.

6). There are adaxial calyx and corolla stomata; elsewhere this combination is found only in some of the *Phyllodoceae*. The inside of the corolla always has long unicellular hairs.

The Arbutoideae are distinguishable in fruit, flower and leaf from all other Ericaceae. It is perhaps only on the borderline of subfamilial rank, but it is a very coherent group and there are no intermediates between it and the Vaccinioideae, to which it shows most similarities. The anthers dehisce by resorbtion tissue (Matthews & Knox, 1926; Doyel, 1942). Palser (1954) found that it was not particularly remarkable in floral anatomy, being but moderately advanced as regards the amount of reduction and non-divergence of the floral traces. Embryologically too it was unremarkable, and in both these respects the group as a whole showed rather little variation.

The Arbutoideae and the Ericoideae are the only two large groups of the Ericaceae for which it is possible to make a coherent anatomical description.

The stem of the Arbutoideae has an homogenous pith and cortex; the nodes are always simply unilacunar. The medullary rays are prominent and flare out in the phloem, as Cox (1948b) found. He also thought that this was a distinctive and natural group
from the point of view of wood anatomy. (He studied 5 species of *Arbutus*, 5 of *Arctostaphylos* and one of *Arctoius*.) Alone in the Arbutoideae sensu Drude it lacked scalariform perforation plates with more than eight bars and had heterogenous type 2a medullary rays (see Kribs, 1935). The group as a whole tends to have ring porous wood and the vessels are relatively broad. There are usually few fibres in the pericyclic sheath position in the stem, and phloem lignification is very poor; in the inflorescence the pericyclic sheath is more prominent. The development of the phellogen is often very irregular.

The midrib bundles are usually the *Lyonia*-type, always transcurrent ("looking like the strings of an harp", Niedenzu, 1890). Both they and the petiole bundle are almost devoid of any associated fibres (Figs. 58 & 59), although some species have a few. They are better developed on the lateral bundles. The leaf epidermis is type 2 except in *Arctoius*; the stomata are anomocytic and usually unorientated. The cuticle may be smooth/papillate. There is no hypodermis except at the leaf margin and immediately next to the bundles. "Mucilaginous" epidermes are of sporadic occurrence through the group. The palisade tissue is usually poorly developed even in those species with only abaxial stomata; the cells rarely exceed 70μ in height. The only exception is *Xylococcus*. In some species of *Arctostaphylos* the leaf may be almost isobilateral.
The basic chromosome number for the subfamily is \( x = 13 \), so far as is known.

5.4.2. THE LIMITS OF THE ARBUTOIDEAE.

Only two genera have ever been included in this group which are excluded here. Klotzsch (1851) included both *Enkianthus* and *Pernettya* in his Arbuteae. *Enkianthus* does not even have fleshy fruit, although it was originally described as being baccate. *Pernettya* differs from the Arbutoideae sensu restricto in its usually axillary inflorescence, two pairs of stamen awns, better development of stem and leaf lignification, etcetera. De Candolle (1836) and Hooker (1876) both included *Pernettya* in the Arbuteae. Miedenzu (1890) finally transferred *Pernettya* to a position close to *Gaultheria* on anatomical evidence; both his and Drude's concept of the Arbuteae agree with the Arbutoideae as here recognised.

5.4.3. GENERA INCLUDED, WITH KEYS.

Drude recognised 3 genera in his Arbuteae. I recognise 6 genera; in the following list all the genera starred were included in *Arctostaphylos* sensu Drude:—

*Arbutus*, *Comarostaphylis*,* Ornithostaphylis*,
*Xylococcus*,* Arctostaphylos* and *Arctoüüs*

All these genera are retained in a single tribe, the Arbuteae.

Two keys are given below.
External Morphological Characters

1. Leaves deciduous; inflorescence surrounded by well-developed bud scales 6 Arctoïs.

1. Leaves evergreen; inflorescence/without well-developed bud scales

2. Leaves 3-whorled 3 Ornithostaphylis.

2. Leaves scattered

3. Ovary smooth

4. Flowers large, ca. 8 mm.; filaments not abruptly swollen at the base 4 Xylococcus.

4. Flowers usually smaller; filaments abruptly swollen at the base 5 Arctostaphylos.

3. Ovary papillate

5. Several ovules per loculus in the ovary; fruit a berry 1 Arbutus.

5. One ovule per loculus in the ovary; fruit a "drupe" 2 Comarostaphylos.

Anatomical characters

1. Midrib bundle ± circular in T. S., rarely unifacial

2. Cuticle at least 6 thick; epidermal cell walls straight 5 Arctostaphylos.

2. Cuticle less than 3 thick; epidermal cell walls sinuous 6 Arctoïs.

1. Midrib bundle ± elliptic in T. S., always bifacial
3. Abaxial epidermis with 30\(\mu\) papillae 2 Comarostaphylis.

3. Abaxial epidermis not as above

4. All cells of the abaxial epidermis with long unicellular hairs 3 Ornithostaphylis.

4. Not as above

5. Palisade mesophyll cells 70\(\mu\) tall 1 Arbutus.

5. Palisade mesophyll cells about 100\(\mu\) or more tall 4 Xylococcus.

5.4.4. THE ARBUTEAE.

ARBUTEAE De Candolle, Prod. 7 (2): 580 (1839).

The tribe has the characters of the subfamily. See table 11 for some of the variation to be found in this tribe.


*Unedo Hoffman. & Link, Fl. Port. 1: 415 (1809).

Trees or large shrubs with large, scattered, evergreen leaves, entire or serrate; convolute in bud. Indumentum of "unicellular" hairs, or glands with stalks of varying lengths. Inflorescence terminal, paniculate, many flowered; no protective perulae. Bracts and basal bracteoles present, ± persistent, not indurated; pedicels not articulate with the calyx. Flowers 5-merous. Calyx lobes small, free, green. Corolla urceolate, 10-pouched at the base or not. Stamens 10; base of the hairy filament swollen, filament attached to the top of the anther;
anther ovoid, with two apical introrse pores. Ovary 5-locular, covered with multicellular papillae; placentae slightly bilobed, ovules few; style continuous with the ovary, stigma truncate. Fruit a few-seeded berry, seeds large (2mm.). Testa well developed, cells elongated, with thick, pitted walls. Embryo large, spatulate in shape.

Ca. 20 species in the genus; 13 were studied. The type species is *A. unedo*.

This is probably the least specialised genus in the subfamily. The glandular hairs are very robust with a multiseriate stalk, they never have uniseriate stalks, nor are there long-celled hairs in the genus. These last two hair types are found in the *Arctostaphylos-Schizococcus* group, *Ornithostaphylyis* and *Arctoïs* which can be considered derived on other grounds.

The large terminal panicle is the starting point of a reduction series culminating in the abbreviated racemes of *Arctoïs* and some *Arctostaphylos* species.

The fruit is unspecialised when compared to other genera. The papillate ovary and mature fruit may or may not be derived, but it is certainly unspecialised in endocarp and testa structure and in seed number. *A. menziesii* and other species have a much thickened endocarp wall, about 300μ thick in T.S. (c.f. the normal two layers of fibres in the other members of the Ericaceae).
Its component cells are lignified and about 180\(\mu\) long; the cell walls are so much thickened (ca. 7.5\(\mu\) thick) that the lumen is almost obscured. It is this layer which becomes developed to form the stony part of the fruit in other genera of the Arbutoideae. There is considerable variation in the number of seeds per fruit in \textit{Arbutus}. With the limited material available it was hard to establish detailed trends, but in general the larger the seeds, the fewer they are in number. \textit{A. petiolaris} has seeds about 1.8 mm. long and ca. 39 per fruit, whilst those of \textit{A. unedo} are about 3 mm. long and ca. 15 per fruit. This trend culminates in the other genera of the subfamily, in which there is usually only a single large seed per loculus.

Correlated with these trends is the fact that the cells of the testa in \textit{Arbutus} have thick walls and do not easily dissociate, whilst those in the other genera have very prominent plasmodesmata and are not so tough, easily dissociating.

The cuticle of most species of \textit{Arbutus} is very striate, and in \textit{A. arizonica} the striae on the abaxial surface of the leaf are about 9\(\mu\) tall and the underlying epidermal cell has a tendency to develop an outpushing as well. In \textit{Comarostaphylis} all these cells have 30\(\mu\) papillae, whilst in \textit{Ornithostaphylis} each abaxial epidermal cell is effectively an unicellular hair. Other genera have striate or smooth cuticles.

Two species, \textit{A. unedo} and \textit{A. xalapensis}, have stomata on
both surfaces of the calyx, thus approaching the condition found in *Comarostaphylis*. However, neither species has stomata on both sides of the corolla, as in the latter genus. Watson’s (1965) observations of the stomatal distribution of *A. canariensis* and *A. andracne* do not agree with mine.

The anthers of *A. unedo* are notable for the prominent beak at the bottom of the thecae (Fig. 60); this also occurs in some other species of *Arbutus* and in *Arctostaphylos*. Most species of *Arbutus* have small, paired, rather fragile appendages at the apex of the thecae between the spurs (Fig. 60: 2); perhaps the terminal portion of the connective. These are also to be found in *Ornithostaphylis*, but they have not been seen elsewhere in the Ericaceae.

In floral anatomy *Arbutus* is distinguishable from the other genera (Palser, 1954; all other details of the floral anatomy for this subfamily are taken from this paper). The vascular supply to the sepal whorl is from 15 separate traces; this is the heaviest and least derived supply of the group. *A. xalapensis* has 5 traces going to each sepal; Palser considered that this was a secondary condition.

**Comments on Niedenzu’s anatomical work on Arbutus.**

Niedenzu (1890) missed the difference in midrib bundle type when separating *Arbutus* from *Arctostaphylos*, although he mentioned that in the former genus the bundle protruded on the abaxial
FIG. 57: ARBUTOIDEAE - HAIRS.

FIG. 58: ARBUTOIDEAE - LAMINA ANATOMY (1).

1. Arbutus menziesii, x35; 2. A. densiflora, x33; 3. Comarostaphylis longifolia, x33;
4. C. glabrata, x33; 5. Ornithostaphylis oppositifolia, x50; 6. Xylococcus bicolor, x25 (e = epidermis, me = "mucilaginous" epidermis).
FIG. 59: ARBUTOIDEAE - LAMINA ANATOMY (2).

1. Arctostaphylos sensitiva, x50; 2. A. nummularia, x50; 3. A. uva-ursi, x50;
4. A. cratericola, x50; 5. A. pungens, x33; 6. A. glauca, x33; 7. A. drupacea,
x33; 8. Arctoús rubra, x50 (e = epidermis, me = "mucilaginous" epidermis).
FIG. 60: ARBUTOIDEAE - STAMEN AND COROLLA.

5. Ornithostaphylis oppositifolia; 6. Arctoës alpina; 7. Xylococcus bicolor;
11. A. myrtifolia (all x10).
FIG. 61: ARBUTOIDEAE - FRUIT AND SEED.

<table>
<thead>
<tr>
<th>Character</th>
<th>Arbutus</th>
<th>Comarostaphylis</th>
<th>Ornithostaphylis</th>
<th>Xylococcus</th>
<th>Arctostaphylos</th>
<th>Arctous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf margin</td>
<td>serrate (usu.)</td>
<td>serrate</td>
<td>entire</td>
<td>entire</td>
<td>entire-serrulate</td>
<td>serrulate</td>
</tr>
<tr>
<td>Plant evergreen</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Leaves borne</td>
<td>scattered</td>
<td>scattered</td>
<td>whorls of 3</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
</tr>
<tr>
<td>Epidermis type</td>
<td>2</td>
<td>2</td>
<td>(1) - 2</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Abaxial epidermis</td>
<td>usu. striae</td>
<td>papillate</td>
<td>densely hairy</td>
<td>smooth</td>
<td>smooth</td>
<td>smooth</td>
</tr>
<tr>
<td>Stomata orientated</td>
<td>-</td>
<td>-</td>
<td>right angles</td>
<td>cuticle</td>
<td>-</td>
<td>parallel</td>
</tr>
<tr>
<td>Midrib bundle shape in T.S.</td>
<td>semi-lunate</td>
<td>lunate</td>
<td>lunate</td>
<td>lunate</td>
<td>circular</td>
<td>(inapplicable)</td>
</tr>
<tr>
<td>Midrib bundle type</td>
<td>Lyonia</td>
<td>Lyonia</td>
<td>Lyonia</td>
<td>Lyonia</td>
<td>Lyonia/Pieris</td>
<td>Pieris</td>
</tr>
<tr>
<td>Druses in petiole</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
</tr>
<tr>
<td>Inflorescence perulate</td>
<td>-</td>
<td>- (†)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Flower size (mm.)</td>
<td>6 - 7.3</td>
<td>4.5 - 7.5</td>
<td>2.75</td>
<td>8</td>
<td>3.3 - 7.3</td>
<td>3.0 - 4.5</td>
</tr>
<tr>
<td>Stomata on flower</td>
<td>+ - + (usu.)</td>
<td>++</td>
<td>++</td>
<td>++ ++</td>
<td>++ ++</td>
<td>++ - ++</td>
</tr>
<tr>
<td>Swollen filament base</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Drupaceous fruit</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Ovary papillate</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ovary loculi</td>
<td>5</td>
<td>4 - 6</td>
<td>10</td>
<td>5</td>
<td>5 - 9</td>
<td>5</td>
</tr>
<tr>
<td>Embryo spatulate</td>
<td>+</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

adaxial corolla, abaxial corolla, adaxial calyx, abaxial calyx

**TABLE II** VARIATION OF SOME CHARACTERS IN THE ARBUTOIDEAE
The midrib bundle is Lyonia-type and elliptic in Arbutus, usually Lyonia-type and circular in Arctostaphylos. The "deckhaare" of the two genera have the same structure. He thought that the bast and libriform tissue was much better developed in Arctostaphylos than in Arbutus; in fact it is poorly developed in both genera. He correctly noted that the cuticle was never striate in Arctostaphylos, although it sometimes was in Arbutus.

He followed de Candolle (1839) in dividing Arbutus into two sections. One, the Gerontogae, were supposed to have glandular hairs with a prominent foot (= stalk) and palisade cells three times as tall as the spongy cells; the other, the Americanae, had almost isobilateral leaves and glandular hairs with a less prominent stalk. Of the Americanae, both A. glandulosa and A. densiflora have glandular hairs with very well developed stalks and A. glandulosa and A. menziesii have a very easily distinguishable palisade layer just like the European species. However, there is a general tendency for the species of the two continents to behave as Niedenzu mentioned. He also claimed that the European species were characterised by having a "mucilaginous" epidermis. This is poorly developed in some individuals of these species; also it is to be found in A. prunifolia and A. densiflora, two American species.


Large, evergreen shrubs with large, scattered, serrate leaves,
convolute in bud. Indumentum of bi- and unicellular hairs, stalked glandular hairs; all the cells of the abaxial surface of the leaf papillate. Inflorescence terminal, sometimes axillary, racemose or paniculate, tending to be perulate; bracts and bracteoles ± persistent, not indurated; pedicel not articulated with the calyx. Calyx lobes small, free. Corolla urceolate. Stamens 10; hairy filaments swollen at the base; anthers ovoid, with a pair of ± straight, apical, granular spurs, dehiscing by a pair of terminal pores. Ovary 4-6-locular, with only one ovule per loculus; covered with multicellular papillae. Fruit drupaceous, with 5-6-seeded, ridged stone which does not separate into one-seeded portions very easily; cells of the testa easily dissociating; embryo large, ± curved and spatulate.

There are ca. 20 species in this genus; 6 have been studied exhaustively. The type species of the genus is C. arguta.

This is a well-defined genus. Although early workers have tended to include it in Arctostaphylos (Hooker, 1876; Drude, 1897), most recent authors have considered it to be generically distinct (Adams, 1940; Abrams, 1951; Munz, 1959). It may be distinguished from Arbutus by its drupaceous fruit, papillate epidermis and the distribution of stomata on its flowers; from Arctostaphylos in its midrib anatomy (c.f. Figs. 58 & 59), papillate epidermis and again the distribution of stomata on its flowers. None of the species of Arctostaphylos which I have
seen have a papillate ovary wall, although Palser reports this from A. tomentosa. The specimens of this species examined do not have such an ovary wall, although the situation is rather obscured by the unicellular hairs densely covering the ovary. (see also p. 345). Also no species of Arctostaphylos have the coarsely serrate leaves of Comarostaphylis and several species of Arbutus; those species of Arctostaphylos with serrate leaves, e.g. A. andersonii, have only a few small serrations restricted to the base of the leaf.

Stomata occur on both surfaces of the calyx and corolla in six out of the seven species examined for this character. The exception was C. mucronifera, where abaxial calyx stomata were not seen; this might have been due to the state of the material. In all the species it is tedious looking for the stomata, owing to confusion with papillae.

The midrib bundle character is a perfectly good distinction between Comarostaphylis and Arctostaphylos. In the latter genus the bundle, although often of the Lyonia type, is always basically circular in shape whilst in Comarostaphylis, and the other genera apart from Arctous, it is a modified ellipse. Comarostaphylis is the only genus in the subfamily with a papillate epidermis.

In floral anatomy the genus is characterised by a rather strong calyx vascular supply which nevertheless arises from a
single trace. This trace branches much subsequent to its departure. However, this difference should be treated with caution, since Palser studied only two species, *C. polifolia* and *C. diversifolia*; other species may have a different arrangement of their floral vasculature.

3. **ORNITHOSTAPHLIS** Small, N. Am. Fl. 2ª: 101 (1914).

Much-branched evergreen shrub with narrow, 3-whorled leaves, entire and with slightly revolute margins when mature. Indumentum of dense, unicellular hairs on the abaxial surface of the leaf, also small capitate hairs elsewhere. Inflorescence a terminal, eperulate, much-branched panicle; bracts and bracteoles persistent, not indurated; pedicel not articulated with the calyx. Calyx small, lobes free. Corolla urceolate, small (3 mm. in length), slightly 10-pouched at the base. Stamens 10; filaments hairy, swollen at the base; anthers ovoid with paired, apical, granular spurs and paired apical processes, dehiscing by two terminal, introrse pores. Ovary 10-locular, smooth, about two ovules per loculus; ovary attenuate into the style, stigma truncate. Fruit drupaceous, the ribbed stone not easily separating into one-seeded portions; cells of the testa tending to dissociate; embryo large, curved and pathulate.

The only species, *O. oppositifolia*, was studied.

**Ornithostaphylis** is instantly recognisable by its delicate
facies. This is due to its narrow, whorled leaves and small flowers borne on the slender branches of the paniculate inflorescence.

In floral stomatal distribution it is unremarkable. Like *Arbutus*, but apparently unlike the other genera, there is a pair of small, apical appendages besides the paired spurs (Fig. 60). There are, on the average, two separate traces to each calyx lobe; in this it agrees with *Xylococcus*, but differs from the other genera of the subfamily. The fruit of this genus is smooth, and in this it approaches the three remaining genera and differs from the two preceding. However, it has two ovules per loculus, although this also seems to occur at least sometimes in *Arctoës*. The embryo is large and spathulate (Fig. 61).

The midrib bundle of *Ornithostaphylis* is rather like that of the two preceding genera (Fig. 58). Unlike both, however, all the cells on the abaxial surface of the leaf bear an unicellular hair. The multicellular hairs on the leaf show an extreme reduction when compared to those of *Arbutus* (Fig. 57). These hairs are similar to those of some species of *Comarostaphylis* and *Arctostaphylos*. Another difference is that most of the Arbutoideae, apart from *Arctoës*, have unorientated stomata, whilst those of *Ornithostaphylis* are rather poorly, but definitely, orientated at right angles to the long axis of the leaf.

Evergreen shrub with entire, scattered leaves; slightly revolute when mature but convolute in bud. Indumentum of unicellular and small capitate hairs. Inflorescence a terminal drooping panicle; bracts and bracteoles ± persistent, the former a little indurated; calyx not articulated with the pedicel. Flower 5-merous; Calyx lobes small, ± free. Corolla rather large (8 mm.), urceolate. Stamens 10; long, hairy filaments tapering gradually from the slightly swollen base; thecae ovoid, with two terminal, recurved granular spurs, dehiscing by two terminal, introrse pores. Ovary 5-locular, smooth; one ovule per loculus. Style continuous with the ovary; stigma truncate. Fruit drupaceous, stone spherical and slightly ridged, not dissociating. Testa cells elongated, tending to separate one from another; embryo large and very spathulate.

The only species, *X. bicolor*, was studied.

*Xylococcus* was proposed as a genus on the grounds that it differed from *Arctostaphylos* in having long filaments only gradually swollen towards the base, and a smooth stone. The first difference is satisfactory, although the filaments of *A. sensitiva* are less abruptly swollen towards the base than those of other species of *Arctostaphylos* (Fig. 60). The fruit character cannot be maintained, since *A. glauca* also has a smooth stone not easily separating into one-seeded portions.
However, they differ in embryo shape (Fig. 61). The embryos of *Arctostaphylos* are allantoid (sausage shaped), those of *Xylococcus* are spathulate and are similar to those of the three preceding genera. More work is needed on this character.

*Xylococcus* differs in facies from the other genera. Its broad leaves are slightly revolute when mature although convolute in bud, as are those of the rest of the subfamily. Its flowers are larger than (all?) other species of *Arctostaphylos*, the genus with which it is often merged. It has stomata on both surfaces of the calyx and corolla, again like *Comarostaphylis* and different from *Arctostaphylos*.

In floral anatomy Palser found that *Xylococcus* had two traces to each calyx lobe like *Ornithostaphylis*. Unlike that genus it had only a single ovule in each loculus.

Anatomically *Xylococcus* is distinct from all other members of the Arbutoideae. It is the only *Arctostaphylos*-like species to have a considerably wider than high midrib bundle. It has the tallest palisade tissue in the whole subfamily - two layers of palisade tissue, each ca. 100 μ high and made up of very slender cells. It also has a mucilaginous epidermis, although this is almost obscured by the thickening of the cell walls.

All this evidence supports the maintenance of *Xylococcus* as a genus.

5. **ARCTOSTAPHYLOS** Adanson, Fam. Pl. 2: 165 (1763).
Prostrate to erect evergreen shrubs with scattered, usually entire, leaves, convolute in bud. Indumentum of unicellular, glandular or, rarely, long-celled hairs. Inflorescence a terminal raceme or panicle, few or many flowered, eperulate; bracts and bracteoles, especially the former, tending to be foliaceous and becoming indurated, rarely deciduous; calyx not articulate with the pedicel. Calyx lobes small. Corolla urceolate. Stamens 10, hairy bases of the filaments usually swollen; only appendages two apical, often recurved, granular spurs, dehiscing by two terminal, introrse pores. Ovary 4-10-locular, smooth, one ovule per loculus; style continuous with the ovary, stigma truncate. Fruit usually a fleshy drupe with 4-10 seeds, rarely schizocarpic; cells of the testa moderately elongated, dissociating easily; embryo large, + allantoid in shape, often strongly curved.

Ca. 70 species in the genus; 18 have been studied. The type species is *A. uva-ursi*.

*Mairania* and *Uva-Ursi* were both published as alternative names to *Arctostaphylos*, but the three other names mentioned in
the synonymy are those of genera segregated from *Arctostaphylos*.

*Xerobotrys* was proposed because Nuttall thought that there was a group of genera differing from *Arctostaphylos* sensu stricto in having prominently angled, dry fruits with 3-5 stones; each stone had 1-3 seeds and the loculi were tortuous in shape. It was an hotch-potch genus even when originally proposed and included some species as to whose correct affinities Nuttall was unsure (*X*. *cordifolia* and *X*. *glaucan*). The type species of the genus is *X. tomentosa*.

The fruit characters on which the original separation were based are not very significant ones. Both *A. uva-ursi* and *A. drupacea* have almost straight embryos and ovary loculi, yet they differ greatly in anatomy and indumentum. There is also no dividing line between tortuous and straight ovary loculi, in the number of loculi and the strength of their attachment in the mature drupe. *A. manzanita* has a strongly-ridged fruit which is very variable in the way that it breaks up: one fruit remained intact whilst another broke up very easily into five, one-seeded portions. The fruit of *A. numila* is variable in both the number of its loculi and in the way that it dissociates. The stone of *A. patula* is ridged, but cannot easily be separated into one-seeded portions, whilst in *X*. *glaucan* and *A. drupacea* the stone is smooth and very strong indeed.

*Xerobotrys tomentosa* is rather different from the other 16
species of *Arctostaphylos* whose floral anatomy has been studied in that the vascular supply to its calyx is better developed; in this respect it approaches *Comarostaphylis*. In view of the report that this species also has a papillate ovary wall, this observation should be treated with caution as it may be based on a misidentified specimen. *X. tomentosa* also has long-celled hairs which are otherwise rare in *Arctostaphylos*, but since there do not appear to be any differences, other than those mentioned, separating it from *Arctostaphylos* sensu stricto, it cannot be maintained, alone or in combination with other species, as a separate genus.

*Daphniodostaphylis* was separated from *Arctostaphylos* by Klotzsch for rather similar reasons to *Xerobotrya*, and it even included those two species which Nuttall had doubtfully assigned to the latter genus. The only feature distinguishing it from *Arctostaphylos* which can be gleaned from the original account is that *Daphniodostaphylis* has 6-10-locular ovaries. This character, as has been shown above, is of no use for segregating genera in the Arbutoideae.

In leaf anatomy *D. hookeri*, the first described species of the genus, has a Pieris-type midrib bundle, but at the very base of the lamina it is Lyonia type (see also *Schizococcus* sensitive). *D. pungens*, on the other hand, has an almost completely circular bundle without any break at all. Other species of *Arctostaphylos* have Pieris-type bundles, e.g. *A. uva-ursi*, and
although I have not found any other species with such a completely circular bundle as occurs in *A. duniens*, it is only a variation on the basic *Arctostaphylos* theme and is connected to the more normal types by intermediates (Fig. 59).

Schizococcus was proposed as a genus because its fruits split up, whilst still attached to the plant, into four (or five) one-seeded portions. The pericarp apparently is dry. This group of species has a rather distinct facies, but in this respect it is approached by species like *A. hookeri*. *S. nummularia* has long-celled hairs; these are an extreme development of the very long-stalked, small-headed hairs found in the other two species of this group studied (*S. sensitiva* and *S. nummularia*, Fig. 57). Florally this group is unremarkable except for often having 4-merous flowers, and for the rather less swollen filaments and the tendency for the corolla lobes to be serrulate in *S. sensitiva*. *S. nummularia* links it up with the more normal *Arctostaphylos* species in these last two respects. All three species placed in this genera have a *Pieris*-type midrib bundle (Fig. 59), although in *S. sensitiva* at least it is *Lyonia*-type at the very bottom of the petiole. Schizococcus, although not to be maintained as a genus, is probably to be given some form of taxonomic recognition. The exact level of the group awaits a monograph of the genus.

Notes on *A. drupacea*

*A. drupacea* is one of the most distinctive species of
Arctostaphylos that I have seen. Its bracts and bracteoles are not at all indurated but seem to be deciduous. Its corolla lobes are definitely serrulate (Fig. 60). Its fruit is 5-locular, smooth, and very strong, rather like that of A. glauca. Its hairs are very long and slender and give the plant a very characteristic appearance. Finally its midrib bundle is rather close to that of A. pungens and has a very prominent adaxial bundle (Fig. 59).

Notes on A. cratericola.

A. cratericola was originally described as a variety of A. pungens and then later raised to the rank of a separate species. Wells (1968) reduced it to a subspecies of A. uva-ursi. Anatomical studies support the general direction of this latest transfer, although perhaps not the rank. A. pungens has a prominent circular midrib bundle (Fig. 59); it also has stomata on both sides of the leaf. A. uva-ursi has Pieris-type midrib bundle and stomata only abaxially. Comparison of A. cratericola with a Mexican collection of A. pungens (Purpus 3250) specially selected to agree with it in leaf shape and size showed that Purpus 3250 agreed with A. pungens in the two characters mentioned above, and indeed was practically indistinguishable from it. A. cratericola, on the other hand, agreed with A. uva-ursi in midrib bundle type and stomatal distribution. However, it had some characters which neither of the other two species possessed:
1. Epidermal cells ca. 30μ deep (in the rest of the genus, including *A. uva-ursi* and *A. pungens*, ca. 12μ -15μ deep).

2. Epidermis of the mucilaginous type, with a wall periclinal bisecting the cells. This has not been seen in other species of *Arctostaphylos*, although, according to Starr (1912), the upper epidermal cells are sometimes periclinal divided in *A. uva-ursi*.

3. There are more prominent libriform fibres than in the specimens of *A. uva-ursi* seen; this difference will probably break down in more detailed studies.

4. Anther spurs are only ca. 300μ long (700μ in *A. uva-ursi*, ca. 1200μ in *A. pungens*).

Although clearly related to *A. uva-ursi*, more work is needed to ascertain the exact rank of *A. cratericola*. According to Wells (1968) there are also differences in pedicel indumentum and leaf shape separating it from *A. uva-ursi* sensu stricto.


Prostrate, deciduous shrubs with scattered, serrate leaves convolute in bud, venation prominently reticulate. Indumentum of long celled and unicellular hairs; small stalked glands on the perulae. Inflorescence terminal, five or fewer flowered, shortly racemose, perulate, bracts thin, bracteoles not seen; pedicel not articulate with the calyx. Flowers 5-merous. Calyx lobes small, free. Corolla urceolate, lobes small.
Stamens 10; filaments hairy or not, swollen at the base; anthers ovoid, with two very small, terminal, granulate spurs, dehiscing by a pair of short, apical, introrse slits. Ovary usually 5-locular, smooth; usually one ovule per loculus. Fruit "drupaceous", stone ridged, single-seeded portions tending to separate. Cells of the testa little elongated, tending to dissociate; embryo slightly curved, not spathulate.

3 - ¼ species in the genus, two of which were studied. The type species is *A. alpina*.

Arctoïs was raised to the generic rank (it had previously been a section of *Arctostaphylos*) because Niedenzu found several anatomical characters separating it from that genus. The druses in the petiole were arranged in a circle around the bundle, whilst elsewhere in the family they were irregularly arranged. This has been confirmed in both the species studied and seems to be a diagnostic character. Alone in the Arbutoideae it has a type 1 epidermis, although the cells over the veins are larger than those elsewhere and have straighter walls. The stomata in both species studied are orientated parallel to the long axis of the leaf. Arctoïs has a Pieris-type midrib bundle like some species of *Arctostaphylos* (Fig. 59); there do not seem to be any associated fibres. However, the thinness of the deciduous leaves is a good distinguishing feature from the more coriaceous evergreen leaves of the other Arbutoideae. It would seem that
this type of anatomy cannot be considered as "primitive" (see Howell, 1945), not least because in other characters Arctous seems to be derived.

The leaf margin hairs of A. alpina are long-celled; those of A. rubra are rather curious structures (Fig. 57). Glandular hairs have been found only on the perulae. The inflorescence is the most reduced in the subfamily, being a ca. 3-flowered raceme with a very short axis. The bracts are thin and the bracteoles are lacking, or at least fugaceous. The inflorescence is surrounded by prominent perulae. Watson (1965) did not find corolla stomata in A. alpina; neither species studied here has them. All species of Arctostaphylos have abaxial corolla stomata (Watson, 1965, missed them). The stamens of Arctous are distinctive (Fig. 60). A. alpina, the only species studied by Palser, had the same weak development of the vascular supply to the sepals as did Arctostaphylos, but there was a tendency, not entirely constant, for the lateral sepal trace to arise from the adjacent petal trace. There must also be two ovules per loculus in Arctous rubra, at least occasionally, since some loculi in the fruit have more than one seed. This parallels the condition found in Ornithostaphylis. The fruit and seed of Arctous are very like those of Arctostaphylos; the embryo is only slightly curved and is allantoid in shape.
5.5. THE VACCINIOIDEAE.

The generic limits of the Vaccinioideae with superior ovaries are dealt with in some detail, but in the Vaccinioideae detailed discussion is confined to genera occurring outside C. and S. America. The Vaccinioideae from these last areas are treated only in general terms.

5.5.1. DESCRIPTION AND CIRCUMSCRIPTION OF THE SUBFAMILY VACCINIOIDEAE

Shrubs or trees with leaves convolute or, rarely revolute in bud. Indumentum of long-stalked glands, long-celled hairs, clavate hairs or sometimes non-glandular scales. Inflorescence very variable, rarely terminal, sometimes perulate; bracts and 2—several bracteoles present, the latter variable in position, sometimes two connate at the apex of the pedicel; pedicel articulate with the calyx or not. Flowers 4—6—merous. Calyx lobes free or variously fused. Corolla gamo- or sometimes polypetalous, usually urceolate or tubular; walls sometimes carnose. Stamens 5—12, sometimes very dimorphic; filaments variable in shape and connation, with spurs or not; anthers ± smooth—very granular, appendages spurs, awns or anthers simply muticous or apiculate, often dehiscing via terminal tubules. Ovary superior to inferior, 3—10—locular, placentae apical or basal; style usually impressed in the apex of the ovary, slender or stout, stigma usually ± truncate. Fruit various, usually a loculicidal capsule and/or fleshy; usually
several seeds per loculus, rarely only one; cells of the testa
variable in shape and thickening.

Four tribes are recognised: - Cassiopeae, Enkiantheae,
Andromedeae and Vaccinieae.

**Delimitation of the subfamily.**

It is obvious from the description that the Vaccinioideae is
an heterogenous subfamily, but there are not sufficient
discontinuities to enable one to delimit other groups of a similar
rank. The Vaccinioideae as here recognised includes the
Vaccinioideae sensu Drude with all the Arbutoideae sensu Drude,
with the exception of the Arbuteae, which has already been dealt
with, and Mittsteinia, which is described in section 5.7.1.

The Vaccinoideae sensu Drude were separated from the rest
of the Ericaceae because they alone had an inferior ovary.
Hooker (1876) thought that they were separable at the family
level, and Wernham (1912a) toyed with the idea that they represented
an entirely different line of evolution from the Ericaceae.
However, as can be seen from Fig. 71, there are intermediate taxa
with half inferior ovaries. These are admittedly rare; *Gaultheria
hispidula* and *G. tetramer* are the only two examples of which I
know, although some species of Vaccinium have a small part of
their ovary which might be described as superior. The degree of
non-divergence of the floral traces, which is another measure of
the congestion of the floral axis and is very well developed in
many of the Vaccinieae, shows no clear cut difference between the two groups (see Bames, 1931; Palser, 1961b). Gaultheria, Diplycosia and Pernettyopsis all have fleshy fruits which connect up to those of the inferior-ovaried genera.

Most of the genera of the Vaccinieae have anthers dehiscing via terminal tubules, although in some genera the tubule is not well developed (Notoëora, some species of Vaccinium, etc.). Tepuia, Diplycosia and Pernettyopsis are three notable genera of the Andromedeae which similarly have terminal tubules; it may be significant that neither these genera nor the Vaccinieae seem to have the white deposit on the back of the anthers so common in many of the other genera of the Andromedeae. The spurs of the Vaccinieae appear to be homologous with similar structures in the Andromedeae.

The position is complicated by the considerable anatomical differences between some of the genera most similar to the Vaccinieae and the Vaccinieae in the area where they live together, i.e. S.E. Asia. There are no records of the Vaccinieae having other than paracytic stomata, and these are also found in all species of Diplycosia seen and, well developed, in Gaultheria and Leucothoë (as well as in Chamaedaphne and Oxydendrum). However, all these genera have pericyclic phellogen, whilst the species of Vaccinium in the same area have hypodermal phellogen and also lack the fibres which wander away from the vascular
bundles which are found to be especially numerous in *Diplycosia* and *Pernettyopsis*.

Thus the Vaccinieae are only tribally separable from the rest of the Vaccinioideae because of the overlap with the genera of the Gaultherieae sensu Drude. The only recent authors who have considered this group to be a tribe are Watson et al. (1967).

The Vaccinieae are a distinct entity, although some of the S. American members are, at first sight, very different from all other Ericaceae (see section 5.5.6.). More work is needed to establish the exact relationship of the Vaccinieae to the Andromedeae; chromatography of phenolics might be helpful in view of the distribution of methyl salicylate.

### 5.5.2. KEY TO THE VACCINIOIDEAE WITH SUPERIOR OVARI

1. Leaves <1 cm. long, abaxially grooved or needle-like; anthers with two spurs
   2. Leaves decussate
   3. Leaves scattered

2. Leaves >1 cm. long, never abaxially grooved; anther appendages various
3. Stamens with geniculate filaments or spurred anthers
   4. Corolla ± campanulate; seeds unilaterally winged
   6. *Craibiodendron*.

4. Corolla urceolate or + tubular; seeds not unilaterally winged

---

* *Cassiope*.
* *Harrimanella*.
5. Capsule with very prominent, thickened ribs  7. Lyonia.
5. Capsule ribs unthickened
6. Abaxial leaf venation very dense, all veins ± equally prominent; stamens without appendages
7. Placentae ± apical  
7. Placentae basal  
10. Agauria.
6. Abaxial leaf veins not all equally prominent; stamens spurred
8. Leaves in whorls of three  
11. Arcterica.
8. Leaves scattered or pseudoverticillate  
8. Pieris.
3. Stamens with ± straight filaments, anthers never spurred
9. Inflorescence terminal; anthers with a single pair of awns
10. Bracts and bracteoles deciduous; anthers dehiscing by long slits  
1. Enkianthus.
10. Bracts and bracteoles persistent; anthers dehiscing by terminal, short slits  
4. Andromeda.
9. Inflorescence rarely terminal; if so anthers not with a single pair of awns
11. Indumentum of scales  
12. Chamaedaphne.
11. Indumentum various, but never of scales
12. Inflorescence terminal, paniculate; cells of testa much elongated  
5. Oxydendrum.
12. Not as above
13. Anthers without appendages, dehiscing by terminal tubes; inflorescence always axillary

14. Leaves without marginal glandular spot; inflorescence fasciculate

15. Calyx lobes >8 mm.; ovary fleshy 17. *Pernettyopsis*.

15. Calyx lobes <7 mm.; ovary dry, calyx fleshy in fruit 18. *Diplycosia*.

13. Anthers usually with paired awns, if with terminal tubules then inflorescence terminal and leafy

16. Seeds unwinged; fruit usually fleshy; if not, then inflorescence racemose or paniculate 15. *Gaultheria*.

16. Not as above


17. Seeds usually winged; if not, then the surface of the leaf with multicellular hairs 14. *Leucothoe*.

5.5.3. **THE ENKIANTHEAE**

**ENKIANTHEAE Tribus Nova.**

Deciduous or subdeciduous shrubs; leaves pseudoverticillate, entire or serrulate, convolute in bud. Indumentum of long-celled, subglandular hairs and unicellular hairs.

Inflorescence terminal, perulate, corymbose or umbellate, rarely paniculate; bracts and bracteoles poorly developed; calyx not articulate with the pedicel. Flowers 5-merous. Calyx lobes
free, valvate (always?). Corolla urceolate to campanulate, lobes varying in size, rarely toothed. Stamens 10, strongly dimorphic; filaments swollen at the base, hairy or strongly papillate; anthers smooth or slightly granular with a pair of long, granular awns, dehiscing by a slit the length of the thecae, no dissolution tissue seen; pollen grains single. Ovary 5-locular, with an inconspicuous nectary at the base; placentae slightly bilobed, apical or basal; style impressed or not, slender, stigma truncate. Fruit a loculicidal capsule, the sutures ± thickened; seeds few-several, usually winged; cells of the testa ± hexagonal, rather tall.

There is only a single genus, *Enkianthus*, in this tribe. It is a remarkable genus in a number of respects; in general facies it looks rather like a *Menziesia*, especially *M. pilosa*, but in details of flower, fruit and embryology it is totally distinct. For a Latin description of the tribe, see appendix 1.

The reasons for separating it as a new tribe are as follows:-

1). It lacks a pericyclic sheath of fibres in the stem. There are sometimes a few lignified cells in this position, e.g. *E. quinqueflorus*, *E. subsessilis*, and in these species they may form a ± continuous ring of cells. In the peduncle the pericyclic sheath is much better developed. The endodermis in the stem is slightly lignified and interior to it develops a layer of cells
with hippocrepiform thickenings which seem to be associated with
the late development of the tanniferous phellogen. In the
leaf the lignification associated with the midrib and other
bundles is poorly developed.

2). The multicellular hairs (Fig. 62) have moderately
elongated cells some of which seem to be glandular, since the
terminal cells become necrotic earlier than the basal ones.

3). The terminal, perulate inflorescence with poorly developed
bracts and bracteoles is very unusual in the Vaccinioideae (Table 12).

4). The pedicels are not articulated with the calyx; all other
superior-ovariated Vaccinioideae are articulated.

5). The nectary is indistinct.

6). The anthers with paired, rather reflexed awns (Fig. 62)
are unique in the Ericaceae. They invert very late in the bud.
According to Safijowska (1960) there is a well-developed
endothecium in the three species which he studied (E. perulatus,
E. cernuus and E. campanulatus).

7). The pollen grains are single in all the species examined.
It is the largest genus in the family in which this character is
constant.

8). It is very distinct in other details of floral anatomy
and embryology (data are taken from Palser, 1951, 1952 & 1961a).
The ventral carpellary bundles arise in the septal position, like
Epigaea and Chamaedaphne. In the mature ovule the endothelium
<table>
<thead>
<tr>
<th>Character</th>
<th>Enkianthaceae</th>
<th>Cassiopeae</th>
<th>Lyonia group</th>
<th>Gaultheria group</th>
<th>the rest</th>
<th>Vaccinieae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves channeled or needle like</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Inflorescence a single flower</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>- (rare +)</td>
</tr>
<tr>
<td>Terminal inflorescence</td>
<td>+</td>
<td>- , +</td>
<td>- , (+)</td>
<td>- , (+)</td>
<td>+ , -</td>
<td>- , (+)</td>
</tr>
<tr>
<td>Anthers spurred</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>- , +</td>
</tr>
<tr>
<td>Anthers awned</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+ , -</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Anther slits entire length</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Filaments geniculate</td>
<td>-</td>
<td>-</td>
<td>+ , (-)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pollen grains single</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>- (only one +)</td>
</tr>
<tr>
<td>Polygonum-type embryo sac</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Gvary inferior</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Gland-headed hairs</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Leaf hypodermis</td>
<td>-</td>
<td>-</td>
<td>- , (+)</td>
<td>- , +</td>
<td>- , -</td>
<td>+ , -</td>
</tr>
</tbody>
</table>

**Table 12** Variation of some characters in the Vaccinioideae
is very prominent and the megagametophyte is perched on a "pedestal" of nucellar tissue. The embryo sac itself has ear-like projections. These characters have been found in all three species which have been studied (E. campanulatus, E. cernuus and E. perulatus); the nucellar pedestal is restricted to Enkianthus and the other characters are of very restricted occurrence in the family.

1. **Enkianthus** Loureiro, Fl. Coch. 1: 339 (1793).

   The genus has the characters of the tribe. There are about 10 species in the genus; 9, + 1 unidentified collection, have been studied. The type species is *E. quinqueflorus*.

**Nomenclature.**

*Melidora* was proposed as an alternative name by Salisbury simply because he did not like the name Enkianthus. *Tritomodon* seems to be a synonym of *Meisteria*: *Meisteria* itself was proposed without reference to *Enkianthus*, and refers to *M. cernuus*. This species has trifid corolla lobes (Fig. 6), but this seems to be the extent of the differences between it and the rest of the genus. These trifid lobes are the deepest indentations to be found in the corolla of any Ericaceae, but in the absence of any
supporting characters the genus cannot be maintained.

Bodinierella was segregated from Enkianthus on unspecified differences of the fruit and bract, although the corymbose inflorescence was recognised to be similar. Léveillé thought that Bodinierella was similar to Pieris. The type specimens of the only species of Bodinierella, B. cavaleriei, have been seen and they are undoubtedly members of Enkianthus. Rehder (1934) thought that B. cavaleriei was a synonym of E. chinensis.

Infrageneric variation.

"The eastern Asiatic genus Enkianthus presents four types of structure which almost indicate as many genera, and would do so if the species had not been united by habit, and if the characters were associated, instead of applying each to one species only" (Hooker, 1879). This impression has been reinforced by the present studies; Enkianthus, although a small genus and showing considerable variation, nevertheless holds together because of a basic similarity of habit, inflorescence and stamen, and because the variations are not highly correlated and are to some extent linked by intermediates (see Table 13).

The corolla may be urceolate to campanulate, with lobes 1/6-½ its length (Figs. 4, 6 & 62). The flowers may be pendulous or erect, but if they are the former they become erect in fruit and the capsule dehisces normally (c.f. Ledum). All species have their capsule sutures ± thickened, and this is particularly
<table>
<thead>
<tr>
<th>Character</th>
<th>Campanulatus</th>
<th>Serrulatus</th>
<th>Quinqueflorus</th>
<th>Subsessilis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf margin</td>
<td>serrulate</td>
<td>serrulate</td>
<td>entire</td>
<td>serrulate</td>
</tr>
<tr>
<td>Leaves deciduous</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Inflorescence type</td>
<td>Corymbose-umbellate</td>
<td>umbellate</td>
<td>umbellate</td>
<td>Corymbose</td>
</tr>
<tr>
<td>Flowers pendulous</td>
<td>+ (- perulatus)</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Corolla shape</td>
<td>urceolate-campanulate</td>
<td>+ campanulate</td>
<td>+ campanulate</td>
<td>+ urceolate</td>
</tr>
<tr>
<td>Corolla lobes trifid</td>
<td>- (+ E. cernus)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Style impressed</td>
<td>+ (- E. perulatus)</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Placentae apical</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Capsule sutures thickened</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Seeds winged</td>
<td>+ (fringed)</td>
<td>+ (entire)</td>
<td>+ (entire)</td>
<td>-</td>
</tr>
<tr>
<td>Stomatal type</td>
<td>anomocytic</td>
<td>+ paracytic</td>
<td>paracytic</td>
<td>anomocytic</td>
</tr>
<tr>
<td>Leaf margin lignification</td>
<td>slight, hypodermal</td>
<td>slight, hypodermal</td>
<td>slight, hypodermal</td>
<td>-</td>
</tr>
<tr>
<td>Midrib bundle type</td>
<td>Pieris</td>
<td>tending to Oxydendrum</td>
<td>sub-Oxydendrum</td>
<td>Pieris</td>
</tr>
<tr>
<td>Pith type</td>
<td>heterogenous</td>
<td>+ heterogenous</td>
<td>homogenous</td>
<td>heterogenous/ Calluna</td>
</tr>
<tr>
<td>Pericyclic lignification</td>
<td>slight</td>
<td>slight</td>
<td>moderate</td>
<td>-</td>
</tr>
</tbody>
</table>

**Table 15: The Variation of Some Characters Within Exanthrus**
FIG. 62: ENKIANTHEAE.

well-developed in *E. quinqueflorus* and *E. serrulatus* (Fig. 62). Both these species have entire wings to their seeds, but this is merely an extreme development of the fimbriate wings of the other species. *E. subsessilis*, alone amongst the species studied, has basal placentae and ovoid, practically unwinged seeds, although the structure of the testa is otherwise unremarkable (Fig. 62). This species is otherwise rather similar to *E. campanulatus*, etc. Petrosilot (1904b) figures *E. nikoensis* (= *E. subsessilis*) as having thin-walled cells persisting beneath the testa in the mature seed. This was not so noticeable in the material which I examined, but was very well developed in other species (Fig. 15).

*E. quinqueflorus* is the only species in the genus with paracytic stomata (Fig. 26), a moderately well developed *Oxydendrum*-type midrib bundle and lignification of the leaf margin; in all these respects *E. serrulatus* is intermediate (Fig. 62). This distinctive anatomy may be connected with the fact that *E. quinqueflorus* is the only evergreen species in the genus (albeit only weakly so). *E. serrulatus* has almost homogenous pith, in *E. subsessilis* it is almost *Calluna*-type.

5.5.4. THE CASSIOPEAE.

Characters and relationships of the tribe.

CASSIOPEAE Tribus Nova.

Small, prostrate or erect evergreen shrublets with decussate or scattered needle-like or grooved leaves. Indumentum of uniseriate glandular and branched hairs, or only unicellular hairs. Inflorescence single-flowered, axillary or terminal, if the former then 4-6 basal bracteoles; calyx and pedicel articulate. Flowers 5-merous. Calyx lobes free. Corolla campanulate, 2/3-1/3 lobed. Stamens 10; filaments straight, anther filament attachment near the top of the anther, whence arise paired spurs; anthers slightly granular, dehiscing by wide, terminal slits. Ovary 5-locular, placentae + apical; style impressed, slender or swollen. Fruit a rather thin walled loculicidal capsule; seeds small, ovoid; cells of the testa thin-walled and moderately elongated.

There are two genera, Cassiope and Harrimanella.

Cox's Cassiopeae was a wholly unnatural assemblage of genera here considered to belong to four different tribes from two subfamilies (Rhododendroideae-Epigaeae; Vaccinioideae-Enkiantheae, Cassiopeae and Andromedeae).

Cassiope and Harrimanella are considered to be tribally distinct from the other Vaccinioideae even though Harrimanella, with its scattered leaves, bast fibres in the leaf and homogenous pith, to some extent forms a bridge with the Andromedeae. For a Latin description of the tribe, see Appendix I.

The inflorescence of both genera is unusual, and needs more study. That of Cassiope is a single flower with 4-6 basal
bracteoles produced in the axils of the leaf the year before anthesis. That of Harrimanella is apparently truly terminal, without bracteoles and produced the year of anthesis. Neither is found in any other Vaccinioideae. Cassiope has adaxial calyx stomata, but stomata are not found elsewhere on the calyx and corolla. In this it approaches the Rhododendroideae; however, Harrimanella lacks floral stomata entirely. Their stamens have a pair of spurs at the anther-filament junction (Fig. 63) and invert rather late; they are not very dissimilar to those of Andromeda (c.f. Fig. 64). In fruit they are unremarkable. Cassiope has branched hairs at least superficially like the branched hairs of certain species of Rhododendron (Figs. 17, 20 & 63) and without parallel in the Vaccinioideae. The uniseriate glandular hairs (Fig. 17) are also not known from other Vaccinioideae, although it seems that the heads of the glandular hairs of C. redowskii may not be uniseriate and thus more like the heads of the hairs of the Andromedeae.

Anatomically they differ from most of the Vaccinioideae in that they lack a pericyclic sheath of fibres in the stem, but in this they are approached by other Ericaceae with a similar habit. Although Cassiope has Calluna-type pith and no bast fibres in the leaf, Harrimanella has a more ordinary anatomy in that it has bast fibres and an homogenous pith.

Cassiope mertensiana, C. lycopodioides and C. tetragona, and
possibly *Harrimanella hypnoides* (see Palser 1951, 1952 & 1961a) have an *Allium*-type embryo sac. This is unknown in other Ericaceae (including *Calluna*). The small ovules have a very poorly developed endothelium. The vascular supply to the sepal is reduced to a single trace per sepal, and there is usually a considerable amount of non-divergence of the traces to the other floral organs. Palser (1952) thought that the two genera were closely related and showed little similarity to other members of the Andromedae sensu Drude, with the partial exception of *Andromeda*.

Many of these floral, anatomical and embryological characters seem to be derived ones in agreement with the habit of the plant. The problem of *Calluna*.

Both Nordhagen (1937 & 1938) and Beijerinck (1940) carried out detailed investigations on *Calluna* and came to the conclusion that it was a very distinct genus within the Ericoideae, to which it nevertheless belonged. They emphasised the following characters 1), the large number of bracts (or bracteoles) 2), the coloured calyx and the way that the flower opened 3), the septifragal capsule and the way in which the seeds were dispersed and 4), the chromosome number. Nordhagen (1938) put *Calluna* in a monotypic tribe, the Calluneae, in the Ericoideae.

Hagerup (1953), emphasising the similarity in vegetative form (shape and arrangement of the leaves, growth rhythm),
considered that Calluna and Cassiope were very close in these respects. The similarity is not perhaps so striking as he thought, since although both genera have apparently similar leaves, those of Calluna are tailed and those of Cassiope are auriculate. Also the single, axillary flowers are initiated the year before anthesis in Cassiope and the same year as anthesis in Calluna. Thus the similarity in growth rhythm is not as great as between the Empetraceae and some of the Ericoideae. Watson (1964) found that Calluna and Cassiope both had a Calluna-type pith and had anomocytic stomata on both sides of the leaves. He also emphasised their decussate phyllotaxy, although this is also to be found in some species of Kalmia; Harrimanella has spirally-arranged leaves and homogenous pith. Watson (1964) suggests that Calluna and Cassiope may not be very different in capsule type, but in fact they are very different (Fig. 63). I have not seen the semi-septicidal dehiscence which Don (1834) says occurs in Cassiope. Watson treats the very great differences in the flower of Calluna and Cassiope very superficially; neither he nor Hagerup refers to Harrimanella.

Calluna, Cassiope and Harrimanella are compared with one another and the Ericoideae and the Andromedeae in Table 14. It can be seen that the anatomical and gross vegetative similarities between Calluna and Cassiope are very remarkable, but those between Calluna and Harrimanella are not so great. None of the genera
<table>
<thead>
<tr>
<th>Trait</th>
<th>Andromedeae</th>
<th>Harrimanella</th>
<th>Cassiope</th>
<th>Calluna</th>
<th>Ericoideae</th>
</tr>
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<tr>
<td>Leaf type</td>
<td>flat</td>
<td>needle</td>
<td>channelled and auriculate</td>
<td>tailed, channelled, needle</td>
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</tr>
<tr>
<td>Leaves petiolate</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Leaves decussate</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Indumentum</td>
<td>long-celled</td>
<td>gland-headed</td>
<td>branched uniseriate</td>
<td>gland-headed</td>
<td>long-celled, gland-headed</td>
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<td>axillary</td>
<td>variable</td>
</tr>
<tr>
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<td>one</td>
<td>one</td>
<td>variable</td>
</tr>
<tr>
<td>Bracteoles</td>
<td>(several -) 2(-0)</td>
<td>0</td>
<td>4 - 6</td>
<td>4+</td>
<td>2</td>
</tr>
<tr>
<td>5-merous flowers</td>
<td>+ (-)</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>- (+)</td>
</tr>
<tr>
<td>Calyx coloured</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>- (+)</td>
</tr>
<tr>
<td>Corolla shape</td>
<td>usually urceolate</td>
<td>campanulate</td>
<td>campanulate</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Calyx stomata</td>
<td>(+ +) - + (- -)</td>
<td>-</td>
<td>+ -</td>
<td>-</td>
<td>- + (- -)</td>
</tr>
<tr>
<td>Corolla stomata</td>
<td>- + (- -)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Stamen appendage type</td>
<td>terete or -</td>
<td>terete</td>
<td>terete</td>
<td>flattened</td>
<td>flattened or -</td>
</tr>
<tr>
<td>Fruit type</td>
<td>loculicidal, or indehiscent</td>
<td>loculicidal</td>
<td>loculicidal</td>
<td>septifragal</td>
<td>usu. loculicidal</td>
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<tr>
<td>Thick testa walls</td>
<td>+ or -</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+ (always?)</td>
</tr>
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</table>

**TABLE 14A** COMPARISON OF THE CASSIOPEAE WITH THE ERICOIDEAE AND ANDROMEDEAE
<table>
<thead>
<tr>
<th></th>
<th>Andromedeae</th>
<th>Harrimanella</th>
<th>Cassiope</th>
<th>Calluna</th>
<th>Ericoideae</th>
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<tr>
<td>Leaf epidermis type</td>
<td>1-2</td>
<td>2</td>
<td>1-2</td>
<td>2</td>
<td>1-2</td>
</tr>
<tr>
<td>Stomatal distribution</td>
<td>- + ( )</td>
<td>++</td>
<td>+ +, + -</td>
<td>+ +</td>
<td>- +</td>
</tr>
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<td>Stomatal orientation</td>
<td>parallel or</td>
<td>parallel</td>
<td>transverse</td>
<td>transverse</td>
<td>transverse</td>
</tr>
<tr>
<td>&quot;Mucilaginous&quot;/epidermis</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+ or -</td>
</tr>
<tr>
<td>Bast tissue</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Libriform tissue</td>
<td>+ usually</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+, -</td>
</tr>
<tr>
<td>Petiole bundle lignification</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+ (flanges)</td>
</tr>
<tr>
<td>Pith</td>
<td>various</td>
<td>homogenous</td>
<td>Calluna</td>
<td>Calluna</td>
<td>homogenous</td>
</tr>
<tr>
<td>Pericyclic fibres</td>
<td>+ (usually)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

**Table 14B** Comparison of the Cassiopeaceae with the Ericoideae and Andromedeae
is quite as close to the Ericoideae in these characters as is Ledothamnus, Daboecia or, for that matter, the Empetraceae. A character rather ignored by the earlier workers is the "mucilaginous" nature of the epidermis in Calluna (but see Vesque, 1885). This is not found in the Vaccinioideae (see Lyonia), but is very common in the Ericoideae. None of the three genera has the lignified flange of tissue in the petiole like the Ericoideae, and their stomatal orientation is intermediate between the parallel and the transverse condition. (Harrimanella has its stomata orientated parallel to the leaf.) The transverse stomatal orientation in Cassiope is far more obvious than in Calluna; perhaps this is due to the more prominent abaxial stomatal channel of the former genus.

Both Calluna and Cassiope have uniseriate gland-headed hairs (Fig. 17). I do not know if they are to be found in the Ericoideae; they are certainly an unusual hair type for the Ericaceae. Harrimanella seems to lack multicellular hairs altogether.

In flower Calluna is very like a member of the Ericoideae and quite different to Cassiope and Harrimanella (Fig. 63). Several Ericoideae have a calyx which approaches the corolla in size and colour, e.g. Erica terminalis, Macnabia montana. Abaxial calyx stomata are lacking in Pentapera (= Erica) bocquetii and E. carnea, so the calyx stomatal distribution of Calluna (and
FIG. 63: CALLUNA AND THE CASSIOPEAE (1).

13. Cassiope redowskii - leaf margin hair; 14. C. mertensiana, x10 - capsule (s = septum).
Harrimanella) agrees with that of some of the Ericoideae. The stamens of Calluna, with their flattened appendages, are far more similar to those of the Ericoideae than to those of Cassiope (c.f. Figs. 8 & 63). In this respect, as in other details of the flower, Harrimanella agrees almost perfectly with Cassiope. The persistent corolla of Calluna is of course general within the Ericoideae. Embryologically Calluna is quite different from the Cassiopeae.

The seeds of Calluna have a single-layered testa whose cells are not elongated and have thick walls (Fig. 64). There are large plasmodesmata in the anticlinal walls (see also Petrosilot, 1904b). The testa cells of Cassiope and Harrimanella are rather elongated and have thin walls. At least some of the Ericoideae-Ericaceae have thick-walled testa cells, but knowledge of the testa structure in the whole subfamily is very poor. At present the structure of the testa of Calluna seems more similar to that of the Ericaceae than to the Cassiopeae.

The problem seems to be best resolved by retaining Calluna in the Ericoideae and recognising it as a tribe, the Callunaeae. It certainly shows greater differences in a number of respects from the entire subfamily than the two generally recognised tribes, the Ericaceae and Salaxideae, do from one another. Study of the wood anatomy may throw more light on the question; the vessels of Calluna are much larger than those of the Cassiopeae.
Phloem lignification in Calluna is late in development and does not seem to be the same as that in the other species of the Ericoideae seen, but knowledge on this point is still fragmentary.

The genera of the Cassiopeae.


Prostrate to erect evergreen shrublets with decussate leaves, leaves acicular, tubular, or channelled abaxially and with prominent auricles. Indumentum of branched hairs at the leaf margin and on the pedicel, uniseriate glandular hairs and unicellular hairs. Inflorescence of single axillary flowers on the previous year's growth; bract apparently the leaf, 4 to 6 flat, basal bracteoles; pedicel articulate with the calyx.

Flowers 5-merous. Calyx lobes medium-sized, free, aestivation usually quincuncial. Corolla campanulate, 1/3 lobed. Stamens 10; filaments hairy or not, slender, attached to the top of the anther, whence arise paired, granular spurs; anthers dehiscing by terminal pores, white deposit on the back of the anthers.

Ovary 5-locular, placentae slightly bilobed, subapical, nectary at the base of the ovary; style impressed, slender, stigma truncate. Capsule rather fragile, loculicidal; seeds small, ovoid; cells of the testa thin walled and moderately elongated.

There are about 12 species in the genus, of which 8 have been studied. The type species is C. tetragona.

It may be mentioned here that it is really inapplicable to
FIG. 64: CALLUNA & THE CASSIOPEAE (2); ANDROMEDA.

1. Cassiope tetragona, x1 - shoot; 2. Harrimanella stelleriana, x2 - shoot;
speak of the venation of the leaf in bud in the Cassiopeae, even in those species with needle leaves, see p. 20. Hara (1958) records *C. lycopodioides* as having leaves convolute in bud, as does *Harrimanella stelleriana*. *C. mertensiana* also seems to have leaves convolute in bud.

There are a number of differences between *Cassiope* and *Harrimanella*; although the latter genus was not separated from it until 1901. The main differences are:

1. Leaves decussate (*Cassiope*) - Leaves spirally arranged (*Harrimanella*).
2. Leaves never petiolate - leaves petiolate.
3. Multicellular hairs always present - not seen.
4. Pith Calluna-type - pith homogenous.
5. No bast fibres associated with the midrib bundle - bast fibres present (Fig. 63).
6. Flowers axillary, with 4 to 6 basal bracteoles - flowers apparently terminal, without bracteoles (Fig. 64).
7. Adaxial calyx stomata present - these stomata lacking.
8. Corolla 1/3 lobed - corolla 1/3 lobed (c.f. Figs. 9 & 63).
9. Stigma slender - stigma short and stout (Fig. 9).

Palser (1951 & 1952) thought that *H. hypnoides* would be better placed in *Cassiope* on embryological and floral anatomical grounds. However, she noticed that both this species and
*H. stelleriana* had no apical placental lobe; this is due to the difference in placental position (see description). Palser found that *C. mertensiana*, *C. tetragona* and *C. lycopodiodes* had essentially undiverged traces to the floral organs whilst in *H. stelleriana* they were independant; in this respect and in corolla lobing *H. hypnoides* was intermediate between *Harrimanella* sensu restricto and *Cassiope*. *H. stelleriana* also had very extensive nectariferous tissue extending up the side of the ovary. The species of *Cassiope* examined have a white deposit formed by dissolution tissue, at the base of the spurs. This is lacking in both species of *Harrimanella* (see also Palser, 1951), and in all the other characters listed above *H. hypnoides* agrees with *H. stelleriana*, so the two should be included in the same genus.

Niedenzu (1890) noticed that both the species now assigned to *Harrimanella* had bast fibres associated with their leaf midrib bundle. However, he erroneously thought that the leaf midrib bundle of *C. lycopodiodes* and *C. mertensiana* consisted of xylem surrounded by phloem (see his Taf. 3, fig. 4). All the species of *Cassiope* studied have *Pieris*-bundles without associated fibres, but with a prominent endodermis (Fig. 63). Also he figures *C. fastigiata* (his Taf. 3, Fig. 6) as having uniseriate glandular hairs looking like a string of sausages on a stalk. Although they are uniseriate, they are similar to the ones illustrated in Fig. 17.

Sub-erect or procumbent evergreen shrublets with congested, spirally arranged, acicular leaves. Indumentum of unicellular hairs. Inflorescence a single, terminal flower; bracts and bracteoles not seen; pedicel articulate with the calyx. Flowers 5-merous. Calyx lobes medium-sized, free, aestivation quincuncial. Corolla campanulate, 2/3-½ lobed. Stamens 10; filaments glabrous, rather slender, attached to the top of the anther whence arise paired, granular spurs; anthers slightly granular, dehiscing by terminal pores, no white deposit on the back of the anther. Ovary 5-locular, placentae apical, nectar lobes very extensive or restricted to the base of the ovary; style slightly impressed, very stout, stigma truncate. Capsule loculicidal; seeds small, ovoid; cells of the testa moderately elongated, thin walled.

There are two species in this genus, both of which have been studied. The type species is *H. stelleriana*.

5.5.5. THE ANDROMEDAEE.

**ANDROMEDAEE** DC., Prodromus 7 (2): 588 (1839), *pro parte*.


Usually evergreen shrubs with entire or serrate leaves which are convolute or rarely revolute in bud. Indumentum of stalked glandular or long-celled hairs, also unicellular hairs. Inflorescence usually axillary, rarely terminal, paniculate,
racemose or fasciculate; bracts present, bracteoles usually paired and apical or basal, calyx articulate with the pedicel. Flowers (4-)5(-6)-merous. Calyx lobes usually small and free. Corolla usually urceolate, lobes small. Stamens usually 10; filaments straight or geniculate, with paired spurs or not; anthers slightly granular, with 2 to 4 awns or not, dorsally often a white deposit of dissolution tissue, sometimes a pair of terminal tubules. Ovary 5-locular, placentae variable in position, not strongly bilobed; style impressed, stigma truncate. Fruit a loculicidal capsule or berry, capsule sometimes surrounded by an acrescent calyx. Seeds very variable.

The Andromedeae is still a rather heterogenous group, even after the removal of the Enkiantheae and the Cassiopeae. It includes the Gaultherieae of Niedenzu (1890) and later authors, because the limits of this tribe are very arbitrary and there is no clear cut distinction between it and the rest of the Andromedeae sensu restricto. Niedenzu (1890) proposed the Gaultherieae as a tribe because he thought that the genera in it (Gaultheria, Diplycosia, Pernettya, Chionogetes) were separable anatomically from the other Andromedeae; they also have a fleshy fruit. Niedenzu thought that the Gaultherieae were characterisable by the frequent occurrence of "spicular cells" (= fibres wandering through the mesophyll), the presence of
sub-paracytic stomata and a difference in indumentum.

As regards the presence of fibres, they are not present in by any means all species of the Gaultheria aggregate and are also found in some species of Pieris and Craibiodendron although they are most common in the genera placed in the Gaultheria group (see below). Paracytic stomata are found in Chamaedaphne, Oxydendrum and Leucothoë; this last genus Niedenzu noted was similar in this respect to the Gaultherieae. There is no clear-cut difference in indumentum. Some species of Gaultheria have dry fruit similar in most respects to that of Zenobia and Leucothoë; these two genera also have the same anther awns as are to be found in Gaultheria. Diplycosia, with its numerous leaf fibres, paracytic stomata and anthers with paired, terminal tubules merely represents one extreme of the Andromedeae since it is connected to other members of the tribe by intermediates.

The following genera are recognised in the Andromedeae:-
Isolated - Andromeda and Oxydendrum.
Lyonia-group - Craibiodendron, Lyonia, Pieris, Azauria, Agarista, Arcterica.
Rather isolated - Chamaedaphne.
Gaultheria-group - Zenobia, Leucothoë, Gaultheria, Pernettyopsis, Tepuia, Diplycosia.

Evergreen shrubs with alternate, entire leaves revolute in bud. Multicellular hairs lacking, but a pair of marginal glands near the base of the lamina and unicellular hairs on the abaxial surface of the leaf. Inflorescence terminal, eperulate, + corymbose; bracts leafy, bracteoles paired, basal, small and persistent; calyx poorly articulate with the pedicel. Flowers 5-merous. Calyx lobes small, imbricate. Corolla urceolate, lobes small. Stamens 10; filaments gradually swollen towards the base, hairy, attached to the midpoint of the anther; anther slightly granular, dehiscing by a terminal short slit, with a pair of almost smooth awns, no white deposit seen. Ovary 5-locular; sub-apical placentae with few ovules and slightly bilobed. Fruit a loculidical capsule; seeds rather large, few, ovoid; cells of the testa not elongated, thick-walled, testa multi-layered.

There is a single species in the genus, *A. dolifolia*. It has been examined.

This is an interesting genus immediately recognisable by its small, terminal, drooping inflorescence (Fig. 64) and scattered leaves without any multicellular hairs. (see Table 15).

The lack of multicellular hairs was the main reason why Niedenzu (1890) did not place the genus. The paired marginal glands near the base of the lamina are similar to those of *Vaccinium, Gaultheria*, etc., but these are almost certainly of
independant polyphyletic derivation. The adaxial epidermis tends to be lignified, although this lignification may be restricted to the leaf margins. In this *Andromeda* agrees with the *Lyonia* group, but there is no close relationship to any group anatomically (Fig. 64).

In general facies *Andromeda* approaches some species of *Kalmia*, but differs both in anatomy and in most details of flower and fruit. This apparent similarity may have been responsible for the inclusion of *Andromeda* in the Rhododendroideae - Phyllodoceae by Watson (in Airy-Shaw, 1966); later (Watson et al., 1967) it was restored to the Vaccinioideae.

In several details of flower and fruit this is a deviant genus, and has similarities to other groups. The terminal inflorescence with a poorly-articulated pedicel is very rare in the Vaccinioideae, although common in the Arbutoideae and the Rhododendroideae. The entire absence of floral stomata is known only from the Vaccineae and Cassiopeae in the Vaccinioideae, and although its stamens are rather similar to those of the Cassiopeae they differ both in the point of attachment of the anther to the filament and in the type of appendage.

In floral anatomy Palser (1951) found that there was only a single trace to each sepal lobe, and that the rest of the floral vasculature showed a considerable degree of non-divergence. In these respects it was similar to *Cassiopea* although in details of
<table>
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<th>Andromeda</th>
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<th>Chamaedaphne</th>
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</thead>
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<td>-</td>
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<td>- +</td>
<td>- +</td>
</tr>
<tr>
<td>Corolla stomata</td>
<td>- -</td>
<td>- +</td>
<td>- - (- + once)</td>
</tr>
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<td>Anthers spurred/tubules</td>
<td>+/-</td>
<td>+/-</td>
<td>+/-</td>
</tr>
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</tr>
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<td>-</td>
<td>+</td>
<td>partially</td>
</tr>
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<td>1 - 2!</td>
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<td>1</td>
</tr>
<tr>
<td>Cuticle</td>
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<tr>
<td>Midrib bundle type</td>
<td>Pieris</td>
<td>Oxydendrum</td>
<td>Pieris</td>
</tr>
<tr>
<td>Bundle transcurrent</td>
<td>+</td>
<td>+</td>
<td>+, lignification of girder</td>
</tr>
<tr>
<td>Pith</td>
<td>heterogenous</td>
<td>Calluna</td>
<td>homogenous</td>
</tr>
<tr>
<td>Cortex</td>
<td>heterogenous</td>
<td>heterogenous</td>
<td>homogenous</td>
</tr>
<tr>
<td>Phloem lignification</td>
<td>-</td>
<td>-</td>
<td>hippocrepiform</td>
</tr>
</tbody>
</table>

**TABLE 15** VARIATION IN THE ISOLATED GENERA OF THE ANDROGEEAE
the megagametophyte and in embryology it was quite distinct (Palser, 1952). The embryo sac was of the normal Polygonum type and was very much elongated when mature. The few, large ovules were campylotropous and the integument was very thick (ca. 8-10 cell layers thick). On cutting a T. S. of the seed, the structure figured by Petrosilot (1904b) was confirmed. The testa is several layers thick all round, and not just over the raphe. The cells of the inner layers have very thick walls, just like the outer layer; in this it differs from all other species in the Ericaceae which have a multi-layered testa (Fig. 14).

Andromeda is thus a very distinct genus with no close affinities to other genera.

5. **OXYDENDRUM** DC. Prodr. 7 (2): 601 (1839).

Deciduous tree with large, prominently serrate leaves. Indumentum of long-celled multicellular and unicellular hairs. Inflorescence terminating the year's growth, paniculate, many-flowered; bracts small, deciduous, bracteoles ± deciduous, ¼ - 2/3 up the pedicel; pedicel articulate with the calyx. Flower 5-merous. Calyx lobes small, valvate. Corolla urceolate, covered by dense, white, unicellular hairs; lobes small. Stamens 10, without appendages; filaments rather stout, straight, densely hairy; anthers slightly granulate with a white deposit dorsally, tubes ca. ½ the length of the anther, dehiscing by a long introrse slit. Ovary 5-locular, with slightly bifid, basal
placentae; style very deeply impressed, stigma truncate.
Capsule elongated, loculicidal, many seeded; seeds ±
spindle-shaped; cells of the testa very long, cell walls
moderately thickened (ca. 7.5μ thick).

The only species in the genus, *O. arboreum*, has been studied.

Anatomically *Oxydendrum* may be distinguished from all other
genera of the Vaccinioideae by its combination of *Oxydendrum*-type
midrib bundle (Fig. 29) and *Calluna*-type pith. Niedenzu (1890)
noted that the midrib bundle was very prominent; since he did not
observe the difference in structure he compared it to the Arboriteae
sensu Drude, although he did not reach a decision as to the
affinities of the plant. Cox (1948b) found that *Oxydendrum*
differed from all the other Arbutoideae (sensu Drude) which he
studied in the type of medullary ray and the high percentage of
porous vessel perforations in the xylem. He thought that
*Oxydendrum* should be put into a monogeneric tribe, the Oxydendreae.

Palser (1951) found that *Oxydendrum* was the only genus in
the Andromedeae sensu Drude with a tapered floral receptacle with
the traces to all the floral organs totally distinct (Fig. 32).
However, in megagametogenesis it was unremarkable (Palser, 1952).
I was unable to see the two apical awns which Palser described as
occurring on each anther; it is possible that she was referring
to the bifidly-apiculate appearance of the anther caused by the
process of dehiscence, rather than definite appendages.
FIG. 65: ANDROMEDAEA - OXYDENDRUM AND THE LYONIA GROUP.

The terminal paniculate inflorescence of *Oxydendrum* fruiting in the same year as it is initiated, although not unique in the Ericaceae (c.f. Lems, 1962), is unique in the Vaccinioideae; terminal inflorescences with a longer period of development are more common. The dense unicellular hairs covering the flowers give them a distinctive look; the stamens too are distinctive (Fig. 65). Its long, loculicidally dehiscent capsule with basal placentae (Fig. 65) is approached elsewhere only by *Azauria*, but this differs both in capsule shape and in the thickening of the elongated cells of the testa.

Although it is not thought that tribal separation of this genus is desirable, it is clear that *Oxydendrum* is a very isolated genus. In its paracytic leaf stomata, long-celled hairs, bracteoles and perhaps also in its stamens, whose long tubes parallel those of *Diplycosia*, *Oxydendrum* is similar to the *Gaultheria* group of genera. Its fruit characters are perhaps more similar to the *Lyonia* group, whilst yet other characters (floral and vegetative anatomy) are restricted to it alone in the Andromedeae.

The *Lyonia* group of genera.

This group of genera is characterised by having stamens with slender, prominently geniculate filaments and short anthers with a white deposit (dissolution tissue) at the anther filament junction. Appendages, if any, are spurs on the filament or at
the anther-filament junction. The style is often swollen. The cells of the testa are usually very long and not very thick walled. Foliar stomata are anomocytic and epidermal lignification is very common. There are bands of fibres in the phloem. The variation of characters in this group is summarised in Tables 16 and 17.

Hooker (1876) had a fairly good idea of this group. Agauria, Agarista and Lyonia were placed together since they had dorsally muticous anthers and, supposedly, valvate sepal aestivation in common. Hooker also noticed a connection to the genus Pieris, but since he had over-weighted the presence of appendages on the stamen he placed Pieris with Zenobia, Andromeda and Enkianthus. All of these genera had dorsally aristate stamens, the aristae being on the anther or the filament. However, as Matthews and Knox (1928) showed, there is a gradual transition in the position of the appendages from the filament to the anther, loss of appendages occurring independently several times. The biggest gap is between the terminal awns and the spurs on the filament or at the anther-filament junction; it is the latter condition which occurs in the Lyonia group, the former in the Gaultheria group. Even if the awns and apiculae of Gaultheria are found to be homologous to those of Lyonia, etc., there are still considerable differences in the stamen type of the two groups.

Drude (1897) did not recognise this group. Agarista was
placed in *Leucothoe* as section *Agastia*; this differed from *Euleucothoe* in style type. He could not find Hooker's difference in sepal aestivation. Drude was perhaps influenced by Niedenzu (1890) who included *Agauria, Agarista* and *Leucothoe* as a subtribe of the Andromedeæ, the Leucothoeineæ. Niedenzu created this subtribe even although he correctly recognised that *Leucothoe* had the same type of stomata as did many Gaultherieæ. Most workers have followed Drude in their treatment of these genera; thus Sleumer (1938 & 1959) also included *Agarista* in *Leucothoe* as section *Agastia*. Drude also included *Pieris* in *Andromeda*.

*Agarista* may be separated from *Leucothoe* as follows. (The characters referring to *Leucothoe* are in parentheses; those characters starred are the ones which suggest that *Agarista* belongs to the *Lyonia* group itself.)

1). Stomata anomocytic (Stomata paracytic).

2). 10/12 species examined have an epidermal cell height; breadth ratio of >1; the epidermis is lignified (ratio of ca. 0.5; epidermal cells un lignified).

3). The petiole and lamina bundle have very well-developed lignification associated with them (Fig. 69) (Not such heavy lignification).

4). The higher order lateral veins are very prominent on the abaxial side of the leaf (not so prominent).

5). The pith is *Calluna*-type (near *Calluna*-type).
6). There are bands of lignified fibres in the phloem (cells with hippocrepiform thickening to the outside of the phloem).

7). The stamens have slender, geniculate filaments; the anthers are ovoid, there are no awns or spurs, but there may be apiculae (filaments stouter, straight; anthers longer; 1 to 2 pairs of awns are present).

8). The seeds are elongated and the cells of the testa are much longer than broad (+ ovoid seeds, cells of the testa are not elongated).

There may also be differences in the venation of the leaves: they are definitely convolute in *Leucothoe*, perhaps revolute in *Agarista*. Lems' (1964) work suggests that the vein endings may be different, since *Agarista* (his *Leucothoe acuminata* and *L. mexicana*) had much shorter vein endings than did *Leucothoe* sensu stricto.

Smith (1911), when first describing *Craibiodendron*, correctly noticed its affinity to *Lyonia* and *Pieris*. Later (1912) he thought that it was closer to *Leucothoe* because they had winged seeds, imbricate sepals and muticous anthers in common.

The dorsally muticous anthers of *Craibiodendron* are not comparable to the awned anthers of *Leucothoe* (see p. 471). Although valvate sepals occur in several members of the *Lyonia* group (*Arcterica*, *Pieris*, some species of *Lyonia*), some species of *Lyonia* at least have imbricate aestivation, thus the character
is not very important. The winged seeds of Leucothoe have their wings formed from the outpushings of single cells; the other cells of the testa are very little elongated (Fig. 71). In Craibiodendron all the cells of the testa, including those over the wings, are much elongated.

Relationships of the group.

In both Pieris and Arcterica there are some species with straight, rather stout filaments. The anthers of some species of Gaultheria are muticous and lack appendages; the filaments too tend to be rather slender (c.f. Figs. 67 & 72). Perhaps the differences between the two types of stamen are not so very great, but even so there is never any trouble in assigning stamens to one of the two types. P. swinhoei and P. phillyreifolia both have + isodiametric testa cells, whilst those of Diplycosia are elongated. Pieris and Arcterica also have their bracteoles about 1/3-2/3 up the pedicel; many species of the Gaultheria group also do not have basal bracteoles.

As already mentioned, some species of Pieris and Craibiodendron have fibres free in the leaf. Although lignified epidermes are very rare indeed in the Gaultheria group, both Diplycosia and Zenobia have bands of fibres in the phloem. The few chromosome numbers which are known from the Lyonia group are based on \( x = 11 \). More work is needed to establish this comparison on a sounder basis.
<table>
<thead>
<tr>
<th></th>
<th>Arsenacoccus</th>
<th>Lyonia</th>
<th>Lyonia</th>
<th>Pieridopsis</th>
<th>Craibiodendron</th>
<th>Pieris S.E. Asian species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves borne</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
<td>scattered</td>
</tr>
<tr>
<td>All veins equally</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>prominent</td>
<td></td>
<td></td>
<td></td>
<td>-</td>
<td></td>
<td>+ pseudo-verticillate</td>
</tr>
<tr>
<td>Plant evergreen</td>
<td>- (++)</td>
<td>- or +</td>
<td>+</td>
<td>- or +</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Hair type</td>
<td>swollen-headed glandular, on both sides of the leaf</td>
<td>eglandular scales</td>
<td>swollen-headed glandular</td>
<td>small-headed glandular hairs, usually on both sides of the leaf</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Inflorescence position</td>
<td>single, axillary, along the stem</td>
<td>inflorescences scattered</td>
<td>inflorescences scattered</td>
<td>often several inflorescences per axil, if latter then near along length of stem</td>
<td>terminal or axillary, if latter then near end of the shoot</td>
<td></td>
</tr>
<tr>
<td>Inflorescence type</td>
<td>+ paniculate</td>
<td>fasciculate</td>
<td>racemose/</td>
<td>raceme</td>
<td>panicle</td>
<td>panicle</td>
</tr>
<tr>
<td>Bracteole position</td>
<td>basal</td>
<td>basal</td>
<td>basal</td>
<td>basal</td>
<td>basal</td>
<td>basal</td>
</tr>
<tr>
<td>Sepal bundles + fibres</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>few</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Calyx stomata</td>
<td>- +</td>
<td>- +</td>
<td>- +</td>
<td>- +</td>
<td>- +</td>
<td>- +</td>
</tr>
<tr>
<td>Corolla stomata</td>
<td>- + 3</td>
<td>- +</td>
<td>- + or -</td>
<td>- +</td>
<td>- +</td>
<td>- +</td>
</tr>
<tr>
<td>Stamen appendages</td>
<td>filament</td>
<td>filament</td>
<td>none</td>
<td>filament or none</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>Filament geniculate</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Style swollen</td>
<td>-</td>
<td>+ bottom</td>
<td>+ bottom</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Placenta position</td>
<td>+ apical</td>
<td>sub-apical</td>
<td>sub-apical</td>
<td>+ apical</td>
<td>apical</td>
<td>apical</td>
</tr>
</tbody>
</table>

**TABLE 16A VARIATION OF SOME CHARACTERS IN SOME OF THE LYONIA GROUP (1)**
<table>
<thead>
<tr>
<th>Character</th>
<th>Arsenococcus</th>
<th>Maria</th>
<th>Lyonia</th>
<th>Pieridopsis</th>
<th>Nuihonia</th>
<th>S.E. Asian species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Multicellular ovary hairs</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Capsule with sutures</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Seed shape</td>
<td>all species with spindle-shaped seeds</td>
<td>prominent</td>
<td>wing</td>
<td>?</td>
<td>spindle-shaped (P. swinhoii ovoid)</td>
<td>+ (P. swinhoii -)</td>
</tr>
<tr>
<td>Testa cells elongated</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>?</td>
</tr>
<tr>
<td>Epidermal cell - height</td>
<td>0.4</td>
<td>0.3</td>
<td>0.5</td>
<td>&lt;1.0 (1.5 - L. rubrovenia)</td>
<td>0.4 - 0.7</td>
<td>0.6</td>
</tr>
<tr>
<td>breadth ratio</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.5 - 0.8</td>
</tr>
<tr>
<td>Hypodermis</td>
<td>-</td>
<td>-</td>
<td>1 - 2</td>
<td>(L. compta +)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Epidermal lignification</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>or -</td>
</tr>
<tr>
<td>Papillate epidermis</td>
<td>-</td>
<td>-</td>
<td>slight in</td>
<td>slight in some species</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Leaf margin lignification</td>
<td>slight</td>
<td>+</td>
<td>+ or -</td>
<td>+</td>
<td>+</td>
<td>+ or -</td>
</tr>
<tr>
<td>Free leaf fibres</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>few</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Midrib bundle type</td>
<td>Lyonia</td>
<td>Lyonia (L. maria Pieris)</td>
<td>Lyonia</td>
<td>Lyonia</td>
<td>Lyonia</td>
<td>Lyonia</td>
</tr>
<tr>
<td>Bundle transcurrent</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Pith type</td>
<td>heterogenous homogenous</td>
<td>homogenous</td>
<td>homogenous</td>
<td>homogenous</td>
<td>homogenous</td>
<td>homogenous</td>
</tr>
<tr>
<td>Epidermal cells divided</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

**Table 1.6B** Variation of Some Characters in Some of the Lyonia Group (1)
<table>
<thead>
<tr>
<th></th>
<th>Pieris</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>floribunda</td>
<td>cubensis</td>
<td>phillyriifolia</td>
<td>Agauria</td>
<td>Agarista</td>
</tr>
<tr>
<td>Leaves borne</td>
<td>leaves are pseudo-verticillate</td>
<td>scattered</td>
<td>scattered</td>
<td>whorls of 3</td>
<td></td>
</tr>
<tr>
<td>All veins</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>equally prominent</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Plant evergreen</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Hair type</td>
<td>long-celled</td>
<td>small gland-headed on the leaves</td>
<td>if present, long-stalked gland-headed hairs</td>
<td>small, gland-headed</td>
<td></td>
</tr>
<tr>
<td>Inflorescence position</td>
<td>terminal</td>
<td>axillary, near the end of the shoot</td>
<td>axillary, scattered along the shoot, rarely terminal</td>
<td>axillary, at the end of the shoot</td>
<td></td>
</tr>
<tr>
<td>Inflorescence type</td>
<td>panicle</td>
<td>raceme</td>
<td>raceme</td>
<td>racemose</td>
<td>raceme</td>
</tr>
<tr>
<td>Bracectole position</td>
<td>top 1/3</td>
<td>ca. middle-top 1/3</td>
<td>basal</td>
<td>basal</td>
<td>near top</td>
</tr>
<tr>
<td>Sepal bundles + fibres</td>
<td>+</td>
<td>?</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Calyx stomata</td>
<td>++</td>
<td>- +</td>
<td>++</td>
<td>- +</td>
<td>- +</td>
</tr>
<tr>
<td>Corolla stomata</td>
<td>- -</td>
<td>- -</td>
<td>- -</td>
<td>- +</td>
<td>- -</td>
</tr>
<tr>
<td>Stamen appendages</td>
<td>at anther/filament junction</td>
<td>+ filament</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Filaments geniculate</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Style swollen</td>
<td>-</td>
<td>-</td>
<td>apex</td>
<td>apex</td>
<td>-</td>
</tr>
<tr>
<td>Placenta position</td>
<td>apical</td>
<td>+ middle?</td>
<td>basal</td>
<td>+ apex</td>
<td>basal</td>
</tr>
</tbody>
</table>

**TABLE 17A** VARIATION OF SOME CHARACTERS IN SOME OF THE LYONIA GROUP (2)
<table>
<thead>
<tr>
<th>Character</th>
<th>floribunda</th>
<th>cubensia</th>
<th>phillyrifolia</th>
<th>Acauria</th>
<th>Acaarista</th>
<th>Aretterica</th>
</tr>
</thead>
<tbody>
<tr>
<td>Multicellular ovary hairs</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Capsule with sutures</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Seed shape</td>
<td>wings both</td>
<td>?</td>
<td>ovoid</td>
<td>spindle-shaped seeds</td>
<td>+ ovoid</td>
<td></td>
</tr>
<tr>
<td>Testa cells elongated</td>
<td>+</td>
<td>?</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Epidermal cell - height:</td>
<td>0.6</td>
<td>0.6</td>
<td>0.7</td>
<td>0.5 - 1.5</td>
<td>1.0 - 2.5</td>
<td>0.4</td>
</tr>
<tr>
<td>Epidermal lignification</td>
<td>- or slight</td>
<td>slight</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Papillate epidermis</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Leaf margin lignification</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Free leaf fibres</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Midrib bundle type</td>
<td>Pieris</td>
<td>+ Lyonia</td>
<td>Pieris</td>
<td>Pieris (very hooked)</td>
<td>Pieris</td>
<td>Pieris</td>
</tr>
<tr>
<td>Bundle transcurrent</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Pith type</td>
<td>heterogenous</td>
<td>?</td>
<td>heterogenous</td>
<td>heterogenous</td>
<td>Calluna</td>
<td>homogenous</td>
</tr>
<tr>
<td>Epidermal cells divided</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Hypodermis</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+ (discontinuous)</td>
<td>-</td>
</tr>
</tbody>
</table>

* exceptions - A. chlorantha and A. ericoides

**Table 17B** VARIATION OF SOME CHARACTERS IN SOME OF THE LYONIA GROUP (2)
Other work perhaps suggests that the two groups may be closer to one another. Lems (1964) found that Lyonia lucida showed greater overall similarity to Pieris (3 species) and to Leucothoe axillaris and L. fontanesiana than to other species of Lyonia. Overall similarity between Lyonia species and the others was less than 50% (26 characters studied). Palser (1951 & 1952) also suggested that Leucothoe was close to the Lyonia group.


Evergreen trees with large, scattered, entire, coriaceous leaves convolute in bud. Indumentum of unicellular hairs and small, clavate-headed glandular hairs. Inflorescence axillary, eperulate, at the end of the previous year's growth. One to few panicles or racemes per axil; bracts and basal, paired bracteoles small, deciduous; pedicel articulate with the calyx. Calyx lobes small, imbricate, free. Corolla ± campanulate, lobes small; walls thick and tending to be bistratose. Stamens 10; filaments geniculate with large papillae and no appendages; anthers slightly granular, tending to be bifidly apiculate, dorsally with a white deposit, dehiscing by short, gaping slits. Ovary 5-locular; rather few ovules from the apical, slightly bilobed placentae; short, stout style impressed, stigma truncate. Capsule
thick-walled, loculicidal; seeds large, few, with unilateral, entire wings; cells of the testa much elongated, thin walled.

There are ca. 8 species in this genus; 4 have been studied. The type species of the genus is C. shanicum (= C. stellatum (Pierre) W.W. Sm.).

The unilaterally winged seeds are unique amongst the Ericaceae (Fig. 66). Otherwise the genus is characterised only by its large inflorescences, several per axil, and its thick-walled, campanulate corolla.

Anatomically the genus is characterised by a lignified epidermis, although this lignification is not always so prominent on the adaxial surface of the leaf. The midrib bundle is the Lyonia-type with lignification spreading into the cells of the collenchymatous / parenchymatous tissue of the transcurrent vascular bundle (Fig. 68). C. Yu 17070 had two layers of lignified mesophyll next to the abaxial epidermis and also a partial adaxial hypodermis; this latter was fully developed in C. henryi. In these leaf characters there are similarities to both Pieris and Lyonia: Craibiodendron agrees with the former in its small, clavate-headed hairs occurring on both sides of the leaf and with the latter in midrib bundle type.

The distinctive thick campanulate flowers are weakly 2-layered rather like those of Dimorphanthera (Fig. 6). The stamens are of the same type as Agauria, Agarista and the
FIG. 66: ANDROMEDA - HAIRS AND SEEDS OF THE LYONIA GROUP.

FIG. 68: ANDROMEEDEAE - STAMENS AND ANATOMY OF THE LYONIA GROUP.

1. *Pieris phillyrriifolia*, x10; 2. *P. cubensis*, x10; 3. *P. floribunda*, x30;
4. *P. formosa*, x10; 5. *Arcterica nana*, x20; 6. the same, x5 - flower; 7. *Muilonia*
(= *Craibiodendron*) *sclerantha*, x50; 8. *C. henryi*, x38; 9. *C. yunnanense*, x30 (e =
epidermis, l = lignified, h = hypodermis).
FIG. 69: ANDROMEDAE - LAMINA ANATOMY OF THE LYONIA GROUP.

1. Lyonia ferruginea, x50; 2. L. lucida, x50; 3. Pieris phillyreifolia, x50;
4. P. swinhoei, x33; 5. P. cubensis, x50; 6. Leucothoë (= Agarista) pistrix, x40;
7. Agauria salicifolia var. buxifolia, x33; 8. A. goetzii, x33 (e = epidermis,
h = hypodermis, l = lignification, p = papillae).
unappendaged species of *Lyonia* (Fig. 67). The seeds are so large that there are only a few per fruit loculus. The seeds most nearly approaching this type are the flattened seeds of *Pieris floribunda*; these are winged on both sides and the wings themselves are not nearly so well developed. The capsules are very robust (Fig. 65), but are not basically different from those of the other genera of this group.

**Synonyms.**

The genus *Nuihonia* was proposed by Dop because he thought that *N. scelerantha* (the only species of the genus) had arillate seeds. He described the ovule as being arillate and anatropous, borne on a slender funicle which arose from the apical interior angle of the loculus. The isotype at Kew has only flowers, so it is probable that his description of the ovule was based on material of a similar age. As already shown (p. 151), the ovule is not arillate; he was confused by the ovules sticking together.

In the anatomical details given by Dop (1931), as well as in the other details of the flower, especially the slender geniculate filaments of the anther (Fig. 67), *Nuihonia* agrees perfectly with *Craibiodendron*. Dop noticed that the epidermis on both sides of the leaf had thickened inner periclinal walls; they are in fact lignified. He also described the midrib bundle as having two bundles on the adaxial side; in the material examined there was only a single bundle (Fig. 68), but it is probable that it would break up into two higher up the
A peculiarity of *N. scleranthea* is that both leaves examined (one half the size of the other) had three bundles at the very base of the petiole which soon joined up to form a single bundle (Fig. 24). Presumably the node had three traces from a single gap, although it was impossible to obtain material to confirm this. Five nodes of *C. yunnanense* were sectioned; two had three traces from a single gap which fused in the base of the petiole, the other three had a single trace from a single gap.

Thus the genus *Nuihonia* cannot be maintained. Formal reduction of *N. scleranthea* to *Crabiodendron* is deferred until the genus is revised.

   *Desmothamnus* Small, Shrubs of Florida 96 (1913).

Shrubs or trees with deciduous or evergreen leaves, usually entire, convolute in bud. Indumentum of scales or very swollen-headed hairs and unicellular hairs. Inflorescence axillary, often near the end of the branch, paniculate, racemose or fasciculate-corymbose; usually small bracts and paired basal bracteoles present, often deciduous; calyx articulate with the pedicel. Flowers usually 5-merous. Calyx lobes small to large,
free; aestivation variable. Corolla urceolate or tubular/campanulate, lobes small. Stamens usually 10; filaments geniculate, with hairs or papillae, spurs present on the filaments or lacking; anthers rather ovoid, slightly granular, apex tending to be bifidly apiculate, dorsally with a white deposit, dehiscing by short, broad, introrse slits. Ovary 5(-6)-locular, often with multicellular hairs; placentae usually apical, slightly bilobed, ovules numerous. Capsule loculicidal, the sutures usually very thickened and remaining intact even after dehiscence. Seeds spindle-shaped, the cells of the testa very much elongated.

Ca. 30 species, 18 of which have been studied intensively. The type species is *L. ferruginea*.

This genus is immediately distinguishable from all others by its combination of geniculate filaments, capsule with very thickened suture walls and a *Lyonia* midrib bundle.

There has been much confusion of *Lyonia* and *Pieris*. Don, in his original description of the genus *Pieris*, included *P. ovalifolia* (= *Lyonia*). Nuttall's original description mentioned the "awnless" nature of the stamens in *Lyonia*, and since at that time the presence or absence of stamen appendages was thought to be very important Don naturally included *L. ovalifolia*, which has spurs, along with *P. formosa* and *P. lanceolata*. Hooker (1876) followed this mistake, as Rehder (1924) noted.
Of Hooker's four sections of *Pieris* only *Portuna* and *Phillyreiodes* belong to *Pieris*, the other two, *Maria* and *Eupieris*, both belong to *Lyonia*. Drude (1897) included *Pieris* in *Andromeda* since he thought that they both had the same corolla and seed type whilst not possessing the thickened sutures of the capsule of *Lyonia*. He included *Chamaedaphne* in *Lyonia*. Although both genera have scale hairs they differ in leaf anatomy, inflorescence, stamen and fruit (see p. 442).

*Lyonia* may be distinguished from *Pieris* on the following characters:

1). Capsule with a well-developed suture which may or may not remain intact during dehiscence (Fig. 11). Although this is rather poorly developed in *L. compta* it is a good character on the whole. None of the *Pieris* species which I have seen has this character.

2). Adaxial calyx stomata never present. These occur in all the species of *Pieris* seen except *P. cubensis*, where they may be present but obscured by the rather dense adaxial calyx hairs. These unicellular hairs occurred on all *Pieris* species but only on some *Lyonia* species. *L. macrocalyx*, with a very large calyx superficially like that of *Pieris*, lacked adaxial stomata. There are abaxial corolla stomata, these have not been found in *Pieris* (c.f. Watson, 1965).

3). There is a rather unsatisfactory difference in stamen type
between the two genera. In Matthew & Knox's table (1926) there are a large number of species listed, all under *Pieris*, with the position of attachment of the spur noted. All species now put in *Lyonia* occur in the top part of the table with spurs on the filaments (*L. nitida* is mentioned as having spurs at the apex of the filament - in fact they occur near the top).

*P. swinhoei* has its appendages on the filaments; they are fused to the top part of the filament but are free below. Both it and *P. phillyreifolia* have geniculate filaments; other species of *Pieris* have straight filaments; either slender, as in *P. cubensis*, or stout, as in *P. floribunda* (Fig. 68). According to Palser (1951) the filaments of *Lyonia* are horizontally S-shaped in bud, whilst those of *Pieris* are vertically S-shaped. There does not seem to be any basic difference between the filaments of *P. phillyreifolia* and *P. swinhoei* and those of *Lyonia* (see Figs. 67 & 68).

4). The bracteoles of *Lyonia* are basal; those of *Pieris* are usually about 1/3 the way up the pedicel.

5). According to Palser (1951) *Pieris* has prominent fibre strands associated with the vascular bundles in the sepals (as in Fig. 33); *Lyonia* does not have these and there are, on the whole, fewer traces to the sepals than in *Pieris*. The former difference especially needs more study, since examination of species from *Lyonia* section *Pieridopsis* shows that small fibre strands are to
be found in *L. macrocalyx* and *L. ovalifolia*. It would also be very interesting to study *L. rubrovenia* and other species.

6). The two genera are easily distinguishable using indumentum since *Lyonia* either has scales or glandular hairs with very swollen heads (Figs. 17, 18 & 67), whilst the hairs of *Pieris* are small and club-shaped, or long-celled (Fig. 66).

7). All species of *Lyonia* except *L. lucida* have a *Lyonia*-type midrib bundle; all species of *Pieris* except *P. cubensis* have a *Pieris*-type midrib bundle (Figs. 29, 30 & 69).

8). Most species of *Lyonia* have homogenous pith, although that of *L. doyonensis* and *L. foliosa* is slightly heterogenous and that of *L. ligustrina* and *L. foliosiflora* is very heterogenous. All species of *Pieris* examined have very heterogenous pith.

**Generic Segregates.**

Three genera have been proposed as segregates from *Lyonia* (*Xolisma* itself is an alternative name to *Lyonia*).

*Desmothammnus* (the only species of which is *D. lucidus*) was separated from *Lyonia* sensu restricto because it had spurs on the filaments (Small, 1913). Small may not have considered the Himalayan species here included in the genus to belong to *Pieris*, but within these species (*Pieris* section *Eupieris*, Hooker, 1876) there is variability in this character, even at the infraspecific level. From the other *N. American* species with spurred filaments and recognised as a genus (*Neopieris*; only species, *N. mariana*) it
differed in being evergreen (Neopieris is deciduous), having leaves with intramarginal veins (not so), an urceolate corolla (tubular/campanulate) and in having a fusiform style (columnar). The persistence of the leaves varies within section Pieridonsis, and N. mariana has its style slightly swollen at the base and thus approaching that of Desmoothannus. The other two differences are good ones, and D. lucidos is also the only member of this group with a Pieris-type midrib bundle. Both genera are rather similar in appearance, and Palser (1951) noted that they both had ovules borne only on the placenta face opposite the ovary wall, they also have a tendency for their placentae to be borne towards the base of the loculus. This is better developed in Desmoothannus. Although neither taxon is maintainable at the generic level, since they have the same stamen, fruit and indumentum as several other species, they are both distinct species. Rehder (1924) was probably correct in assigning them together to a separate section, Maria, of the genus.

Arsenococcus (A. ligustrinus) was believed to lack stamen appendages and to differ from the other New World species without such appendages in the shape and angularity of the capsule, indumentum and inflorescence. The last two characters are satisfactory, although the difference in inflorescence is not very great, since some of the Antillean species of Lyonia have a congested raceme; the paniculate inflorescence of Arsenococcus.
might be a less reduced form of the fasciculate inflorescence so common in the Antillean species. *Arsenococcus* is not generically separable from these species. The hairs of *L. ligustrina* and *L. foliosiflora* (only doubtfully distinct as species) are very like those of the other species of the group from N. America and the Himalayas, so it is perhaps not surprising to find that both species have small filament spurs. However, both species have a very heterogenous pith. Sectional rank is probably the best level at which to recognise them (Rehder, 1924).

The Antillean species of the genus are perhaps the most distinct group. Their inflorescence is ± fasciculate, as is that of *L. mariana* and *L. lucida*. Their indumentum of eglandular scales is found elsewhere only in *Chamaedaphne*, a superficially similar genus which differs in anatomy, stamen type, seeds, etc., but nowhere else in the Vaccinioideae. Some species seem to lack corolla stomata; all species seem to lack filament spurs. I was unable to find filament spurs in *L. fruticosa*, although Palser (1951) said that they occurred there.

Some species of this group have a lignified adaxial hypodermis, the cells of which are about the same size as the epidermal cells. Those species lacking such an hypodermis nevertheless have a curious epidermal structure suggesting a very low epidermis + hypodermis, a divided epidermis of sorts, or even a "mucilaginous" epidermis with all the walls very much thickened. The epidermis on both
surfaces is lignified. *L. compta*, of section *Pieridopsis*, is the only other species of *Lyonia* known to have an hypodermis.

Palser (1951 & 1952) studied one species each from the sections *Lyonia, Arsenococcus, Neopieris* and *Desmothamnus*, and found that they were more similar in floral anatomy and embryology to one another than to the *Pieris* and *Leucothoe* groups. They had in common relatively small antipodal cells and hence the antipodal swelling was not great; in general the ovules were rather small.

Section *Pieridopsis* comprises the S.E. Asian species of *Lyonia*. *L. rubrovenia* has two layers of lignified spongy tissue next to the abaxial epidermis, but otherwise this section is not remarkable in anatomy. The epidermis is not lignified. The hairs are of the same basic type as in sections *Maria*, etc. (Fig. 67) and the style is swollen (Fig. 65). Members of this section are deciduous or evergreen and are characterised by their elongated, one-sided racemes and rather weak development of the capsule sutures. As a result the line of dehiscence tends to go through the suture, rather than leaving the thickened rib of tissue intact.


*Ampelothamnus* Small, Shrubs of Florida 96 (1913).

Evergreen shrubs with serrate leaves convolute in bud.
Indumentum of small, clavate-headed glands or long-celled hairs, and unicellular hairs. Inflorescence terminal or axillary, paniculate or racemose; bracts small, paired bracteoles ca. >1/3 up the pedicel; pedicel articulate with the calyx. Flowers 5-merous. Calyx lobes valvate, well developed. Corolla urceolate, lobes small. Stamens 10; filaments geniculate or not, stout or not, hairy, spurs on the filaments or on the back of the anther; anther rather elongated, slightly granulate, dorsally with a white deposit, dehiscing by terminal introrse pores. Ovary 5-locular, placentae slightly bilobed, apical or basal. Style impressed, usually columnar; stigma truncate. Loculicidal capsule without thickened sutures; seeds winged or spindle-shaped with very long cells in the testa, or ovoid with ± isodiametric testa cells.

There are about 10 species in this genus; 8 have been studied. The type species is *P. formosa*.

The relationships of this genus to *Lyonia* have been dealt with above. *Pieris* differs from *Craibiodendron* in midrib anatomy, pith type, stamen and seed type, and in calyx stomatal distribution. *P. floribunda* is closest to *Craibiodendron* in seed structure, but it differs from it in the other characters mentioned above and also in indumentum. *Pieris* differs from *Agauria* and *Agarista* in leaf anatomy and stamen and leaf type.

*Fortuna* (only species, *P. floribunda*) was proposed by Nuttall without reference to the genus *Pieris*. Nuttall thought that its
closest relationships were to Leucothoe. *P. floribunda* is an odd species in that it has a terminal paniculate inflorescence, hairs of the long-celled type and large, therefore few, flattened seeds. On the inflorescence the hairs are glandular and like those of the other species of *Pieris*. Although a very distinct species it is not worth generic recognition.

*Aegilaeae* was published without reference to any particular species, but the name is probably to be referred to *P. phillyraifolia* since this was the only *Pieris* then known which had bent filaments (referred to in the description). The name could possibly refer to a species of *Lyonia*, although the spurs are specifically referred to as arising from the back of the anther.

*Ampeloalthamnus* (the only species is *A. phillyraifolius*) was proposed by Small in 1913, but de Candolle had earlier (1839) suggested that this species might be given generic recognition. Small separated it on the grounds that it differed from *P. floribunda* in inflorescence and stamen. It is similar to all the S.E. Asian species of *Pieris* in this first respect and is rather similar to *P. swinhoei* in the second (Figs. 67 & 68). These two species have a geniculate filament in common although in *P. swinhoei* the spurs seem to arise from the filament rather than from the anther/filament junction. Further, previously unnoticed, similarities between these two species are the basal position of the placenta (apical elsewhere) and the polygonal cells
of the testa (elongated elsewhere). *P. phillyraifolia* has the most strongly lignified epidermis amongst the species of *Pieris* studied whilst that of *P. swinhoei* is un lignified. Other species in the genus link these two species in this respect.

Palser (1951 & 1952) concluded that there was no floral anatomical or embryological evidence to keep the two separate. They both had prominent fibre strands in the sepal and a three trace gap supply to each sepal lobe. I agree with Palser. *P. phillyraifolia* is an odd species and the possibility of a relationship to *P. swinhoei* and perhaps other S.E. Asian species and even to *P. cubensis* (the fruits of which I have not seen) should be investigated further.

9. **AGARISTA** D. Don in G. Don, Gen. Syst. 3: 837 (1834), pro parte.  
**Amechania** DC., Prodr. 7 (2): 579 (1839).

Evergreen shrubs with entire or, rarely, serrate leaves, leaves scattered, sometimes long-petioled, all lateral veins about equally prominent. Indumentum of long-stalked glands and unicellular hairs. Inflorescence usually axillary, racemose, eperulate; small bracts and paired, basal bracteoles present; pedicel articulate with the calyx. Flowers 5-merous. Calyx lobes small, free. Corolla ± urceolate, lobes small. Stamens without appendages; filaments hairy and geniculate; anthers ovoid, dehiscing by short, wide slits, tending to be (bifidly) apiculate, dorsally with a white deposit. Ovary 5-locular; slightly bilobed
placentae near, or at, the apex of the loculi; style impressed, swollen just below the apex; stigma usually truncate. Capsule loculicidal, sutures unthickened; seeds numerous, spindle-shaped; cells of the testa very long, little thickened.

There are about 30 species in the genus; 12 have been studied in detail.

*Agarista* is most easily distinguished from the genera mentioned above by its unappendaged stamens, capsule with unthickened sutures, leaf type and racemose inflorescence.

There has been much confusion over this genus. Malagasy species now placed in the genus *Agauria* were included with the S. American species of *Agarista* sensu stricto in the original description. De Candolle transferred the whole genus into *Leucothoë*; the S. American species were put in a section *Agastia* and the Malagasy species into section *Agauria*. He also described two species in the new genus *Amechania*; he did not realise at that time that this genus was indistinguishable from *Leucothoë* section *Agastia*. Hooker (1876) raised *Agauria* to generic rank and also reinstated *Agarista*. Most later authors have followed Hooker in maintaining *Agauria* as a genus distinct from *Leucothoë* because of the difference in placental position in these two genera, whilst *Agarista* is recognised at the sectional level within *Leucothoë*. Reasons have already been given for separating
Agarista from Leucothoë (see p. 409).

Agauria and Agarista are very similar despite their difference in placental position. This difference should not be overweighted, since in both Pieris and Enkianthus there is great variation in this character within otherwise natural genera. Even in Agarista itself there is some variation in this character; most species, like A. revoluta, have apical placentae whilst a few, like A. oleifolia, have placentae in the middle of the loculi (Fig. 65).

The two genera both have the characters of the Lyonia group in common: the other important similarities between the two genera are listed below:

1. They agree in most details of habit, inflorescence and indumentum. Their glandular hairs have multiseriate stalks and small heads (Fig. 67); such hairs are unknown elsewhere in the Lyonia group.

2. They both have all the veins almost equally prominent on the abaxial side of the leaf; the veinlet reticulum is very dense (see section 2.1.2.).

3. At least some species in both genera have very tall epidermal cells. (height:breadth ratio = >1) - see Fig. 27. Niedenzu (1890) correctly noted the similarity of the two genera in leaf anatomy, although he included them both in his subtribe, the Leucothineae. His suggestion that Agarista linked on to Leucothoë via A. serrulata and A. numularia is not borne out by this work. A. serrulata
has the midrib bundle and the epidermis of an *Agarista* rather than a *Leucothoe*. *A. nummularia* has not been seen.

4). Both genera have a *Pieris*-type midrib bundle with very heavy associated lignification (Fig. 69). This is rather less well developed in *Agauria*, and the bundle tends towards the *Oxydendrum* type as well.

Also both genera have abaxial corolla stomata, although Watson (1965) fails to record them from *Agauria*. *Agauria salicifolia* has leaves revolute in bud; this is probably the condition in *Agarista*. There may also be a similarity in the type of veinlet ending in the leaf (see Lems, 1964).

The two genera may be separated as follows:-

1). *Agarista* has heterogenous pith, that of *Agauria* is *Calluna*-type.

2). *Agarista* does not have an hypodermis and several species have their epidermal cells divided periclinaly. *Agauria* does have an hypodermis, although it is not always continuous, and in the material examined the epidermal cells are not divided periclinally (Niedenzu, 1890, reports that there is sometimes periclinal division of these cells).

3). *Agarista* has a smooth abaxial epidermis whilst that of *Agauria* is papillate.

4). The placenta in *Agarista* is + apical; that of *Agauria* is basal (Fig. 65). There is no difference in seed shape.
5). Agarista has a swollen tip to its style. I could not see this in Agauria, although fresh material would be desirable to confirm this point.

According to Cox (1948b), there are significant differences in the wood anatomy of the two genera. This needs more study.

Thus the generic separation of Agauria and Agarista is borderline, although they live on different continents between which close taxonomic relationships are not common (see Chapter 6). Whatever rank is assigned to these taxa, it is important to note that they are more closely related to each other than to any other genera, but at the same time they show definite relationships with the other members of the Lyonia group. They are not close to Leucothoe.


Evergreen trees or shrubs with scattered, entire leaves revolute in bud. Abaxial leaf covered with a whitish or greyish bloom, the venation very reticulate. Indumentum of long-stalked glands and unicellular hairs. Inflorescence axillary, racemose, near the ends of the branches; small bracts and paired basal bracteoles present; calyx articulate with the pedicel. Flowers 5-merous. Calyx lobes small, free. Corolla + urceolate, lobes small. Stamens without appendages; filaments geniculate and hairy; anthers slightly granular, dorsally with a white deposit, dehiscing
by an apical introrse slit, slightly apiculate. Ovary 5-locular, placentae basal; style impressed, columnar, stigma truncate. Capsule loculicidal, many seeded, sutures unthickened; seeds spindle-shaped; the testa with very long cells.

1 to 7 species according to the author; 4 taxa have been studied. The type species is *Agauria salicifolia*.

In addition to the close relationship of this genus to *Agarista*, it also shows similarities to other genera of the *Lyonia* group. In anther type it is just like *Crabiodendron* and *Lyonia* section *Lyonia*. Anatomically too there is some correspondence with *Lyonia*. Section *Lyonia* has rather tall epidermal cells (ratio ca. 1), and hypodermis and epidermal lignification. *L. rubrovenia* of section *Pieridopsis* has very tall epidermal cells (ratio ca. 1.5), and some species of this section have scattered papillae on their abaxial epidermis, e.g. *L. macrocalyx*, *L. sphaerantha* and *L. doyonensis*; *L. compta* has an hypodermis.


Small evergreen shrubs with entire leaves in whorls of three, convolute in bud. Indumentum of small, clavate-headed glandular hairs and unicellular hairs. Inflorescence axillary at the end of the shoot, eperulate, a few flowered raceme; bracts leafy, bracteoles paired, subapical; calyx and pedicel poorly articulate. Flower 5-merous. Calyx lobes rather large, free, valvate in
aestivation. Corolla urceolate, lobes small. Stamens 10; filaments glabrous, slightly swollen towards the base, slightly granular spurs at the anther-filament junction; anthers smooth, with a white deposit dorsally, dehiscing by a short, introrse slit. Ovary 5-locular, slightly bilobed placentae near the base of the loculi; style impressed into the swollen apex of the ovary, stout, stigma truncate. Fruit a loculicidal capsule; seeds several, ovoid; cells of the testa moderately elongated, walls slightly thickened; the testa several layers deep over the raphe.

The single species in this genus, *A. nana*, has been studied.

This is a somewhat isolated genus, but with a number of points in common with *Pieris*. It differs from all other Vaccinioideae in its 3-whorled leaves. Prior to 1901 the single species had been included in *Pieris, Andromeda* or *Cassiope*.

Anatomically it is distinguishable from the other members of the *Lyonia* group in the poor development of the libriform tissue and the very prominent bast (Fig. 70); the spongy mesophyll has very large spaces. In these characters it approaches the *Gaultheria* group, but its epidermis is lignified at and near the leaf margin. This is a point of similarity to the *Lyonia* group. Banded phloem lignification has not been observed.

Its multicellular hairs are very similar to those of *Pieris* and *Craibiodendron* (Fig. 66), having a two-ranked stalk and only
slightly expanded head. The leaf hairs of the *Gaultheria* group have a more robust construction, nearly always being multiseriate.

Its inflorescence develops about August of the year preceding flowering, in the axils of the topmost whorl of leaves of the current year's growth. There are sometimes one or two whorls of leaves below the one or two whorls of flowers. The bracteoles, rather near the top of the pedicel, are rather similar to those of *Gaultheria*, *Pieris*, etc. Its anthers are very similar to those of some species of *Pieris*, having paired spurs arising from the anther filament junction and a white deposit dorsally (Fig. 65). It entirely lacks corolla stomata, but has abaxial calyx stomata. This is the same distribution as is found in *Pieris cubensis*, and of course the lack of corolla stomata is general in that genus.

Some aspects of its floral anatomy have been studied, and they agree almost perfectly with that of *Pieris*. There is usually a total of 10 traces supplying the sepal whorl; the traces are reflexed (Fig. 33). Alternate traces are the fused, adjacent lateral sepal traces; by the time the bundles enter the base of the sepals there are 5-7 bundles supplying each calyx lobe. Each bundle is accompanied by a prominent bundle of fibres, and there are apparently air spaces on the adaxial side of the calyx, so the epidermis there is very easily removed. The sepals are valvate in aestivation, and there are numerous adaxial, unicellular hairs.
The seeds of *Arctera*ica are different from all others in the family, but are rather similar to those of *Chamaedaphne*, although that genus differs in anatomy, indumentum, inflorescence, etc. The testa cells are about 5x as long as broad, with 3-5 thick walls. The seed is ovoid in shape, but on the chalazal side there is a wing formed by the testa being locally several layers thick. These observations agree with those of Petrosilot (1904b).

12. **CHAMAEDAPHNE** Moench, Meth. 457 (1794).

Subevergreen shrubs with small, serrate leaves, convolute in bud. Indumentum of scales and unicellular hairs. Inflorescence eperulate, terminal on the vegetative shoots, racemose or paniculate, flowers borne on one side; bracts leafy, bracteoles small, paired, apical; pedicel articulate with the calyx. Flowers 5-merous. Calyx lobes free, quincuncial. Corolla urceolate, lobes small. Stamens 10; filaments straight, glabrous; anthers slightly papillate with tubes ca. 1/2 their length, dehiscing by short, apical, introrse slits. Glabrous ovary with 5+ apical, slightly bilobed placentae; style impressed, slender, stigma ± truncate. Capsule loculicidal with unthickened sutures; seeds few, ovoid; testa several layers thick over the raphe, cells of the testa ± oblong, rather thick walled.

The single species in the genus, *C. calyculata*, has been studied.
This is an interesting little genus looking superficially like Lyonia, but differing from it in anatomy, inflorescence, stamens and fruit. See table 15 for characters (p. 402).

Bentham (1876) correctly recognised this genus (as Cassandra). However Drude (1897) thought that it was a subgenus of Lyonia. He distinguished it from the other Lyonia species on the lack of prominently thickened sutures in the capsule and the presence of a protruding raphe.

There are some apparent similarities to Lyonia. Thus the one-sided inflorescence with prominent, leafy bracts approaches the condition of Lyonia section Pieridopsis, although in this section the inflorescence is axillary. The scaly indumentum is at least superficially similar to that of Lyonia section Lyonia, although a developmental comparison of the two has not been undertaken since living material of section Lyonia has not been available. Niedenzu (1890) was misled by this apparent similarity in indumentum and he thought that Lyonia (= Lyonia section Lyonia) and Cassandra were so close anatomically that they should be put in the same genus - Cassandra. However, this is improbable even on anatomical grounds, since he overlooked differences in the midrib bundle, epidermal lignification and the hypodermis which do not support such a transfer. Chamaedaphne differs from Lyonia in the following characters:

1. The stomata are positionally paracytic.
2. The midrib bundle is of the *Pieris* type.
3. The inflorescence terminates the year's growth.
4. There are paired bracteoles at the apex of the pedical.
5. There are no corolla stomata (a single stoma was found on the abaxial surface of the corolla in var. *longifolia*), although it should be remembered that they may also be lacking in some species of *Lyonia* section *Lyonia*.
6. The straight filaments are somewhat swollen at the base and there are long tubules on the anthers (Fig. 70). Palser (1951) records the presence of two short awns terminating the tubules. There are no awns in the sense here used, although the tubules may be apiculate.
7. The capsule lacks thickened sutures (Fig. 71).
8. The testa has rather short cells with thickened walls; it is several layers thick over the raphe (Fig. 14), as Petrosilot (1904b) noted.
9. Palser (1951 & 1952) considered that it was a very distinct genus in floral anatomy and embryology within the Andromedae sensu Drude, although it did have some affinity to the *Lyonia/Leucothoe* group of genera, especially in the 10 traces which supplied the sepal whorl. The ovules were campylotropous; this is unusual in the Ericaceae.

*Chamaedaphne* does seem to be an isolated genus. In stomata, bracteole, seed and general anatomical characters it shows some
FIG. 70: ANDROMEDEAE - GENERAL.

1. Arcterica nana, x33; 2. Chamaedaphne calyculata, x100; 3. Zenobia speciosa, x50;
similarity to the Gaultheria group, but its remarkable scale hairs are similar to those of Lyonia and the seed is grossly similar to that of Arcterica. In inflorescence, floral stomatal distribution and stamen type it seems to be isolated, although in the first and last of these characters there is possibly some similarity with Oxydendrum.

The Gaultheria group.

The multicellular hairs of this group of genera are often very robust, with a multiseriate stalk of some size, the cells of which usually have no particular regular arrangement. The stamens have straight, rather stout filaments, although in Diplycosia they are more slender. There are one or two pairs of awns, but the stamens are never spurred; there is a white deposit (dissolution tissue) at the back of the anther in most genera. Diplycosia, Tenuia, Pernettyopsis and some species of Gaultheria lack any appendages and dehisce via terminal tubules. The fruit is often fleshy; the cells of the testa are elongated in Diplycosia alone of those genera of which seed has been seen. Stomata are very frequently paracytic or positionally paracytic. There are often fibres wandering through the mesophyll; epidermal lignification has not been seen. Bands of fibres are found in the phloem of this group; also cells with hippocrepiform thickenings.

The relationships of this group to the Lyonia group were dealt with under the latter. The Gaultheria group includes the Gaultherieae of Niedenzu (1890) with the addition of Zenobia and
Leucothoe. Although these two genera do not have fleshy fruits or leaf fibres (but see also some species of *Gaultheria*) they agree with the rest of the group in the other characters, and cannot logically be excluded. Their stamens are very similar to those of *Gaultheria* (see Figs. 70 & 72); indeed, in this respect most species of *Gaultheria* are different from *Diplycosia*, *Pernettyopsis* and *Tepuia*. Cox (1943b) thought that the *Gaultheria*ae itself might be divided into two groups on wood anatomy, with *Gaultheria* and *Pernettya* in one group, *Chiogenes* intermediate, and *Diplycosia* and *Wittsteinia* (sic) in another.

It is not thought worth while to recognise this group taxonomically, although it does seem to represent a distinct entity which shows a number of points of similarity to the *Vaccinieae*.


Weakly evergreen shrub with ovate, serrulate leaves convolute in bud. Indumentum of unicellular hairs, stout, clavate hairs restricted to the leaf margin. Inflorescence eperulate, axillary, fasciculate, borne towards the end of the previous year's growth; bracts and basal, paired bracteoles present; calyx articulate with the pedicel. Flowers 5-merous. Calyx lobes small, free. Corolla urceolate, lobes small. Stamens 10; filaments swollen at the base, papillate; anthers with a white deposit dorsally,
granulate, two pairs of awns. Ovary 5-locular, placentae apical, slightly bilobed; style slender, impressed, stigma truncate. Fruit a loculicidal capsule; seeds several, ovoid; cells of the testa polygonal in shape and with somewhat thickened walls.

There is a single species in the genus, *Z. speciosa*. It has been studied.

Hooker (1876) maintained *Zenobia* as a genus which he compared to *Lyonia*. Drude (1897) included *Zenobia* in *Andromeda*, although it differs in facies, indumentum, leaf venation, inflorescence, stamen, seed, etc.

Lems (1964) found that, when overall similarity in leaf anatomy was considered, *Zenobia* came so close to the deciduous species of *Lyonia* as to warrant a re-evaluation of the generic limits in that area. This apparent similarity does not stand up to close scrutiny. No species of *Lyonia* have the same, heavily lignified hypodermis at the leaf margin as does *Zenobia*; they also have a *Lyonia*-type midrib bundle and a lignified epidermis, neither of which are found in *Zenobia*. Although the inflorescence of *Zenobia* is the same as that of *Lyonia mariana*, they differ in stamens, fruit and seed, as well as indumentum. However, they do agree in their anomocytic stomata and the bands of fibres in the older part of the phloem.

The closest relationship of *Zenobia* seems to be to *Leucothoë* and *Gaultheria*. *Zenobia* differs from *Leucothoë* in having
anomocytic stomata in the type of the lignification at the leaf margin (see Table 18). Anomocytic stomata are to be found in some species of Gaultheria, but no species have been seen with such strong marginal hypodermal lignification. Bands of phloem fibres have not yet been found in either Leucothoe or Gaultheria, although they are to be found in Diplycosia of the Gaultheria group. In indumentum Zenobia is rather closer to Gaultheria, where several species have similar clavate hairs on the leaf margin.

In inflorescence Zenobia is similar to Leucothoe keiskei and G. dumicola; Airy Shaw (1940) noted that the latter species was similar to Zenobia in this respect, although they have been found to differ in fruit, anatomy and indumentum. Although Watson (1965) did not find abaxial corolla stomata in Zenobia they do occur there, so in the distribution of stomata on the flower it agrees with the Andromedeae in general. The same basic type of anther as occurs in Zenobia also occurs in the other two genera (see Figs. 70 & 72). There is no difference in fruit between Zenobia, Leucothoe and species of Gaultheria like G. oppositifolia and G. wardii, although in the latter the calyx lobes may stay greener longer. Material has not been adequate to establish this point. Fertile seed has not been seen, but from observations on apparently normal (but actually sterile) seed and from Petrosilots' (1904b) excellent illustration, it is clear that the testa is only a single
FIG. 71: ANDROMEDAEE - FRUIT OF CHAMAEDAPHNE AND THE GAULTHERIA GROUP.

<table>
<thead>
<tr>
<th>Character</th>
<th>Zenobia</th>
<th>Acranthes</th>
<th>Leucothoe</th>
<th>Paraleucothoe</th>
<th>Oligariate</th>
<th>Eubotroides</th>
<th>Eubotrya</th>
</tr>
</thead>
<tbody>
<tr>
<td>speciosa</td>
<td>daviesae</td>
<td>axillaris</td>
<td>fontanesiana</td>
<td>keiskei</td>
<td>griffithiana</td>
<td>grayana</td>
<td>racemosa</td>
</tr>
<tr>
<td>Leaf in bud</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>?</td>
<td>?</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Leaf evergreen</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Leaf hairs clavate (c) or glandular (g)</td>
<td>c</td>
<td>e</td>
<td>e</td>
<td>e</td>
<td>c</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Inflorescence position</td>
<td>all species have axillary inflorescences borne on the previous year's growth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inflorescence type</td>
<td>fascicle</td>
<td>raceme</td>
<td>raceme</td>
<td>fascicle</td>
<td>raceme</td>
<td>raceme</td>
<td>raceme</td>
</tr>
<tr>
<td>Bracteoles basal</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Corolla urceolate</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>?</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Corolla length (mm.)</td>
<td>11</td>
<td>7.5</td>
<td>ca. 6.5</td>
<td>11.5</td>
<td>5</td>
<td>5</td>
<td>6 - 7</td>
</tr>
<tr>
<td>Calyx stomata</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Corolla stomata</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Anthers awned</td>
<td>+, 2 prs.</td>
<td>-</td>
<td>apiculate</td>
<td>+, 2 prs.</td>
<td>2 prs.</td>
<td>+, 2 prs.</td>
<td>-</td>
</tr>
<tr>
<td>Filaments swollen, straight</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>White deposit on anthers</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>?</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Seeds winged</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+, -</td>
</tr>
</tbody>
</table>

**TABLE 13A** VARIATION OF SOME CHARACTERS IN ZENOBIA AND LEUCOTHOE
<table>
<thead>
<tr>
<th></th>
<th>Zenobia</th>
<th>Acranthes</th>
<th>Leucothoe</th>
<th>Paraleucothoe</th>
<th>Oligarista</th>
<th>Eubotryoides</th>
<th>Eubotrys</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf epidermis</td>
<td>1</td>
<td>+2</td>
<td>2</td>
<td>1</td>
<td>1 (-2)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Stomata paracytic</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+ (position)</td>
<td>+</td>
</tr>
<tr>
<td>Cuticle striate</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Hypodermis</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Leaf epidermis lignified</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Leaf margin lignified</td>
<td>-</td>
<td>hypodermal</td>
<td>fibres</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Fibres in mesophyll</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Midrib tissue lignified</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Midrib bundle Pieris-type</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Cortex</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Pith</td>
<td>hetero.</td>
<td>hetero.</td>
<td>all these species heterogenous/Calluna type</td>
<td>+ homo.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bands of fibres in phloem</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

**Table 18B** Variation of some characters in *Zenobia* and *Leucothoe*
layer of cells, the cells themselves are ca 60\(\mu\) in diameter, ± polygonal, and with walls about 3-5\(\mu\) thick. The outer periclinal walls are also thickened, and in this it agrees with several species of the Gaultheria aggregate (see Fig. 15).

Detailed study of the floral anatomy has not been undertaken, but there are no prominent tracts of fibres associated with the vascular bundles in the sepals, and the whole vascular supply of the flowers seems to be rather compressed and non-diverged. There are 5 traces supplying the sepal whorl.

This genus is not a very distinct entity, but it seems best to maintain it until the relationships of this part of the Gaultheria group are fully worked out. It is quite possible that it would be better included in Gaultheria.

14. Leucothoe

- Oreocallis Small, Fl. N. Am. 29 (1): 58 (1914).

Evergreen or deciduous shrubs, leaves ± serrate, convolute in bud. Indumentum of stalked, glandular hairs or clavate hairs and unicellular hairs. Inflorescence axillary, eperulate, at the top of the preceding year's growth, racemose, eperulate; bracts and small, paired bracteoles present, the latter variable
in position; calyx ± articulate with the pedicel. Flowers 5-merous. Calyx lobes small, free. Corolla urceolate, lobes small. Stamens 10; filaments swollen towards the base, hairy or not; anthers slightly granular with one or two pairs of terminal awns, these sometimes reduced and anthers muticous, a white deposit dorsally. Ovary 5-locular, placentae apical, slightly bilobed style usually slender, impressed, stigma ± truncate. Fruit a loculicidal capsule; seeds winged or ovoid; cells of the testa little elongated or thickened.

There are about 8 species in the genus; 8 have been studied. The type species of the genus is *L. axillaris*.

The separation of *Leucothoë* from *Gaultheria* is not at all easy. *Leucothoë* never has fleshy fruits and the calyx withers soon after flowering. The fruit of *Gaultheria* is nearly always fleshy, and the seeds are never winged as is some species of *Leucothoë*; those species of *Leucothoë* with unwinged seeds have rather thinner testa cell walls than are found in *Gaultheria*, although the sampling of the latter genus is still inadequate in this respect. There is no absolute difference in the indumentum (Figs. 19 & 73); *L. graviana* and *L. griffithiana* especially are very close to species of *Gaultheria* in this. The latter species is very similar to *Gaultheria* section *Leucothoides* in general facies and all details of flower and anatomy except in its winged seeds, lack of an hypodermis (Fig. 74) and dry calyx. *Leucothoë*
has all the characters of the Gaultheria group in general and so may be distinguished from the genera of the Lyonia group on these characters.

Cox (1943b) thought that Leucothoe formed a group with "Andromeda" and Chamaedaphne, but on the evidence which he gave it might just as well have been placed in the Gaultherieae sensu Drude.

**Generic segregates.**

Most of the species in Leucothoe are very distinct, and several generic segregates have been recognised. Small (1914) recognised three genera from N. America alone.

Cassandra was proposed by Spach but was antedated by Cassandra D. Don, published in 1834. Nuttall's genus Eubotrysis is based on the same species as Cassandra Spach. There are two species included in Eubotrysis, E. racemosa, the type species, and E. recurva. Small (1914) maintained it as generically distinguishable from the other N. American species of Leucothoë (L. axillaris and L. fontanesiana) and Oreocallis (see below) in having terminal, as against axillary, panicles and awned, as against awnless, anthers. All three genera have axillary racemes, but the difference in anther type holds; in addition Eubotrysis may be separated from the other two genera on its homogenous pith and thin, deciduous leaves. Lems (1964) found that in general leaf anatomy the two species placed in Eubotrysis were very similar to
one another and rather distinct from the other species of the genus Leucothoë.

Palser (1951 & 1952) found that Eubotrys differed from the other species of Leucothoë studied in having quincuncial sepal aestivation (imbricate), a reflexed 3-trace 15-gap sepal vasculature (non-reflexed 1-trace 5-gap), and the ovule was campylotropous, its micropylar end much enlarged and the antipodal cells were multiplied (unremarkable in these respects).

Oreocallis (only species, O. davisiae) was proposed by Small on very slender evidence. It differed from Leucothoë in inflorescence position (this was a difference of degree only), calyx shape and the thickness of the capsule wall. In his key he also mentioned "flower stalks scaly at the base". In fact both genera have paired, basal bracteoles, so what is meant by this difference is obscure. Leucothoë also has unwinged seeds whilst those of Oreocallis are winged (Fig. 71) and Leucothoë has a marginal band of fibres to its leaf which is lacking in Oreocallis. The differences between these two genera are hardly greater than between the two species placed in Eubotrys, which also differ in whether or not the seed is winged and also in the number of awns; these latter are similar in facies whilst Oreocallis and Leucothoë are rather different.

Eubotyroides (only species, E. grayana) is another deciduous species and has seeds with fringed wings. Its urceolate flowers
are the smallest in the genus, and its stomata are also positionally paracytic; the stomata of the other species of the genus are simply paracytic. Its stamens do not have prominent apical awns, and in this it is similar to Oreocallis. Anatomically it is unremarkable.

Paraleucothoë (only species, P. keiskei) is superficially similar to Leucothoë sensu Small, and Palser (1961a) found that they were similar in embryology and floral anatomy. Paraleucothoë was separated because of its very long, subtubular corolla, long paired anther awns (Fig. 70) and its fasciculate inflorescence. It was also claimed that the seeds had little appendages at both ends, but in the material seen they are simply apiculate (Fig. 71) and are rather similar to those of Leucothoë, although those of the latter genus seem to have a rather looser testa. Paraleucothoë lacks the marginal band of fibres of that genus, and its midrib bundle is of a different shape (Fig. 74). No white deposit was seen on the back of the anthers as has been found in all the other species of the genus, but this may have been due to the fact that the anthers examined were rather immature.

As mentioned earlier L. griffithiana and L. cavaleriei (probably con-specific) are very close to Gaultheria in all aspects except for fruit and seed. They are rather different in facies form other species of Leucothoë and, as Sleumer (1959) noted, one member of each pair of awns is smaller than the other.
also found in *Eubotrys*, where one of each pair of awns may even be missing, and in some species of *Gaultheria*.

It is not thought that generic recognition of any of these segregates would be insupportable. Further work on *Gaultheria* and *Zenobia* may help to elucidate the relationships of these species; meanwhile the classification proposed by Sleumer (1959) seems to be most satisfactory. He recognised 6 sections:—

*Acranthes* (= *Oreocallis*), *Oligarista* (= *L. griffithiana* and *L. cavalryi*), *Paraleucothoe*, *Eubotryoides*, *Eubotrys* and *Leucothoe*. *Paraleucothoe* and *Leucothoe* seem to be quite close to one another and *Oligarista* may also be of this affinity. Lems (1964) found that members from these three sections had a similar density of veins in the leaf and similar vein endings. Sections *Eubotryoides* and *Acranthes* are rather more distinct, whilst section *Eubotrys* is the most distinct of all. It is interesting to see that the two members of this section, although so similar in many respects, differ in seed type and anther appendages, both characters which are not usually so variable.

*Phalerocarpus* G. Don, Gen. Syst. 3: 841 (1834).

Large and erect to small and procumbent evergreen shrubs, leaves alternate, very rarely opposite, entire or serrulate, convolute in bud. Indumentum of gland-headed, long-celled or clavate hairs and unicellular hairs. Inflorescence axillary or terminal, perulate or not; fascicate, racemose, paniculate; reduced to a single, axillary flower; bracts leafy or not, ± persistent, bracteoles several-two, variable in position; calyx articulate with the pedicel. Flower usually 5-merous; often apparently gynodioecious. Calyx lobes small to medium-sized, free. Corolla urceolate or, rarely, campanulate, small, lobes small. Stamens (5, 8) or 10; filaments usually swollen, hairy or not; anthers slightly granular, dorsally with a white deposit, dehiscing by a short (sometimes elongated) slit, appendages one or two pairs of awns, or anthers simply muticous, rarely with a pair of terminal tubules. Ovary 5-locular, placentae ± apical, fruit usually with a fleshy accrescent calyx enclosing a loculicidal capsule, rarely baccate or entirely dry; seeds small, numerous, ovoid or angular; cells of the testa little elongated, with thickened walls.

There are about 220 species in the genus, of which about 83 have been studied. The type species is *G. proculbens*.

This is a large and variable genus which it is both difficult to separate from related genera such as *Leucothoe* and *Zenobia*.
(see above) and also to classify satisfactorily at the infrageneric level.

Generic segregates.

Brossaea. **Brossaea** (type species, *B. coccinea*) was considered to be a genus separate from *Gaultheria* because its calyx lobes were large and hardly accrescent in fruit. The two species studied here both have rather large (>½ mm.) calyx lobes with acute apices and prominent veins, they are definitely accrescent in fruit; their bracteoles also are large. Their stamens have rather slender filaments and small awns (Fig. 72). Anatomically they may be distinguished from all other S. American species in having homogenous pith and a strongly lignified adaxial hypodermis; there is also strong hypodermal lignification at the leaf margin.

Species like *G. barosmoides* have a rather similar calyx, although it does not agree in the other details mentioned. There is considerable variation in stamen type in the genus as a whole, as well as in the nature and extent of the fleshiness of the fruit; species like *G. malayana* are more remarkable anatomically. Thus it is thought that **Brossaea** cannot be maintained as a genus, although it is a distinct group.

Pernettya. **Pernettya** was distinguished from *Gaultheria* on the nature of the fruit - it is truly baccate in **Pernettya** whilst in **Gaultheria** the calyx is the part of the fruit which is fleshy. Most workers have followed Niedenzu (1890) who considered that
Gaultheria was close to Pernettya on anatomical grounds, and who also quoted Hooker himself (who had considered that Pernettya was close to Arbutus, etc.) to show that there were intermediates between the two genera in fruit type.

There is much confusion between the two genera when they are out of fruit and most species of Pernettya have been described under Gaultheria at one time or another. As Burtt and Hill (1935) remarked, they are "... two genera, which, in the Southern Hemisphere especially, cannot be very clearly separated." Pernettya is predominantly a Southern Hemisphere group.

In all details of indumentum the two genera are comparable. Camp (1939) thought that Pernettya species generally had strigose and not setose hairs; where the latter occurred in Pernettya (P. ciliata and P. hirsuta) it was under suspicion of having been introduced by introgression from Gaultheria. A number of species of Gaultheria do have strigose hairs (G. antipoda, G. wardii, G. arachnoidea, sections Hispidulae and Trichophyllae, etc.). In leaf, flower, inflorescence and general facies there is the same similarity between the two.

The fruit character itself is not an all-or-nothing break. P. furiens has a slightly, although definitely, fleshy calyx, whilst that of the Antipodean species, e.g. P. tasmanica, comprises about half the total bulk of the fruit (Fig. 12). In species like P. mucronata the calyx is simply green and persistent.
G. procumbens, and possibly some species of Diplycosia, have brightly coloured ovaries which are slightly fleshy. Although, by the nature of the fruit types involved, one would not expect a wholly intermediate type of fruit, P. lanceolata comes very close to filling this category (Fig. 71). This has both its calyx and ovary wall fleshy; the latter is dehiscent. Dehiscence was observed both in the type and another specimen with mature fruits; in neither case did it give the impression of being caused by the preservation of the specimen. Even if this species is an hybrid (Burtt, in verb.), it can be seen that there are no other characters supporting generic separation.

Anatomical work has not led to the discovery of any distinguishing features (Figs. 74 & 75). Niedenzu (1890) thought that the two were separable on the shape of the spongy mesophyll cells; Pernettya had spreading arms on its spongy mesophyll cells, but these were lacking in Gaultheria. This has not been confirmed by my studies. Both genera have pericyclic phellogen, a pith varying from heterogenous to homogenous, druses in the pith and the cortex, etc. Sleumer (1935) noted that P. mucronata and G. florida were indistinguishable in leaf anatomy, and, apart from a possible difference in the thickness of the leaf, this appears to be true. Stomata and hypodermis, Pieris-type midrib bundle with a variable development of associated fibres all vary in parallel in the two groups. Some species, apparently similar,
may be separated by anatomical differences, but these differences are not of any high level taxonomic significance. Thus *G. antartica* may be separated from *P. pumila* since it has a fibrous "rindbast" the latter lacks. Similarly *G. caespitosa* lacks an hypodermis and has stomata on both sides of the leaf, *P. leucocarpa* has an hypodermis but only abaxial stomata.

The general impression one gets is that Pernettya is a "grade" genus. *P. furiens* seems to show some similarity to the *G. saltensis/G. arachnoidea* group, *P. mucronata* is similar to the *G. florida* group, and the *P. nana/tasmanica* group is similar in general facies to *G. caespitosa*. In the first and last pairs there are substantial differences, e.g. the numerous leaf fibres of *P. furiens*, the presence of only two bracteoles and lack of an hypodermis and libriform tissue in *G. caespitosa*. Further work is needed to establish the exact relationship of the Pernettyoid Gaultherias to the rest of Gaultheria proper, but there can be no doubt that *Pernettya* is not maintainable as a genus.

This is supported by the frequency of hybridisation between the two genera. Many workers have commented on the occurrence of sometimes considerable numbers of hybrids in the field. These hybrids are known, or suspected, from many parts of the range of *Pernettya*. A list is given below:-

P. *pumila* x *G. antartica* (1, 2)  P. *mucronata* x *G. shallon* (5)
*P. mexicana* x *G. conzattii* (4)  *P. macrostigma* x *G. oppositifolia* (6)
P. macrostigma x G. colensoi (3, 6)  P. nana x G. depressa (6)
P. macrostigma x G. depressa (3, 6), P. macrostigma x G. crassa (6, 7)
P. macrostigma x G. antipoda (3, 6), P. nana x G. depressa (6, 7)
P. macrostigma x G. rupestris var rupestris (3, 6)
P. nana x G. rupestris var parvifolia (3)


All these hybrids occurred in the field, apart from P. mucronata x G. shallon which produced the well-known horticultural plant, x Gaulthetta wislevensis. This was the result of an heteroploid cross between the N. American G. shallon (2n = 88) and the S. American P. mucronata (2n = 66). The parents are under suspicion of being autopolyploids or segmental allopolyploids, since they form multivalents at meiosis. This may make the survival of the offspring, some of which are dysploid, more likely; but the Antipodean crosses at least are at the diploid level.

Ten per cent of the seeds of x Gaulthetta wislevensis are fertile (Callan, 1941). Hair (1964) noticed that the hybrids and their parents showed the same low chiasma frequency, and that the pollen was apparently viable. Back-crossing, or recombination amongst the hybrids themselves would seem to be possible from Burtt and Hill's data (1935) on the variability of P. macrostigma x G. depressa at Waimaro in New Zealand.
Chiogenes. The genus Chiogenes was proposed by Salisbury, who noted that it was nearly related to the cranberry. Not until Torrey (1843) published a good description of the plant do the generic characters seem to have been mentioned: the ovary is half inferior and the flowers are 4-merous, also the plant has a distinctive creeping habit. Hooker (1876) was so impressed by the semi-inferior nature of the ovary that he included Chiogenes in his Vacciniaceae, and Watson et al. (1967) still maintain it in the group with inferior ovaries. However, it differs from all other members of that group in its anthers with 4 terminal awns (Fig. 72), definitely partially superior ovary (Fig. 71) and only positionally paracytic stomata. Also it smells of methyl salicylate, like some other species of Gaultheria, and has long-celled hairs. Niedenzu (1890) showed that Chiogenes was similar to the other members of his Gaultherieae in leaf anatomy (Fig. 74), and it is usually considered to be related to these genera today.

Airy Shaw (1910) considered a little known species of Gaultheria, G. subdiviculare, to be close to C. hispidula (he thought that both should be placed in the same series of Gaultheria). Both species usually have 4-merous flowers; these are only rarely to be found in other species of Gaultheria. Their stamen type is very distinctive (Fig. 72), but there are species of Gaultheria series Trichophyllae which link them up to
the more normal type of *Gaultheria* stamen (see especially *G. sinensis*). All members of series *Trichophyllae* have 5-merous flowers with superior ovaries. In the two species mentioned above the fleshy part of the fruit is formed from the floral axis below the ovary, in most other species of *Gaultheria* the calyx lobes are very fleshy whilst the axis is less prominently fleshy. *G. suborbicularis* definitely has a superior ovary, and in this forms a bridge between the more normal species of *Gaultheria* (Fig. 71) and *Chiogenes*. A final floral difference is that these two species lack abaxial corolla stomata, although one was found in this position in *C. hispida*. They are of general occurrence in *Gaultheria*.

In inflorescence *Chiogenes* is unremarkable, both it and *Gaultheria* series *Trichophyllae* having single, axillary flowers with paired, apical bracteoles. Although *Chiogenes* and *G. suborbicularis* are prostrate with almost circular leaves and series *Trichophyllae* is erect with more elongated leaves, there is no major difference in anatomy between the two. Neither has an hypodermis, the stomata are only positionally paracytic and the midrib bundle and the spongy mesophyll are the same. The hairs of *C. hispidula* are very distinctive (Fig. 75); those of *G. suborbicularis* do not seem to have such a regular arrangement of cells at the base. Series *Trichophyllae* has long-celled hairs or hairs with a small, presumably glandular, head (Fig. 75).
Although Palser (1958) found that *Chiogenes hispidula* was very different to *Gaultheria* in floral anatomy only six species of *Gaultheria* sensu lato have been studied, so it is a little early to evaluate the significance of this difference.

It is thought that Airy Shaw (1940) was correct in considering *Chiogenes* to be generically indistinguishable from *Gaultheria*. Although *G. hispidula* is a very distinct species, it is connected to the other species of *Gaultheria* via *G. suborbicularis* and series *Trichophyllae*. The names *Lasierpa*, *Phalerocarpus* and *Glyciphyllla* all seem to be nomenclatural synonyms of *Chiogenes*.

Notes on the infragenetic classification of *Gaultheria*.

The following discussion will be based on the classification of *Gaultheria* in S.E. Asia proposed by Airy Shaw (1940). The variation of some of the characters used is summarised in Fig. 73.

**Section Brossaeopsis.** This section has leaves with palmate or Melastomataceous venation and paired, basal bracteoles. It was thought to form a possible link with the New World species of the genus. Series *Dumicolae* and *Atihehenses* both have a tendency for the midrib bundle at the very base of the lamina to be of the *Lyonia* type; this also occurs in the S. American species. The inflorescence is the same, but some of the S.E. Asian species under consideration have campanulate corollas; these are not found in the S. American species with racemose inflorescences. There may also be a difference in stamen type, but this needs more study.
FIG. 72: ANDROMEDAE - STAMENS OF GAULTHERIA.

FIG. 73: VARIATION OF SOME CHARACTERS WITHIN GAULTHERIA.
FIG. 74: ANDROMEDAEE - GAULTHERIA & LEUCOTHEAE.

1. Leucothoe keiskei, x50; 2. L. axillaris, x50; 3. L. griffithiana, x33;
4. Gaultheria griffithiana, x50; 5. G. antipoda, x50; 6. G. codonantha, x33;
7. G. malayana, x33; 8. G. hispidula, x33; 9. G. suborbicularis, x50;
10. G. sinensis, x50; 11. G. rupestris, x50 (e = epidermis, h = hypodermis,
m = mesophyll, l = ligulation).
FIG. 75: ANDROMEDAEE - GAULTHERIA, GENERAL.

1. "Pernettya" rigida, x50; 2. "P." ciliata, x50; 3. "P." leucocarpa, x40;
4. Gaultheria antarctica, x50; 5. G. caespitosa, x100; 6. "P." furiens, x50;
7. G. adenothrix, x3.5 - small podium (p) at the base of the pedicel; 8. G. eriophylla
stem hair; 9. G. sinensis - stem; 10. G. hispidula - stem hair (e = epidermis,
h = hypodermis).
since the S. American species are very imperfectly known in this respect. The pith is homogenous in these Old World species and heterogenous in the many New World species, but there are no basic anatomical differences. It is not yet clear whether the similarities mentioned are indicative of a real relationship.

All members of section Brossaeopsis have an homogenous pith, positionally paracytic stomata, a single-layered hypodermis and no fibres free in the leaf. *G. codonantha*, of series Dumicolae, has a Lyonia-type midrib bundle even in the middle of the lamina, and this differs from all other members of the section (Fig. 74). It is quite distinct in appearance and has the largest flowers of the genus; its anthers are very long and narrow (c.f. Figs. 72 & 74). It should perhaps be put in a series by itself.

*G. codonantha* has sparse hairs on its filaments and these are rather more common in *G. dumicola* and *G. notabilis*, although according to Airy Shaw they should be lacking in this series (Dumicolae). It is not thought that the difference in distribution of filament hairs which he notes for the three series of section Brossaeopsis have any great significance; this also applies to the occurrence of unicellular ovary hairs.

*G. atjehensis*, *G. notabilis*, and *G. nummularicoides* seem to form a group, although stamens have not been seen of the first-named species. There is a trend in the reduction of the inflorescence culminating in the single, axillary, multibracteolate
flower of *G. nummularioides*. The three species have the same facies and anatomy, although there is difference in corolla shape. *G. dumicola* and *G. abbreviata* are similar to one another and are closer to the *G. atiehensis* group than to *G. codonantha*. They have an inflorescence with a shortened rachis, but which is still several flowered. In this they approach *Diplycosia*, and this similarity is heightened by the sub-Melastomataceous venation the two groups have in common. This was probably the reason for the description of *G. dumicola* under *Diplycosia*, although it differs in stamen type and in the absence of free leaf fibres.

**Section Amblyandra.** This section usually has single, axillary, multibracteolate flowers, anthers without aristae (awns) and leaves with pinnate venation. All three species have long-stalked, gland-headed hairs, and a single flower in the axil of each leaf. *G. adenothrix* has more bracteoles than the other species, but all three have a small "podium" at the base (Fig. 75) of the pedicel. The single flower is a reduced inflorescence, since some individuals of *G. adenothrix* have more than one flower per axil. The anthers are simply muticus (Fig. 72), rarely slightly two-awned, and as Airy Shaw noticed, the corollas are campanulate. Stomata are anomocytic or positionally paracytic; all three species lack an hypodermis and have a marginal band of leaf fibres. *G. adenothrix* has heterogenous pith; the other two species have homogenous pith and may be distinguished from one another in the
sterile state by having, among other differences, a difference in stomatal distribution. *G. humifusa* has stomata on both sides of the leaf; *G. procumbens* only abaxially.

**Section Leucothoides.** This section has a perulate raceme, usually urceolate flowers and ± obovate, pinnately-veined leaves. The group of species centred on *G. fragrantissima* is a fairly natural entity (Fig. 73). All species do have the same inflorescence type, and their anthers are similar, having two pairs of awns. Anatomically, all species have positionally paracytic stomata, a single-layered, rather low, hypodermis and moderately heterogenous pith. *G. griffithiana*, the only species with a campanulate corolla, is not otherwise remarkable. *G. discolor* is the most distinct species anatomically, since its hypodermal cells are very tall (ca 50 μ, in the other species only 30 μ in height); this does not seem to be correlated with any other important characters. The specimens of *G. wardii* seen have dry fruits; this is an unexpected character. I have not seen fertile stamens of this species.

Another group of species in this section centred on *G. pyroloides* was characterised by Airy Shaw as having a ± sympodial inflorescence; the group just dealt with is the same in this respect. Nevertheless, it does seem to form a natural group. In general facies it looks like a reduced version of the *G. fragrantissima* group, its inflorescence is smaller and with
fewer perulae, the flowers are not so congested on the peduncle, the leaves are smaller and the indumentum is generally less prominent, being mostly of the clavate-haired type. As in the previous group the stomata are positionally paracytic, but there is no hypodermis and the pith is very heterogenous. The most reduced member of the *G. fragrantissima* group, *G. pyrolifolia*, which Airy Shaw included in this group but is here allied to the *G. fragrantissima* group, has an hypodermis and its pith is moderately heterogenous; its inflorescence is congested.

The third informal group was characterised by having consistently apical bracteoles (the two other groups were variable in this) and a terminal raceme or leafless panicle. This group has an eperulate inflorescence (c.f. the characters of the section, above), but it does not seem to be natural group. *G. pullei* and *G. punctata* seem to connect on to section *Gymnobotrys* which has an eperulate inflorescence and paired, apical bracteoles. All have the same inflorescence; there is also no difference in anther or indumentum. Section *Gymnobotrys* itself has a very delicate facies which is not so well marked in the other species; it also has a campanulate corolla (the other two species are urceolate), although this may not be an important difference. They all have homogenous pith, and only *G. punctata* has an hypodermis. *G. malayana* superficially fits into this group, but it is very remarkable anatomically, having a lignified
hypodermis and lignified spongy mesophyll cells next to the abaxial epidermis (Fig. 7). G. novaguineensis, with single flowers in the axils of leaves and paired, apical bracteoles (i.e. a terminal leafy raceme), was also placed in the third group, but it and a number of the Malaysian species need much more study before they can be satisfactorily placed.

Section Eugaultheria. This section has small, pinnately veined leaves and solitary, axillary flowers with paired, apical bracteoles. This work fully supports the three series proposed by Airy Shaw, but whether or not they form a natural section is another matter. Series Hispidulæ has been dealt with already under Chiogenes. Although G. hispidula has rather different hairs to G. suborbicularis, a half-inferior ovary and homogenous pith (both varieties have been examined) whilst G. suborbicularis has heterogenous pith (c.f. section Amblyandra) and a superior ovary, the two species are otherwise very similar.

As already mentioned, series Hispidulæ is close to series Trichophyllæ; the two differ in the nature of the fleshiness of the fruit, habit, the 5-merous flowers and partially in stamen and indumentum type.

Series Procumbentes has a single species, G. procumbens, which is isolated both in the section and the genus as a whole. It has relatively large leaves and long pedicels, and its flowers are rather urceolate for a member of section Eugaultheria.
The leaves tend to be pseudo-verticillate, and they have a very prominent fibrous margin. The pith is homogenous, there is no hypodermis and the stomata are paracytic. Despite the fibrous margin to the leaf, there does not seem to be any close connection to section Amblyandra.

The following species have not been definitely placed in an infrageneric hierarchy, and since the sampling of species leaves much to be desired informal groups of species are established as a basis for further, more thorough, studies (see Fig. 73).

G. shallon is in some ways isolated. Its inflorescence, flowers and indumentum are rather like those of the G. saltensis group of S. America, and like them it has a deeply-hooked petiole bundle and heterogenous pith. However, it lacks an hypodermis, and there seems to be a tendency for there to be a very reduced vascular bundle near the leaf margin, thus giving the impression of having a fibrous margin to the leaf. In some ways it is like section Amblyandra, although its inflorescence is much better developed, and the stamens and corolla shape differ.

The Caribbean species of the old genus Brossaeopsis have been dealt with already. The species studied form a distinct entity, and will probably have to be given infrageneric recognition.

There is a large group of S. American species, the G. saltensis group, the members of which are similar in a number of respects. They all have perulate, racemose inflorescences,
bracteoles usually near the base of the pedicel, and urceolate flowers. The stamens usually have slender filaments and anthers with two pairs of awns and dehiscing by slits which are sometimes rather elongated (Fig. 72). Their indumentum is usually well-developed (long-celled hairs or gland-headed hairs), although their leaves are sometimes simply punctate. All have positionally paracytic stomata, a single layered hypodermis which is usually quite un lignified, + heterogenous pith and a deeply-hooked petiole bundle causing the lamina bundle to be transitionally of the Lyonia-type at the very bottom of the lamina, and this may persist further up the lamina, e.g. G. bracteata, G. remayana. About one half the species studied have a few fibres free in the lamina (Fig. 76). Some of the species are superficially very similar to the S.E. Asian species, e.g. G. glabra - G. punctata, G. arachnoi des - G. wardii. It would seem unlikely that it will be possible to separate these S. American species from the S.E. Asian ones at any high taxonomic level.

Three other species, G. conferta, G. barosmoides and G. anastomosans are similar to the preceding in most details of anatomy and morphology. Their inflorescence is reduced to a single, axillary, multibracteolate flower and their leaves are smaller, with the petiole bundle not so deeply hooked (perhaps consequentially). They are probably reduced members of the G. saltensis group. In facies they tend to approach "Pernettya". 
G. florida and G. phillyreifolia are even more similar to "Pernettya" mucronata, etc. in facies and anatomy, (Fig. 74), although they may be distinguished from them in stamens and fruit. They also agree with the G. conferta group in most details of anatomy, inflorescence and indumentum!

Many of the S. American species seen at the Edinburgh and Kew herbaria fall into the G. saltensis and G. florida groups, but there are a number of deviant species. G. nubigena has the anatomy of the G. saltensis group, but has a very delicate facies and a somewhat reduced inflorescence. The stamens are distinctive (Fig. 72), although it seems that they may sometimes be simply apiculate. G. foliosa, G. secunda and G. tenuifolia all lack an hypodermis, although they are otherwise not very remarkable anatomically. G. tenuifolia has the appearance of a member of the G. florida group, but the material seen had only 5 stamens. G. foliosa and G. secunda have single, axillary, multibracteolate flowers, and in this they approach some of the Brazilian species such as G. myrtilloides, G. ulei and G. itatiaiae. G. itatiaiae has ± urceolate flowers, those of the other species seem to be campanulate; there also seems to be a tendency for the bracteoles to become reduced to two and G. itatiaiae, at least, has rather unusual stamens for a member of Gaultheria; they are more like those of Tepuia (c.f. Figs. 72 & 77).
The whole situation is as yet very unclear, but there does not seem to be any link-up of these species, or the G. conferta group, to section Amblyandra, as Sleumer (1952) suggested. No S. American species apart from G. antarctica has been found with a band of fibres at the leaf margin. As Sleumer (1952) noted, it is remarkable that G. itatiaiae (with single, axillary flowers and anthers with terminal tubules) and G. eriophylla (with axillary racemes and anthers with two pairs of awns) should cross, since the species were so very distinct and were representatives of the two main groups of Gaultheria in S. America.

G. caespitosa is an odd species, perhaps because it is so reduced in habit. It has only two bracteoles, stamens in some ways similar to the "Pernettya" tasmanica group (Fig. 72) and a campanulate corolla (c.f. "P", macrostigma). Anatomically it is characterised by lack of libriform tissue and hypodermis (Fig. 75) and stomata on both sides of the leaf.

G. antartica is also distinct. It too lacks libriform tissue and an hypodermis, but it does have a "randbast". Leaf stomata are to be found abaxially only. Its stamens are the normal ones for Gaultheria, in this and to some extent in general facies it seems to approach G. depressa and G. antipoda.

G. depressa and G. antipoda from New Zealand and G. Mundula from New Guinea seem to be rather close, as Sleumer (1966) noted; Airy Shaw (1940) tentatively included the last species in section
Leucothoides. They all have an hypodermis, heterogenous pith and the libriform tissue is very prominent (Fig. 74). They also agree in inflorescence and indumentum. Sleumer's (1952) suggestion that these species belong to section Amblyandra is probably incorrect, since they lack marginal leaf fibres and have an hypodermis. The anthers of G. antipoda have fairly well developed awns, but those of the other two species are less prominent and so are similar to those of section Amblyandra (Fig. 72).

The other species of Gaultheria in New Zealand (G. rupestris, G. oppositifolia and G. paniculata) are very similar to the G. depressa group in all characters apart from inflorescence and fruit (Fig. 74). Burtt and Hill (1935), and Franklin (1962 & 1963) noted that there was hybridisation between members belonging to the two groups. G. rupestris var parvifolia looks very much like G. antipoda/G. depressa. The rupestris group has axillary and terminal inflorescences with many flowers, and their fruits are apparently quite dry: the calyx seems not to become fleshy in fruit.

Finally, in Australia there are two species of Gaultheria, G. appressa and G. hispida, which are similar to the G. rupestris group in anatomy and details of inflorescence and indumentum. The two species have a prominently fleshy calyx and a dense indumentum of long-celled hairs. G. appressa has urceolate
cortex, but it is definitely close to G. hispida. They are similar to the S.E. Asian section Leucothoides.

In the following discussion on the Pernettyoid Gaultherias the classification followed is that of Sleumer (1935).

P. furiens is the most distinct species, and Sleumer placed it in the monotypic section Pseudogaultheria. It is the only species with a combination of paracytic stomata, dense, long-celled hairs and numerous fibres in its leaf (Fig. 75). It also has a racemose inflorescence and a slightly, although definitely, fleshy calyx. In facies it is very like the S. American G. saltensis group, although there are numerous differences between the two (see above).

Sleumer's other section, Archipernettya, was divided into three series. One, the Pumilae, comprises to species "P." Pumila and "P." Leucocarpa. This is a very distinct section with ovoid leaves devoid of serrations or an acute apex. There are usually no libriform cells and I did not see any multicellular hairs on the stem. The style is often not very deeply sunk into the ovary, but more work is needed on this character since a collection of "P." prostrata was found with a non-impressed style.

The other two series, the Purpurae and Mucronatae, were separated because the former had a less pungent leaf apex and its stems and pedicels usually had multicellular hairs. These characters are very variable in the Ericaceae as a whole, both
between and within species. This is especially true of the hair
difference. All the species examined from both series had
multicellular hairs on the stem, and some from both had them on
the pedicel also; there was no difference in hair type. The size
of the leaf overlaps (Purpureae, 1 - 2.5 cm. long; Mucronatae,
0.8 - 2.0 cm. long). Sleumer noted that both series had much
libriform tissue and that the Purpureae quite lacked fibres free
in the leaf. In fact the amount of libriform tissue is very
variable. As Sleumer (1935) noted in the material that he studied,
cultivated plants of "P." mucronata lacked libriform tissue but
this was usually present in wild material. The material in the
garden at Edinburgh also lacked libriform tissue, and this was
even lacking in some of the herbarium material studied; in the
rest there was every gradation between none to a considerable
amount (9 specimens were studied). Exactly the same state of
affairs is to be found in "P." prostrata, of series Purpureae.
This character must be treated with caution throughout the group.
A few fibres are to be found in the mesophyll of species from
both series.

It is possible that there is a group distinguishable within
the combined Purpureae-Mucronatae. Sleumer (1935) keys out the
Australian/New Zealand species together because they have a
fleshy calyx as well as a fleshy ovary. Three of the four
species involved have small leaves (exception "P." lanceolata),
three have an only partially developed hypodermis. The exception, "P." macrostigma, may have its hypodermis well lignified at the leaf edge. Thus Sleumer's claim that all species of Pernettya have a single layered hypodermis is not strictly true; also "P." rigida has a second hypodermal layer, albeit not continuous. Other unusual characters found in this group are the almost awnless anthers of "P." tasmanica and the very slender filaments of "P." nana (Fig. 72). I have not seen the stamens of "P." lanceolata.

The problem of G. pernettyoides

G. pernettyoides is superficially similar to G. novaguineensis and grows in the same region. It was described from material in young fruit, but anatomically it is very similar to Diplycosia. Its pith is homogenous, the midrib bundle is of the Pieris type, the leaf lacks an hypodermis and there are numerous fibres traversing the mesophyll, more than in any other species of the Gaultheria aggregate apart from "P." furiens, G. sphagnicola and G. domingensis. Unfortunately the stomatal type was not observed. In facies G. pernettyoides is very similar to some species of Diplycosia (e.g. D. rupicola) with its single, axillary flowers (probably a reduced fascicle) which have paired, apical bracteoles. It would not be surprising to find that this was a species of Diplycosia, but this must await discovery of flowers.
These notes have, of necessity, been somewhat disjointed. In S.E. Asia the groups proposed by Airy Shaw do seem to represent natural entities, apart from some species of sections Brossaeopsis and Leucothoides. However, a monograph of the genus on a world basis is badly needed to elucidate the relationships of the Australian and S. American species in particular.


Small evergreen shrubs with scattered, evergreen, entire leaves with very revolute margins when mature; a pair of marginal glands near the base. Densely cinerous, or hispid, indumentum. Inflorescence axillary, of few-flowered racemes near the ends of the branches; bracts present; paired, apical, connate bracteoles; calyx apparently articulated with the pedicel. Flowers 5 (-6) merous. Calyx lobes rather large (ca. 6-8 mm.), free. Corolla urceolate, lobes small. Stamens 10 (-12); filaments swollen towards the base, hairy; anthers without appendages, slightly granular in their bottom half, produced into two tubules dehiscing by short apical slits. Ovary 5-locular, placentae subapical. Style impressed; stigma truncate. Fruit probably a dry, loculicidal capsule.

There are ca. 7 species in this genus, but none have been studied. The type species is *T. tatei*.

This genus is distinguishable from all others in the *Gaultheria*
group by its combination of paired apical bracteoles, dry fruit and shortly racemose inflorescence.

In anther type Tepuia is rather like Diplycosia (Fig. 77), although it has somewhat expanded, hairy filaments; it also differs in inflorescence, leaf type etc. Camp (1939) looked at the leaf anatomy of two of the species which he described. He noted that the cuticle was very thick (to be expected from the Ericaceae growing in this region of S. America), that there were abaxial foliar stomata and that the fibrous sheath of even the small leaf bundles was well developed. Unfortunately one cannot see if fibres or an hypodermis are present in the leaf. This might clarify its position with regard to Diplycosia. It is thought that the relationship is not likely to be very close.

In general leaf type Gaultheria lanigera is very similar to the photographs of leaves of Tepuia (see Fig. 77). I did not notice any glands at the base of the leaf in this Gaultheria, but it agrees with Tepuia in having leaves which look like cauliflower ears. In general inflorescence type too Tepuia looks rather like some of the S. American species of Gaultheria, but anther type, leaf glands and, to a lesser extent, fruit and bracteoles, serve to separate the two. It is possible that Tepuia is an offshoot from the Gaultheria stock.


Evergreen shrub with thick ovate leaves, margins entire or
serrate, convolute in bud. Indumentum of long-celled hairs on all vegetative parts and also on the calyx lobes, also unicellular and small, uniseriate hairs. Inflorescence of few-flowered axillary fascicles on the previous year’s growth; bracts small, scarious; bracteoles large, paired, + connate at the apex of the pedicel; pedicel articulate with the calyx. Flower 5-merous. Calyx lobes very large (ca. 8 mm.), † enclosing the flower. Corolla small, urceolate; lobes small. Stamens 10; filaments glabrous, hardly expanded towards the base; anthers without appendages, the basal half granulate, the apical part prolonged into paired, smooth tubes with a terminal slit. Ovary 5-locular, the placentae subapical; style impressed, stigma truncate. Fruit a berry; seeds numerous, cells of the testa rather elongated. The single species in the genus, *P. malayana*, was studied.

This genus is easily to be distinguished from related genera by its large calyx lobes. Although it has a fruit rather similar to that of the Pernettyoid Gaultherias, it may easily be distinguished from them by the different type of anther (Fig. 77), the inflorescence, etc. Anatomically it is distinguishable from all the species of *Gaultheria* seen by its combination of numerous fibres in the leaf, no hypodermis and deeply hooked lamina bundle (Fig. 76).

It is rather similar to *Diplycosia* in general facies. The indumentum and inflorescence types are the same; likewise the
FIG. 76: ANDROMEDAEE - ANATOMY OF SOME OF THE GUALTHERIA GROUP.

1. Gaultheria eriophylla, x40; 2. G. domingensis, x40; 3. Pernettyopsis malayana, x33; 4. Diplycosia kinabulense, x33; 5. D. cinnamomifolia, x33; 6. D. abscondita, x50; 7-9. Diplycosia viridiflora, x10 - successive sections through the node
(e = epidermis, h = hypodermis, l = lignification).
FIG. 77: ANDROMEDACEAE - DIPLOCOSIA, PERNETTYOPSIS & TEPULA.

<table>
<thead>
<tr>
<th>Character</th>
<th>Gaultheria - 83 spp.</th>
<th>Pernettyopsis - 1 sp.</th>
<th>Diplycosia - 29 spp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fruit type</td>
<td>calyx usually fleshy, ovary usually dry</td>
<td>ovary fleshy</td>
<td>calyx fleshy, ovary dry</td>
</tr>
<tr>
<td>Seed type</td>
<td>cells little elongated</td>
<td>cells elongated</td>
<td>cells elongated</td>
</tr>
<tr>
<td>Stomatal type</td>
<td>usually positional paracytic</td>
<td>paracytic</td>
<td>paracytic</td>
</tr>
<tr>
<td>Epidermis type</td>
<td>1 - 2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Cuticle</td>
<td>usually striate</td>
<td>peppery</td>
<td>peppery, rarely striate</td>
</tr>
<tr>
<td>Hypodermis</td>
<td>+ or -</td>
<td>+ or -</td>
<td>+ or -</td>
</tr>
<tr>
<td>Free leaf solereids</td>
<td>abundant in only 3 species</td>
<td>abundant</td>
<td>abundant in all species</td>
</tr>
<tr>
<td>Midrib bundle type</td>
<td>usually Pieris-type</td>
<td>deeply hooked</td>
<td>often deeply hooked, sometimes Pieris-type</td>
</tr>
<tr>
<td>Pith</td>
<td>homogenous in only 23 species, heterogenous in the rest</td>
<td>homogenous</td>
<td>homogenous</td>
</tr>
<tr>
<td>Cortex</td>
<td>homogenous or heterogenous</td>
<td>homogenous</td>
<td>homogenous</td>
</tr>
<tr>
<td>Phellogen</td>
<td>pericyclic</td>
<td>pericyclic</td>
<td>pericyclic</td>
</tr>
<tr>
<td>Node</td>
<td>single trace, single gap</td>
<td>single trace and gap</td>
<td>single trace and gap apart from 2 species</td>
</tr>
</tbody>
</table>

**Table 198 Variation of Some Characters in Gaultheria, Diplycosia and Pernettyopsis**
paired apical bracteoles, urceolate corolla and stamens (Fig. 77). Like most species of *Diplycosia* it has abaxial calyx stomata but no corolla stomata. In anatomy it is identical. The numerous leaf fibres, deeply hooked lamina midrib bundle, paracytic stomata and homogenous pith and cortex are all characteristic of *Diplycosia* (Fig. 76).

*Pernettyopsis* differs from *Diplycosia* in its purple, baccate fruit. In *Diplycosia* the calyx lobes and that part of the axis under the ovary become fleshy (Fig. 71); the capsule itself is dehiscent, although sometimes brightly coloured. The calyx lobes of *Pernettyopsis* are larger than any in *Diplycosia* (see Table 19) and it is thought that there are sufficient differences between the two genera to maintain them as separate, although they are obviously very close.


*Amphicalyx* Blume, Fl. Java. 1: Praef. 7 (1828).

Evergreen terrestrial or epiphytic shrubs with entire or serrate leaves convolute in bud. Indumentum of long-celled hairs, sometimes with a glandular head or clavate hairs, and unicellular or shortly uniseriate hairs. Inflorescence a few-flowered, axillary fascicle borne on wood at least one season old; bracts small and obscure, bracteoles paired, connate, at the apex of the pedicel; pedicel articulate with the calyx.
Flowers usually 5-merous. Calyx lobes usually small, free. Corolla urceolate, small, lobes 1/12-1/3 the length of the flower. Stamens usually 10; filaments rather glabrous, little swollen at the base; anthers granular in their bottom half, apically produced into a pair of tubules of varying length, without appendages. Ovary usually 5-locular, glabrous or with unicellular or shortly uniseriate hairs; placentae arise near the base of the loculi; style very deeply impressed, slender, stigma ± truncate. Fruit a loculicidally or, apparently, irregularly dehiscing capsule surrounded by the fleshy, accrescent calyx lobes; seeds numerous, rather angular; cells of the testa elongated, somewhat thickened.

There are ca. 96 species in the genus, of which 29 have been studied. The type species is *D. heterophylla* (see Sleumer, 1957).

Blume seems to have thought that the name *Amphicalyx* was the proper name for *Diplycosia*, but there is no mention of it in the literature before 1828 and so it cannot be used here.

This is a very distinct genus both florally and anatomically. It has the same fruit as most species of *Gaultheria* and, according to Sleumer (1967), methyl salicylate is probably to be found here as well as in *Gaultheria*. Anatomically it is of the same basic type as *Gaultheria*, but it differs in the always abundant fibres in the lamina mesophyll, the often deeply hooked lamina bundle (Fig. 76) and the occurrence of paracytic stomata. Furthermore,
several species of *Diplycosia* have bands of fibres in the phloem, e.g. *D. caudatifolia*, *D. memecyloides*, *D. penduliflora*, etc.; cells with hippocrepiform thickenings occur towards the outside of the phloem in species like *D. aurea*, *D. abscondita*, etc.

As mentioned above, it is very close to *Pernettyopsis* florally. Both genera usually have abaxial calyx stomata (stomata are found in this position in *D. luzonica*, c.f. Watson, 1965) but lack any corolla stomata. Stomata were found on both sides of the corolla in *D. elliptica* and one collection of *D. microphylla*; they were present only on the abaxial side of the corolla (the condition in nearly all species of *Gaultheria*) in another collection of *D. microphylla* and two collections of *D. kinabulense*.

Usually the smaller-leaved species of the genus lack an hypodermis and have a midrib bundle which is only shallowly arcuate; the larger-leaved species have a single-layered, un lignified hypodermis which is about the same height as the epidermal cells, and the midrib bundle is deeply hooked to circular (Fig. 76). The circular bundles seem to change to the *Pieris*-type higher up the leaf by having a single break on the adaxial side of the bundle and so becoming deeply hooked, a *Lyonia*-type bundle transitional form is at most infrequent. Two species in the genus seem to have nodes with three traces coming from a single gap (*D. viridiflora*, Fig. 76; probably also *D. urceolata*). Other
large-leaved species and all other species in the genus examined had a simply unilacunar node.

5.5.6. THE VACCINIEAE.


Usually evergreen shrubs with entire or serrate, often coriaceous, leaves convolute in bud. Indumentum usually of small, short-stalked glandular hairs and unicellular hairs. Inflorescence usually axillary, racemose or fasciculate, rarely terminal; or single, axillary flowers; perulate or not; bracts and paired bracteoles usually present, deciduous or not; pedicels articulate with the calyx or not. Flowers 4-7-merous, usually actinomorphic.

Calyx limb large-small, variously fused; calyx tube winged or not. Corolla usually gamopetalous, winged or not; often carnose, usually tubular or urceolate. Stamens 5-12; filaments various, fused or not; anthers tubular, sometimes with spurs, sometimes very granular, usually dehiscing by slits or pores at the end of long tubules, rarely tubules lacking. Ovary (3-)5(-10)-locular, inferior; usually slender style impressed in the apex of the ovary, stigma truncate. Fruit fleshy, usually several seeds per loculus, but rarely only one seed or a stone; cells of the testa variable in thickening and size, sometimes mucilaginous.

The Thibaudieae and the problem of the S. American Vaccinieae.

Many earlier workers divided the Vaccinioideae/Vacciniaceae
into two tribes, the Vaccinieae and the Thibaudieae, although since about 1940 the boundary line between the two has often been considered to be so vague as to be unmaintainable.

Hooker (1876) separated the two tribes on corolla texture and size and on filament length and connation. Drude (1897) added a further character; whether or not the pedicel was articulate with the calyx. Smith (1932) did not provide any new evidence. Niedenzu (1890) tried to separate the two anatomically; he separated a Thibaudieae, which had a well-developed hypodermis ad- and abaxially (the latter corresponds to lignified mesophyll), from a Vaccinieae, which lacked these characters. Agapetes, Disterigma and Sphyrospermum were shuttled to and fro between the Thibaudieae and the Vaccinieae by successive authors.

It is impossible to separate the two groups by using these characters in combination, and even using one set of characters there are a whole series of intermediates. Thus some species of Agapetes have flowers as large as the Thibaudieae and their stamens have very short filaments, but anatomically they are very close to Vaccinium as Niedenzu (1890) recognised (see also p. 533). Orthaea has long filaments (Fig. 9), but it has always been included in the Thibaudieae, whilst in Paphia there is every gradation between species with long and species with short filaments.

Sphyrospermum and Disterigma are just like Vaccinium in flowers and stamens, but anatomically they are more similar to
species of the Thibaudieae with large flowers and connate filaments. Niedenzu (1890) placed Vaccinium subcrenulatum in the Thibaudieae (as Eurygania) because of its anatomy; but both Vaccinium section Neurodesia (as he noticed) and section Cinctosandra have species which are anatomically like the Thibaudieae. These anatomical peculiarities are not matched by details of the flower and inflorescence, which are those of Vaccinium. The occurrence of abaxial, lignified spongy mesophyll in Vaccinium microphyllum is likewise independant of any marked differences of the external morphology, and in this case occurs in a different line of evolution to the other examples (see the discussion after Vaccinium).

Williams (1965) described a new species of Vaccinium close to V. poasanum and found that there were no characters, apart from the small size of the flowers, to indicate whether or not it should go into the Vaccinieae or the Thibaudieae. Vaccinium sections Oreades, Brachyceratium, Nemochaeton, Disterigmosia and probably Pseudodisterigma are not close to Vaccinium/in atomic, but in flower size, and to a varying extent in other floral characters, the difference is less marked. Hornemannia is as distinct from Vaccinium as is section Oreades, and has stamens as distinctive (Fig. 78), comparable leaf anatomy (although its spongy mesophyll lignification is more extensive c.f. Figs. 30 & 80) and a thick-walled, campanulate corolla (Fig. 78). Its
flowers are 5-6-merous, but this is not a very important difference. Although the problems here are partly caused by the probable misclassification of these sections of Vaccinium (they might be better excluded) it is still true that the main differences are anatomical ones.

The problem is further complicated by the hitherto unknown occurrence of another anatomical type very different from the previous two types. This is found in Findlaya and Notopora. Here the epidermal cells are very tall and lignified (Fig. 27) on both the adaxial and abaxial surface of the leaf; only Notopora has a tendency for the spongy mesophyll to be lignified and neither genus has an hypodermis. Furthermore, both genera have an open petiole bundle; it is not deeply hooked or closed as in even the small leaved S. American genera like Sphyroaspermum and Killipiella. Although both genera have acuminate leaves and a fasciculate inflorescence they are totally different in stamen type (Fig. 79). Those of Findlaya are like those of Orthaea, and indeed Findlaya has often been included in Orthaea (e.g. Smith, 1932). Again anatomy does not tally with floral characters. Both Notopora and Findlaya have been included in the Thibaudieae without any reservations at all, except that Notopora has been considered to be very different from all other Ericaceae in its stamens.

All that can be said is that many S. American genera, together
FIG. 78: VACCINIEAE - FLOWER & STAMENS (1).

1. & 2. Homemanniia racemosa, 1. stamen; 2. corolla; 3. Vaccinium latifolium;
4. V. poasannum; 5. Anthopteropsis insignis; 6. Psammisia ferruginea;
7. Ehibaudia pachyantha; 8. Gaylussacia baccata - T.S. ovary; 9. Cavendishia striata - strong dimorphism (all x10 except 2, x5 and 8, x15).
FIG. 79: VACCINIEAE - STAMENS (2).

1. Notopora schomburgkii - a-c major stamen, various views, d, a minor stamen;
FIG. 80: VACCINIACEAE: - MIDRIB ANATOMY.

1. "Agapetes" scortechinii, x33; 2. Agapetes (= Paphia) vitis-idaea, x50;
3. Paphia meiniiana, x50; 4. Costera loheri, x33; 5. C. cyclophylla, x50;
6. Vaccinium poasanum, x50; 7. V. latifolium, x50; 8. Anthopteropsis insignis,
x60; 9. Macleania salapa, x60 (e = epidermis, h = hypodermis, m = mesophyll,
1 = lignification).
with Costera, Dimorphanthera and Paphia from S.E. Asia, have a complex of anatomical characters which are rare elsewhere in the Vaccinieae. These characters are a well developed, often lignified hypodermis, a more or less extensively lignified spongy mesophyll, expanded vein endings and a petiole bundle which usually forms a closed cylinder of xylem and phloem. Niedenzu's (1890) difference of guard cell size awaits confirmation.

Floral characters are less distinct, although genera in S. America show a very considerable range of stamen type not found elsewhere in the family these types are not basically different to that found in Vaccinium, and in some genera the stamens are apparently identical to those of Vaccinium (Figs. 78, 79 & 84).

Within the S. American genera themselves the taxonomy is very chaotic, as has become apparent even in the limited work carried out (64 species from 20 "genera"). It seems that the variation in stamen type has been misinterpreted and overweighted in classification, and this also applies to the winging of the calyx and the corolla. However, it also seems that a careful reassessment of the stamen types in conjunction with anatomical evidence will be of the greatest help in establishing natural groups. MacBride (1944) is justified in his strictures on the state of classification of these genera.


Schollera Roth, Fl. Germ. 1: 170 (1788).
Acosta Lour., Fl. Coch. 276 (1790).
Epigynium Kl., Linn. 24: 49 (1851).
Rigiolepis Hook. f., Ic. Plant. T. 1160 (1873).
Corallobotrys Hook. f., Gen. Plant. 2: 575 (1876).
Hugeria Small, Fl. S. E. U. S. 896 (1903).
Herbothemnus Small, Man. S. E. Fl. 1017 (1933).

Evergreen or deciduous shrubs with entire or serrate leaves convolute in bud, usually scattered, sometimes with marginal glands near the base of the lamina. Indumentum usually of short, clavate-headed glandular hairs, rarely long-stalked glands, also unicellular hairs. Inflorescence variable, usually an axillary raceme, also single, axillary flowers; bracts and paired bracteoles usually present, + deciduous; pedicel articulate with the calyx or not. Flowers (4-)5(-6)-merous. Calyx lobes usually free,
sometimes reduced. Corolla usually gamopetalous, urceolate, less commonly campanulate, rarely polypetalous. Stamens usually 8 or 10; filaments free, hairy or not; anthers with terminal tubules, thecae granular, spurred or not. Ovary 3-6 or pseudor 10-locular, inferior; style impressed, usually slender, stigma truncate. Fruit fleshy; seeds several to one per loculus; testa usually a single layer of cells, the cells elongated or not, thickening various.

There are about 300+ species in this genus, of which about 120 have been studied intensively. The type species is **V. myrtillus**.

**Nomenclature.**

All the names above refer to species which are included in **Vaccinium** as here delimited, with the possible exception of **Malesia**, **Gavinium** and **Acosta**. There is also a name **Myrtillus** Gilib. apparently referable to **V. myrtillus**. Detailed discussion as to the history of the various segregates is considered to be out of place at this stage.

Although **V. myrtillus** is accepted as the type of the genus, the generic description in Gen. Plant. (1754) is obviously best fitted by **V. vitis-idaea**.

**Sectional limits in Vaccinium.**

The following, necessarily much curtailed, discussion of the sectional limits is based on Sleumer's (1941) classification of
the genus. As mentioned in section 2.1.3., the relative time and position of initiation of the floral and vegetative shoots has been little used here. Characters which have proved to be of most use are the persistence of the leaves, type of inflorescence and corolla, the articulation of the calyx, the number of ovary loculi and a number of anatomical details. Stamen type and the presence of appendages has been less used. Many of the differences in the arrangement are caused by apparent misobservations rather than the application of new characters. The variation of some of the characters used with the groups recognised is shown in Fig. 81.

On the whole, Sleumer's classification is confirmed by the new data added. The main changes have been in the removal of most of the species from section 2, *Vitis Idaea* to a modified section 19, *Conchophyllum*, and the recognition that E. Asian species previously placed in section 8, *Cyanococcus* are close to section 7, *Hemimyrtillus*. It has been found impossible to separate sections 20, *Bracteata* and *Eococcus* in S.E. Asia, so section 20, *Bracteata*, has been enlarged; the C. American species of section *Eococcus* have provisionally been removed from this part of *Vaccinium* (see 12b). The differences between sections 27, *Disterigmopsis* 28, *Brachyceratium*, 29, *Nemochaeton* and 30, *Oreades* and the rest of *Vaccinium* have been shown to be very great. More work is still needed, especially in sections 6, *Cinctosandra*,...
FIG. 81: VARIATION OF SOME CHARACTERS WITHIN VACCINIUM.

(numbers refer to the sections in the text)
MacroDelma and also on the species of group 12b. Section Pachyantha is dealt with under Dimorphanthera.

The sections are numbered consecutively; the numbers in parentheses after the name of the section are the numbers of the sections in Sleumer's classification.

1. Oxycoccus (1). This section, with its polypetalous 4-merous flowers (Fig. 82; Sleumer calls them 5-merous) and leaves with revolute margins, is one of the most distinct entities in Vaccinium as far as is known. The anthers dehisce by terminal pores (Fig. 82); they lack appendages. This might be expected with the lobes of the corolla being so recurved.

The differences between V. macrocarpon and the other members placed in this section are of the order of sectional differences elsewhere in the genus. The testa of V. macrocarpon is more prominently several layered and there are stomata on both sides of the corolla, its flowers are borne singly in the axils of the lowest leaves of the same year's growth. The other species lack corolla stomata (they were not found in 3 collections of V. oxyccoccus, although they are recorded from here by Watson, 1965) and the subfasciculate inflorescence is borne on the previous year's growth, although rare, aberrant inflorescences like those of V. macrocarpon have been seen in V. oxyccoccus.

2. Vitis-Idaea (2). Sleumer lists 15 species in this section,
but it is really monotypic.  *V. vitis-idaea* differs from the other species previously placed in the section in having campanulate, deeply-lobed, 4-merous flowers (urceolate, small lobes, 5-merous), anthers dehiscing by terminal pores (slits, c.f. Figs. 82 & 84) and marginal leaf fibres and a pericyclic phellogen (no such fibres, phellogen is hypodermal). The spongy mesophyll cells of *V. vitis-idaea* are very thick-walled, but un lignified, and they are as a result very rigid, as Niedenzu (1890) noticed. This type of mesophyll is perhaps comparable to that of section *Pyxothamnus*; the affinities of *V. vitis-idaea* certainly seem to be with N. American rather than S.E. Asian sections. Hybrids between it and *V. myrtillus* (*V. x intermedium*) are well known. *V. myrtillus* belongs to section *Myrtillus* which differs in inflorescence, leaf, anatomy, etc.; it is rather surprising that the two should cross.

3. *Herpothamnus* (3). This is a monotypic section; the only species *V. crassifolium*, grows in N. America. Its small, shortly pedunculate, racemose inflorescences are scattered along the growth of the preceding year. Its small stamens dehisc by pores rather than by slits (Fig. 82), and its ovary loculi are not divided by inpushings (undivided loculi are also found in the first two sections). Anatomically it is characterised by its lignified epidermis and the moderately, but not very, thickened walls of the spongy mesophyll. Camp (1945) mentions
that in its swollen stem base it was rather similar to S. American species.

4. Pyxothamnus (14). Here the inflorescences are more restricted to the apex of the shoot and the peduncle is longer. The ovary is again 5-locular, and the stamens rather similar to the previous section, although those of V. ovatum have small spurs (Fig. 82). The three species examined all have thick-walled, rigid, lignified spongy mesophyll cells (Fig. 83); this lignification sometimes spreads to the palisade tissue. Meristic variation is common in members of this group. Rather surprisingly perhaps, V. ovatum is recorded as hybridising with V. darrowii, of section Cyanococcus, an apparently very different species with a pseudo-10-locular ovary (Darrow & Camp, 1945).

5. Neurodesia (13). Sleumer distinguished this section from the preceding by its raised, and not impressed, veins; this difference is reflected in leaf anatomy. All five species examined have tall epidermal cells (height: breadth ratio >1) which tend to be lignified. An hypodermis is erratic in its occurrence, but if it is present it too is lignified; the whole of the girder of tissue surrounding the midrib bundle is also lignified (Fig. 83). The spongy mesophyll is not generally lignified, but abaxially there may be a layer of lignified cells next to the epidermis. The stamens are unremarkable, dehiscing by short slits or pores (Fig. 82). The ovary is 5-locular;
FIG. 82: VACCINIEAE - VACCINUM (1).

1. Vaccinium oxycoccus, x6 - flower; 2. V. oxycoccus - testa; 3. V. macrocarpon;
4. V. crassifolium; 5. V. confertum; 6. V. ovatum; 7. V. vitis-idaea;
8. V. crenatum; 9. V. oxul; 10. V. stanleyi; 11. V. secundiflorum;
12. V. myrsinites; 13. V. canadense; 14. V. hirtum; 15. V. arctostaphylos;
16. V. cylindraceum (all stamens x10).
FIG. 83: VACCINIEAE - VACCINIUM (2).

1. *Vaccinium floribundum*, x50; 2. *V. crenatum*, x66; 3. *V. subcrenulatum*, x66;
x66; 8. *V. uliginosum*, x100; 9. *V. uliginosum*; 10. *V. praestans*; 11. *V. kunthianum*;
12. *V. stamineum* (all stamens x10; e = epidermis, h = hypodermis, m = mesophyll,
1 = lignified).
there is a notable tendency for some species at least to have a terminal, paniculate inflorescence. This section does not seem to be very close to the preceding one.

6. Cinctosandra (11). This is a very heterogenous group of which I have seen very limited material. Relationships have been proposed between this section and the preceding but, although there are some points of similarity, more work is needed on this. The epidermal cells are not tall; the hypodermal cells where present are about 2X the height of the epidermal cells and are lignified. Three out of four of the species studied anatomically have lignified layer(s) of spongy mesophyll adjacent to the abaxial epidermis (Fig. 83). The stamens are very variable (Fig. 82), spurred or not. 3 species seen have very deeply lobed corollas (2/5-⅓) and exserted stamens, another is ± urceolate and with included stamens (V. exul). V. stanleyi is intermediate, it also lacks an hypodermis.

The next group of sections are not close to the preceding.

7. Hemimyrtillus (7). This section has 5-locular fruit and articulated pedicels. The stamens may be with or without spurs (the latter in V. cylindraceum, Fig. 82). Both V. padifolium and V. arctostaphylos have stomata on both sides of the calyx and corolla, but in the sole collection of V. cylindraceum seen they were found abaxially only. The three species have ± tubular flowers. Anatomically they are not remarkable, except that the phellogen is very late in developing.
*V. hirtum* and *V. versicolor* were placed in section *Cyanococcus*, but they both have 5-locular ovaries (all other species of section *Cyanococcus* seen have pseudo-10-locular ovaries); *V. hirtum* also often has the stomatal distribution of *V. padifolium*, although both it and *V. versicolor* seem to have only abaxial stomata at times, thus approaching *V. cylindraceum* and also section *Cyanococcus*. *V. versicolor* also has spurred anthers. Although the anthers of section *Cyanococcus* are supposed to be unspurred, a collection of *V. corymbosum* has been seen with spurred anthers.

Both *V. hirtum* and *V. versicolor* have a short inflorescence axis, and in this too they are similar to section *Cyanococcus*. The phellogen in *V. hirtum* is initiated in wood only one season old, and in this it differs from either section. These E. Asian species are removed from section *Cyanococcus* and are provisionally put in section *Hemimyrtillus*. They seem to be intermediate between the two sections in several respects. According to Darrow and Camp (1945), *V. arctostaphylos* will hybridise with *V. australe* (section *Cyanococcus*).

8. *Cyanococcus* (9). This section has pseudo-10-locular ovaries, stomata only on the abaxial surface of the calyx and corolla and anthers usually without spurs. The inflorescence is a few-flowered raceme with a short peduncle, the pedicels are articulated and the plants are deciduous. All species seen are
anatomically similar to the preceding section; their thin leaves have no hypodermis, the epidermal cells are low and un lignified and the midrib bundle is of the Pieris-type (Fig. 83).

9. Pseudocyanococcus (4). The sole species, *V. myrsinites*, is under suspicion of being a hybrid between *V. tenellum* and *V. darrowii*, two members of the preceding section (Camp & Gilly, 1943), and it is interesting to see that it hybridises with at least 5 species from that section (Darrow & Camp, 1945). Its stamens are similar to section Cyanococcus (Fig. 82), and it also has a similar inflorescence and a pseudo-10-locular ovary. Despite this, it has a very different facies; it is evergreen and they are deciduous. It is superficially like section Rexothamnus, but this similarity is not confirmed by its anatomy which is unremarkable, apart from the rather prominent palisade tissue (4 layers of it, Fig. 83).

10. Uliginosa (6). This section is superficially similar to section Cyanococcus, but its ovary is 5-locular and its anthers always prominently spurred (Fig. 83). Its leaves, although very thin, have very well developed lignification of the midrib bundle (Fig. 83). Neither species seen has corolla stomata, and Watson (1965) also failed to find them here. There are abaxial calyx stomata. Wasscher (1947) found that *V. uliginosum* had large amounts of xylem parenchyma, further work is needed to see if this will be of use in separating it from other sections of Vaccinium.
11. **Praestantia** (5). The sole member of this section, *V. praestans*, agrees with the preceding section in most details. It has the same inflorescence, ovary and general anatomy; it too seems to lack corolla stomata, although the condition of the flowering material was very poor. The petiole is rather broad, and the petiole bundle divides towards the top before entering the lamina. The stamens do have spurs (Fig. 83), although Sleumer records them as being absent. The corolla seems to be ± tubular, with lobes about 1/4 its length. *V. praestans* is also separable from the previous section on its habit; it is a subprostrate shrub, whilst members of section *Uliginosa* are small, but erect, shrubs.

12a. **Batodendron** (8). This section was separated from section *Cyanococcus* by its ± persistent leaves, foliaceous bracts and spurred stamens. The inflorescence axis is much longer than in section *Cyanococcus*, and the two evergreen members have slight hypodermal lignification at the leaf margin. *V. arboreum*, the deciduous species, differs in facies from the other two species; it also has a campanulate corolla, whilst they are urceolate.

12b. The Central and South American species of section *Eococcus*.

These species are similar to the S.E. Asian species of section *Eococcus* in anther type, pseudo-10-locular ovary and racemose inflorescence. However, their phellogen is very late in developing and has not been observed in the herbarium specimens examined.
This suggests that it is pericyclic, and not hypodermal as in the S.E. Asian species. The American species are thus provisionally excluded from section Eococcus. Sleumer (1936) keys out *V. meridionale*, *V. cordatum* and *V. corymbodendron* as having 5-locular ovaries, although later (1941) they were all placed in this section with pseudo-10-locular ovaries. *V. meridionale* definitely has the latter type, *V. corymbodendron* apparently the former. More work is needed on this group of species.

13. Polycodium (10). This is another pseudo-10-locular section with spurred anthers. It differs from all other sections previously considered in having pedicels continuous with the calyx tube. Another peculiarity, found nowhere else in the family, is that the flowers are open even in the young bud, long before anthesis. It is a very distinctive group. The mature flowers are campanulate, and this and the leafy inflorescence give the plants something of the appearance of *V. arboreum*, from which they may be easily distinguished by the above-mentioned characters. The three species seen tend to have laciniate tips to their anther tubules (Fig. 83), but whether or not this is to be found in all species of this group, I do not know. Ashe (1946) considered this section to be generically distinct, and in it he recognised 21 species in six sections.

The four following sections are probably fairly close to one
another. All have single flowers borne in axils of leaves of the current year, pedicels not articulated with the calyx and simply 4- or 5-locular ovaries.

14. *Oxycoccoides* (32). This section is notable for its flowers, which are superficially like those of section *Oxycoccus*. However, it differs from that section in inflorescence, leaf type, distribution of stomata on the flower, etc. Section *Oxycoccoides* is 4-merous, polypetalous and has unspurred stamens. Bracteoles are present and there are abaxial calyx and corolla stomata. The extent of the lignification around the midrib bundle is rather extensive. The flowers are borne towards the ends of the shoots of the same season (compare the two following sections), and in some cases almost every leaf axil on the shoot bears flowers. The main growth of the plant is carried out by shoots other than those which bear flowers.

15. *Myrtillus* (29). The single flowers are borne in the axils of the lowest leaves on the vegetative shoot, the main axis continues and there are ordinary vegetative buds in the highest axils. The flowers are urceolate and 5-merous, no bracteoles have been seen and the anthers are always spurred. This section is notable for the tendency of stomata to occur on both sides of the leaf (4/6 species examined). There is considerable variation in the occurrence of calyx and corolla stomata; the former is sometimes so small that they would not be expected to
occur. Only a single abaxial corolla stoma was found in *V. myrtillus*, Watson (1965) did not find any.

16. *Macropelma* (31). All the Hawaiian species of this section seen have the same inflorescence as section *Myrtillus* and, like it, their anthers are spurred. They are evergreen; members of the preceding section are at best weakly evergreen. Bracteoles are present, and the calyx lobes are especially large in some species. *V. reticulatum* and *V. peleanum* have very prominent bast and libriform tissue, and some species have a well developed, un lignified hypodermis.

Although this group of species forms a distinct entity, the type species of the section (*V. cereum*) and the other southern species examined (*V. rana*) are somewhat different. Although similar in calyx, stamen, general anatomy, etc. they differ in inflorescence, since the growth of the inflorescence axis is determinate and all leaves have flowers in their axils (similar to many collections of species in section *Oxyacccoides*). *V. cereum* definitely has a pseudo-10-locular ovary, although the intrusions of the ovary wall may not be quite as prominent as elsewhere. However, the calyx tube and the pedicel do seem to be continuous. These species may properly belong to some other section, even section *Bracteata*; they are similar in facies to *V. macgillivrayi*, although they do not have the epidermal characters of that species (see below). It would be of help to
know where the phellogen was initiated, since in those Hawaiian species in which a phellogen has been seen it is pericyclic, in section *Bracteata* it is hypodermal.

17. **Cyanophthalmos (30).** This monotypic section (*V. modestum* is the only species) has its flowers borne in the topmost one (or few) axils of the shoot of the same season. It is remarkable chiefly for the long-pedicillate flowers with subapical bracteoles (Fig. 5); its stamens have rather stouter filaments than occur in section *Myrtillus* (Fig. 84), but are basically similar, and its midrib bundle has rather extensive associated lignification. Corolla stomata have not been seen, and in this it agrees with some members of section *Myrtillus*, to which it is similar in most aspects other than those mentioned.

18. **Ciliata (33).** This has the same inflorescence as section *Oxycoccoides*, but it differs in having a pseudo-10-locular ovary, pedicels articulate with the calyx tube and in flower. *V. sieboldii* has very conspicuously campanulate flowers, while the glandular hairs of *V. oldhami* have very long stalks. I am not sure as to the affinities of this section. The phellogen position was not definitely ascertained, although it may be hypodermal.

The next group of sections agree in having an hypodermal phellogen (the only species in the Ericaceae with this), an inflorescence borne on the wood of the preceding season and a
pseudo-10-locular ovary. They link on very closely to Agapetes (for the distinctions of the two genera, see later).

19. Conchophyllum (21). Only three named and one unnamed species have been seen. V. triflorum, V. pseudotonkinense and the unnamed specimen are dealt with under Agapetes. The other species, V. conchophyllum itself, of which I have seen the type, has a shortly racemose inflorescence borne near the end of the branches, an urceolate corolla and differs in these characters from these other species (Sleumer keys out the whole section as having a campanulate or subcampanulate corolla). The species which have been seen and excluded from section Vitis-Idaea (above) agree in all respects with V. conchophyllum (see Fig. 84 for stamens), so they are transferred to section Conchophyllum. For the species involved, see Fig. 81. V. monetarum has leaves serrate at the top and thus approaching the larger, apically serrate leaves of V. sikkimense in type. V. sikkimense is similar to V. glauco-album and V. gaultheriiifolium, both previously included in section Galeopetalum. They differ from that section in corolla shape, shorter inflorescence axis and also in having a petiole bundle which is not deeply hooked. V. manipurense shows some points of similarity to Agapetes (see later).

20. Bracteata (27) and Eococcus (26). The American species of the latter section have already been dealt with. The only
FIG. 84: VACCINIEAE - VACCINIUM (3).

1. Vaccinium plecanum; 2. V. geminiflorum; 3. V. myrtillus; 4. V. chaetothrix;
5. V. conchophyllum; 6. V. sikkimense; 7. V. monstereum (all x10); 8. V. subfalcatum - abaxial leaf; 9. V. sp? (section Garianthe), x10 - swollen style;
10. V. uroglossum, x10; 11. V. uniflorum, x20; 12. V. nuttallii; 13. V. vacciniaceum; 14. "Agapetes" leptantha; 15. V. acuminatum; 16. V. modestum (all x10); 17. V. kachinense, x25; 18. V. vacciniaceum, x75; 19. "A." leptantha, x75 (e = epidermis).
difference which one can find between these two sections from
Sleumer's description is that the bracts and bracteoles are +
foliaceous and persistent in the former group and smaller and
deciduous in the latter. This character breaks down
completely, even within _V. bracteatum_ itself there is much
variation in bract size and persistence. All the S.E. Asian
species seen from these two sections (apart from _V. carlesii_ and
_V. yaoshanicum_) agree in having serrate, pinnately-nerved leaves
which have protuberances on the midrib on the abaxial surface
(Fig. 84), although this last character is not always constant.
There is never an hypodermis, but the group may be recognised
anatomically in that the adaxial epidermal cells are slightly
sinuous (even in _V. macgillivrayi_, from the New Hebrides), the
cuticle is striate/the petiole bundle is shallowly hooked. The
anthers are usually spurred, although Sleumer says that spurs are
rare in section _Bracteata_; this is not so. _V. carlesii_ is
anomalous in having campanulate flowers, but it otherwise agrees
fairly well with this section. _V. yaoshanicum_, also with
campanulate flowers, has the facies of some of the species of
section _Galeopetalum_ and so it is tentatively excluded. The two
sections, _Bracteata_ and _Eococcus_, are indistinguishable and so
they must be combined as section _Bracteata_, since this name was
the first published. The relationships of the section are to
section _Conchophyllum_ and to _Eupigynium_. Copeland (1930)
completely mistook the relationships of species like *V. neilgherrense*, etc. because he thought that they had 5-celled ovaries with only one seed per ovary being produced.

21. *Euepiphytum* (25). This section was included in section *Bracteata* by Sleumer (1967b), but the two sections are distinguishable on several counts. The leaves of section *Euepiphytum* are entire (apart from *V. stapfianum*) and have palmate venation; there may be marginal glands, and if there are protuberances on the abaxial midrib these are never so large as in section *Bracteata*. The adaxial epidermal cells have straight walls and the cuticle is not striate. An hypodermis is very common, and the petiole bundle is deeply hooked, indeed in *V. claoxyylon* the midrib bundle is usually of the *Lyonia*-type. These differences are not very great, but there do seem to be two recognisable entities in section *Bracteata* sensu Sleumer (1967b).

*V. stapfianum* has serrate leaves and is close to *V. coriaceum*. The two agree in their small, rather thick, serrate leaves, a shallowly hooked petiole bundle and very thick-walled, rigid, spongy mesophyll cells which, in *V. stapfianum* at least, are lignified. The lignified cells are towards the centre of the leaf, and not adjacent to the abaxial epidermis.

22. *Rigiolepis* (24). This section has very small flowers and slender peduncles. All species examined have spurred anthers (Fig. 84) and the leaves have marginal glands near the base.
(Fig. 16). Of the five species studied anatomically all lacked an hypodermis. As in the preceding section the occurrence of corolla stomata is variable.

23. Neojunghuhnia (20). Only two species of this section, which is characterised by its large, acute sepal lobes, were studied in detail; no hypodermis was seen. The section is close to both Rigiolepsis and Euepignyrium in floral details.

24. Oarianthe (22). This section is characterised by its small leaves and inflorescence which is reduced to one or two flowers. As in section Euepignyrium, the occurrence of an hypodermis is variable. Anther spurs are not common in this section, and the style is often swollen (Fig. 84). Neither calyx nor corolla stomata have been observed in any of the specimens examined.

25. Eupignyrium (28). This section was separated from the others by its pseudo verticillate leaves which were usually serrate. The racemes were rather long and the anthers generally spurred (in fact most species are without spurs). The inflorescence is perulate at the base, and subcorymbose. All members of this section studied anatomically lack an hypodermis and have a circular or Lyonia-type midrib bundle, often with a dorsal crest of fibres (Fig. 84). The significance of this last character is still unclear. There is a tendency for the spongy mesophyll cells away from the abaxial epidermis to be lignified in some species.
"Agapetes" lentantha and "A", acuminata are included in this section (see the discussion after Agapetes) and V. kachinense is transferred here from section Galeopetalum. These species agree with section Epigynium in all particulars except that the last two have leaves scattered along the stem, and not pseudo verticillate. This varies greatly at the sectional level in Agapetes, and is not very important. Their anthers are similar to those of species of section Epigynium (Fig. 84).

26. Galeopetalum (20). This section is very much the residuum remaining after the other sections have been delimited. All members are supposed to have campanulate flowers, but several are urceolate. V. piliferum, which has urceolate flowers, is included in Agapetes pro tempore, and V. lanigerum will probably have to be placed in a monotypic section. It differs from the other species of this group in its subfasciculate inflorescence with very large bracts and almost sessile flowers (1 mm. pedicels), and its hairs are of a type not yet found in any other Vaccinieae (Fig. 22). Of the other species studied in detail, all that can be said in the way of generalisation is that they lack an hypodermis and have axillary racemes. Midrib bundle type is very variable; some species have similar bundles to those of Epigynium and some to those of Euepignyium. This section needs much more study.

Of the five remaining sections, four are those which show a
close approach to other S. American genera of the Vaccinieae (see above). I have not been able to study section *Pseudodisterigma* (16). Decisions as to the final rank of these sections must await a revision of the S. American genera (see above).

27. *Disterigmopsis* (12). The sole species, *V. didymanthum*, has a large-celled, lignified hypodermis and a layer of spongy mesophyll cells next to the abaxial epidermis. The petiole bundle is circular; no other species of *Vaccinium* with such small leaves is known to have circular bundles. The palisade tissue has banded thickenings on the walls. Its fasciculate inflorescence is also very unusual for *Vaccinium* sensu stricto. I could not find stomata on its tubular corolla or on its calyx; the stamens are unremarkable (Fig. 79).

27. *Brachyceratium* (15). In anatomy this section agrees very well with the preceding, although the hypodermis is not so strongly lignified. The corolla is campanulate and deeply lobed. Again stomata have not been found on the flower. The stamens are not dissimilar to those of section *Disterigmopsis*, and again the inflorescence is fasciculate and the calyx and the corolla tube are continuous. The leaf hairs occurring in both species of this section are of a very unusual type (Fig. 21). Sections *Disterigmopsis* and *Brachyceratium* seem to be fairly close to one another.
29. Nemochaeton (18). *V. latifolia* has a 1-2 layered adaxial hypodermis, the cells of which are very large and slightly lignified. Abaxially there are three layers of lignified spongy mesophyll next to the epidermis (Fig. 80). The racemose inflorescence has large bracts (ca. 18 mm.) and the calyx tube is articulated to the pedicel. The tubular corolla has stomata abaxially, and the anthers dehisce by rather long, introrse slits (Fig. 78). This is a very distinct section from all points of view, and it has the facies of a Cavendishia.

30. Oreades (17). *V. poasanum* is anatomically similar to the preceding section, although there is only a single-layered hypodermis and abaxially only two layers of lignified tissue (Fig. 80). The inflorescence axis is short, the bracts small and the corolla thick-walled and campanulate. Again, most of these characters are unusual for a member of *Vaccinium*, and the distinctness of the section is compounded by the stamens, which are unparalleled in the genus (Fig. 78). Sleumer noted that it was similar to *Hornemannia*, and indeed the differences between *Hornemannia* and *Vaccinium* are no greater than between section *Oreades* and the rest of *Vaccinium*.

AGAPETES D. Don ex. G. Don, Gen. Syst. 3: 862 (1834).

Caligula Kl., Linn. 24: 28 (1851).

Pentapterygium Kl., Linn. 24: 47 (1851).

Epiphytic or terrestrial evergreen shrubs, often with swollen stem bases or roots; leaves small to large, serrate to entire, if entire usually with at least one pair of marginal glandular spots; convolute in bud; scattered or pseudo-verticillate. Indumentum of long-stalked gland-headed hairs or, more rarely, long-celled hairs and unicellular hairs. Bud scales large and like stipules, or small and inconspicuous. Inflorescence always axillary, on wood one season old, or ramiflorous; corymbose or fasciculate, rarely racemose, few-flowered; bracts and basal paired bracteoles small, pedicel articulated with the calyx, often long, sometimes expanded at the apex, or small and flowers ± sessile. Flowers 5-merous, rarely zygomorphic. Calyx tube winged or not, calyx limb large to small, variably fused or lobes free. Corolla usually 1.5 cm. <, tubular, more rarely campanulate or urceolate, lobed for 1/12-1/2 its length, sometimes densely glandular hairy; red or rarely white or yellow in colour, often banded; sometimes with antipetalous wings. Stamens 10, filaments long or short, usually hairy and free from each other; anthers with a granular basal half, very rarely hairy, prolonged apically into smooth tubules dehiscing by introrse slits, spurred or not; anthers often connate by thecae or tubules. Ovary inferior, pseudo-10-locular, style impressed, slender or rarely swollen at the apex, stigma ± truncate. Fruit fleshy; seeds several, testa with rather
elongated cells, cells sometimes mucilaginous.

Ca. 85 species, of which at least 46 have been studied. The type species is *A. setigera*.

In the discussion which follows the infrageneric classification of *Agapetes* is that of Airy Shaw (1959) and that of *Vaccinium* is Sleumer's (1941). The Malaysian plants previously included in *Agapetes* are excluded from *Agapetes* sensu stricto and are dealt with under *Paphia*.

**Generic synonyms.**

*Caligula* was based on two species, *C. pulcherrima* and *C. odontocera*; both these species are now referred to *A. odontocera*. This species is in no way remarkable when compared with other species now placed in *Agapetes* subseries *Coriaceae*, having the same tubular flowers with fairly large lobes, stamens with short filaments and the same anatomy. Subseries *Coriaceae*, as will be seen, is not generically distinct from the other subseries of *Agapetes*.

*Pentapterygium*, as its name implies, differs from *Agapetes* in having a conspicuously winged calyx and corolla; the calyx limb is also very large. The only species mentioned in the original description was *A. serpens*, but about five other species were described afterwards. There is a tendency for several species of *Agapetes* sensu stricto to have angled or slightly winged corollas, e.g. *A. angulata*; *A. miranda* has a very large
corolla wings indeed, although its calyx is unwinged. Airy Shaw (1949) thought that it was close to the species with winged calyces. Although the winged calyx and corolla are very noticeable characters, they are not highly correlated with any other set of characters, and so the other characters of *Pentanterygium* are those of *Agapetes*. The stamens are very like those of series *Robustae*, the leaves dry with either a smooth or a bullate surface and have *Lyonia-* or *Pieris-*type midrib bundles as in other sections. There is a tendency for members of this group to have yellow corollas, although they are red in *P. serpens*, *P. interdicta*, etc. I agree with Sleumer (1941) and Airy Shaw (1959) in considering *Pentanterygium* to be synonymous with *Agapetes*.

*Desmogynae* (type – *D. nerifolia*) was created to accommodate a species with very large, fused calyx lobes and a pedicel much expanded at the apex. As Airy Shaw (1935) noted, there are all transitions in the calyx type between species like *A. linearifolia*, with large, half-fused calyx lobes, and the smaller, free lobes of most other species of *Agapetes*, via species like *D. angustifolia*. The largest calyx lobes in the genus are possessed by *A. burmanica*; these are free, although they are larger than those of any "*Desmogynae*". Some species of *Agapetes* subseries *Robusta* also have the prominently expanded pedicel apex. The *Desmogynae* group of species is characterised by narrow leaves scattered along the stem and an urceolate corolla with very short
corolla lobes. Anatomically it has a + circular midrib bundle tending to become the Pieris-type without an intervening Lyon-type stage (Fig. 86, this needs more extensive sampling to establish properly) and fibres of very large diameter (ca. 45μ or more, in the rest of Agapetes they are less than 30μ) surrounding the petiole bundle. Similar, large fibres are also found in Vaccinium claeyxylon. These species of Agapetes form a distinct group, but not at the generic level.

The Separation of Agapetes from Vaccinium.

There is no really clear-cut difference between Agapetes and Vaccinium. Several authors have noted this problem (e.g. Sleumer 1941, Airy Shaw 1959, etc.), and species like "V. bulbeyanum" and "A. pilifera" have been shuttled backwards and forwards between the two genera. There are two main areas of overlap. The first is between Agapetes subseries Chartaceae and Vaccinium section Epigynium, and the second is Agapetes subseries Cuneatae and Vaccinium sections Conchophyllum and Vitis-Idaea. It is possible that Vaccinium section Aethopus, with its fasciculate inflorescence and colarette of hairs at the apex of the pedicel, may also be rather close to Agapetes, but its flowers are reported to be urceolate. (Sleumer, 1941; Airy Shaw, 1948). The relationship between Vaccinium section Galeopetalum and Agapetes is certainly not via A. pilifera (A. pilifera is placed in this section by Sleumer) since A. pilifera does not have the characters
of the section in which it is placed. However, as mentioned in the discussion on this section, it is/very poorly known and diverse group and may yet hold some surprises.

1. *Agapetes* and *Vaccinium* section *Epigynium*. Airy Shaw considered all species with a corymbose or umbellate inflorescence and elongated flowers to belong to *Agapetes*. Thus he included *V. bulleyanum* in *Agapetes*, although it is perhaps significant that it does not appear in any of his keys. Although its inflorescence is corymbose/sub-umbellate it is not dissimilar in this to the species of *Vaccinium* section *Epigynium*. *V. acuminatum* is also often included in *Agapetes* (subseries *Chartaceae*); this also has a corymbose inflorescence. Both these species have many flowers in each inflorescence, in *Agapetes* there are rarely more than 12 flowers per inflorescence. The flowers of *V. bulleyanum* can hardly be called elongated, being 8 mm. long, those of *V. acuminata* are even shorter and in both species the corolla is urceolate. In this, and in anther type, both species agree with species like *V. nuttallii* and *V. leucobotrys* (see Fig. 34). In leaf anatomy both species are closer to section *Epigynium* than to *Agapetes*, although the differences are not great. *Vaccinium bulleyanum* in particular has a layer of lignified spongy mesophyll cells not immediately adjacent to the epidermis just like *V. vacciniaceum*. If either species is included in *Agapetes* there is no logical reason why the whole of *Vaccinium* section *Epigynium* should not be
included as well (see Fig. 81). This would make the distinction between the two genera very tenuous indeed.

The only differences between the two genera are as follows:

<table>
<thead>
<tr>
<th>Agapetes</th>
<th>Vaccinium</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flowers large, nearly always</td>
<td>Flowers smaller, &lt;1 cm.</td>
</tr>
<tr>
<td>&gt;1.0 cm.</td>
<td></td>
</tr>
<tr>
<td>Flowers usually red, rarely</td>
<td>Flowers often greenish or white, but</td>
</tr>
<tr>
<td>yellow or white.</td>
<td>red in many species.</td>
</tr>
<tr>
<td>Corolla sometimes winged,</td>
<td>Corolla never winged, very often</td>
</tr>
<tr>
<td>usually tubular or campanulate.</td>
<td>urceolate, less often campanulate.</td>
</tr>
<tr>
<td>Inflorescence 1-12 flowered,</td>
<td>Inflorescence (in the problem species)</td>
</tr>
<tr>
<td>fasciculate or corymbose.</td>
<td>a many-flowered raceme or corymb.</td>
</tr>
</tbody>
</table>

This is obviously a very poor separation, and there are no supporting anatomical differences. Both groups have the same basic anatomical pattern and Agapetes agrees with the other S.E. Asian sections of Vaccinium in having an hypodermal phellogen. This is where its closest relationships are, and further work may lead to the merging of the two genera.

Two other taxa are excluded from Agapetes. They are A. leptantha and an unnamed collection of Keenan et al. 3253. Both these would be placed in Agapetes subseries Chartaceae if included in Agapetes. Although they both have tubular corollas ca. 1.2 mm. long and corymbose or subumbellate inflorescences they differ considerably from the rest of subseries Chartaceae.
and Agapetes as a whole. A. leptantha has the same mesophyll lignification as V. vaccinoides; both species have their midrib bundle with a dorsal crest of fibres (Fig. 84). This latter character is unusual in Agapetes (but see p. 523). Their inflorescences have many, greenish flowers; the stamens have very long, slender filaments and are similar to those of V. vacciniaceum, etc. (Fig. 84). In A. angulata and A. miniata (two species of Agapetes correctly placed in subseries Chartaceae) the stamens are just like those of subseries Coriaceae, with very short filaments and long, weakly connate anther tubules. In these two problem taxa the stamens are quite free, as in Vaccinium section Epigynium. They are provisionally placed in this section, but a new combination for A. leptantha is deferred until further studies are made in Agapetes and Vaccinium section Galeopetalum.

2. Agapetes and Vaccinium section Conchophyllum My work on sections Conchophyllum and Vitis-Idaea has made the distinction between these small-leaved species of Vaccinium and Agapetes series Longifiles less clear. A. obovata, of series Longifiles, subseries Cuneatae, is remarkable within that group in having a greenish campanulate corolla with lobes ca. 1/3 the total length of the corolla. Its stem is densely clothed with long-stalked, glandular capitate hairs. A. manji, of the same subseries, has unicellular hairs in groups on raised areas of the epidermis (Fig. 22). This type of hair is also found in A. forrestii, but this species is not very close to those being presently discussed.
Three species previously in *Vaccinium* section *Conchophyllum* have the inflorescence and flower shape of *A. obovata* combined with the indumentum of *A. mannii*. These are *V. triflorum*, *V. pseudotonkinense* and an unnamed specimen, Wang et al. 52,673. All four have their stamens connate by their thecae. This is very rare outside *Agapetes* in this area of the Ericaceae, although the character should be treated with caution (see section 2.1.4.).

Two of the three species of *Vaccinium* (exception, Wang et al. 52,673) have small, clavate, glandular hairs on the abaxial surface of the leaf, like many species of *Vaccinium*. These have not been found in any species of *Agapetes* sensu stricto: they do not occur in *A. obovata*. *A. obovata* also differs from the three species in having very much shorter filaments (Fig. 87).

3. *Agapetes* and *Vaccinium* section *Vitis-Idaea*. *Vaccinium manipurense* was originally described as an *Agapetes*, but was included in *V. section Vitis-Idaea* by Sleumer (*Vaccinium* section *Conchophyllum* here). It agrees with this section in having a small, somewhat drooping raceme borne towards the end of the preceding season's wood and in having small, multicellular hairs on the abaxial surface of the leaf. However, it too has clusters of unicellular hairs on the stem and its flowers, although immature on the specimen seen, seem to be tubular and at least 8.5 mm. long. The stamens are connate via their thecae, as in several species of *Agapetes*, but this also occurs in *V. nummularia*, which is undoubtedly a species of *Vaccinium* belonging to section *Conchophyllum*. 
Although more study is needed on the relationships of species previously placed in the last two sections of Vaccinium to Agapetes, it is clear that the distinction between the small-leaved species of Agapetes and Vaccinium is much less clear than has been generally recognised. It may be that A. obovata is really a species of Vaccinium, but whatever happens it will probably be necessary to recognise a new section of Vaccinium and/or a new subseries of Agapetes.

In view of the difficulties still remaining, it is premature to make any new combinations in Agapetes or Vaccinium.

**Infrageneric groupings within Agapetes.**

The four series of Agapetes section Agapetes are based on habit, the winging of the calyx and corolla, the length of the filament and the possession of anther spurs (Airy Shaw, 1959):

- **Series Robustae** - Generally rather robust plants; leaves large, broad, pseudoverticillate; inflorescence variable, filaments short.

- **Series Pteryganthe** - Variable habit; inflorescence never elongated; calyx tube winged, segments broad; flowers usually yellow; filaments short, anthers usually without spurs.

- **Series Graciles** - Often climbers, leaves variable; inflorescence usually pedunculate; filaments short, anthers without spurs.

- **Series Longifiles** - Rarely climbing, leaves generally small;
FIG. 85: VARIATION OF SOME CHARACTERS WITHIN AGAPETES.
FIG. 86: VACCINIEAE - LAMINA ANATOMY IN AGAPETES.

1. Agapetes macrophylla, x25; 2. A. moorei, x50; 3. A. angustifolia, x50;
4. A. linearifolia, x50; 5. A. forrestii, x50; 6. A. miranda, x33; 7. A. vilifera, x50; 8. A. bracteata, x100; 9. A. mannii, x66; 10. A. lacei, x50 (all species lack an hypodermis).
FIG. 87: VACCINIEAE - STAMENS OF AGAPETES.

1. Agapetes obovata; 2. A. miranda; 3. A. bracteata; 4. "Vaccinium" triflorum;
5. "V." pseudotonkinense; 6. A. lacei; 7. A. wardii - note small size of the spurs; 8. A. pilifera; (all x10); 9. A. moorei, x2.5 - long filaments bent at the bottom, stamens connate via anther thecae.
inflorescence usually fasciculate; filaments elongated, anthers with spurs.

These series seem to be based on a rather arbitrary selection of characters, some of which are not very satisfactory. As a result there are a number of species which would be better assigned to series other than those in which they have been placed. The following is a tentative realignment of the species studied within the framework of the existing classification (see Fig. 85). It is very probable that in any future reclassification of the genus a considerable modification of this hierarchy will be found to be necessary.

Series Robustae. Subseries Coriaceae seem to form a distinct group, with their large, tubular flowers, stamens with short filaments and long, connate tubules and midrib bundle of the Lyonia-type. Pseudoverticillate leaves are also frequent, but too much importance should not be attached to this character since it is very variable. Most species have abaxial calyx stomata, although they could not be found in A. burmanica, which has almost the largest calyx lobes in the genus.

Four species have curved, zygomorphic corollas. A. moorei and A. macrostemon belong to this group and also have long filaments. A. moorei, both in wild and cultivated material, has very large bud scales (ca. 4.5 mm.) filaments bent at the bottom (Fig. 87), and a Pieris-type midrib bundle (Fig. 86);
A. macrostemon has all these characters except the third. Both species also have stamens connate via their anther thecae. The other species with zygomorphic corollas and the rest of subsection Coriaceae differ in these respects, so these two species will probably have to be given taxonomic recognition.

Most species of the Coriaceae have corollas lobed to at least $1/8$th their length. A. auriculata and A. macrophylla are exceptional in this respect, and, like series Graciles subseries Longifoliae, their corollas are less than $1/9$th lobed. In A. macrophylla this similarity is rather superficial, since in other characters it agrees well with subseries Coriaceae (see Fig. 85). Petiole bundle sheath fibres have not been seen in this species, but they would not be expected to be more than $30\mu-40\mu$ in diameter. A. auriculata is dealt with under subseries Longifoliae. A. nuttallii also has a very long peduncle like these two species, but it is otherwise like the Coriaceae. A. nana, with a very short corolla, needs more study.

A. leptantha and A. acuminate have already been removed from subseries Chartaceae. A. angulata, one of the remaining members, is very similar in all details to subseries Coriaceae, although its leaves are somewhat different in texture, serrate, and arc scattered along the stem. A. miniata, with shorter corolla lobes, is otherwise similar to A. angulata. They are both rather like Vaccinium section Epigynium in leaf.
Series Pteryganthe.  *A. serpens* is transferred from series Graciles to this section, since all the species are similar florally. They have large wings on the calyx and corolla, abaxial calyx stomata but no corolla stomata at all. Their stamens have short filaments and long, connate tubules. The lobing of the corolla is variable. Three of the five species of which flowers have been seen have spurred anthers (including *A. serpens*, unspurred). Airy Shaw records only two of the eight species he placed in section Pteryganthe as having spurs.

Series Pteryganthe, as here delimited, includes all the species which have been placed in *Pentapterygium* apart from "P." scortechinii. *A. miranda*, with its winged, yellow corolla, is probably still best excluded although anatomically it is fairly close to *A. serpens*. The section is very diverse in habit. Subseries Bullatae has very bullate leaves with a Lyonia-type midrib bundle, its leaves are larger than the others. Subseries Planifoliae has smaller, smooth-surfaced leaves also with a Lyonia-type midrib bundle whilst the small leaves of *A. serpens* have a deeply hooked midrib bundle and tend to wrinkle transversely on drying. *A. serpens* is reported to hybridise with *A. rugosum*, but it would need a subseries to itself since it differs from the other two subseries as much as they differ from one another.

Series Graciles. From the information given by Airy Shaw the
Graciles-Longifoliae can be distinguished from the Robustae-Coriaceae only by having their leaves scattered along a slender stem. Their inflorescence and stamens are of the same basic type, although the peduncle of subseries Longifoliae is usually longer than that of subseries Robustae. Additional characters to separate the two groups have been mentioned in the discussion on the genus Desmogyne; the large petiole bundle sheath fibres may be mentioned again. Most members of this subsection lack abaxial calyx stomata, and have very short corolla lobes. A. auriculata is included here, because although it has scattered leaves and rather small calyx lobes with abaxial stomata, it has the inflorescence, corolla lobes and petiole fibres of the Longifoliae. It certainly seems to be more similar to the Longifoliae than A. griffithii and A. hyalocheilos; both these species lack broad petiole fibres and their midrib bundle seems to be of a somewhat different type.

Subseries Parvifoliae is an heterogenous group and can be separated from series Longifolies only by its lack of anther spurs. At least some species from the two groups have a similar habit, inflorescence and leaf size. A. similis is in some ways superficially like the Longifoliae, and like this subsection both it and A. refracta and A. forrestii have circular midrib bundles tending to go to the Pieris type without there ever being separate adaxial bundles (Fig. 36). The other species have
rather smaller leaves and *Pieris*-type bundles, although the
bundle of *A. praecclara* is deeply hooked. All these species,
as well as *A. miranda*, have rather thick-walled, rigid spongy
tissue so that the leaf resuscitates quite well.

*A. praestigiosa* would be interesting to study in this respect,
and also to see if it has the bullately-thickened anticlinal
epidermal walls of *A. praecclara* (Fig. 27). The species
mentioned show a trend from a corymbose to a fasciculate
inflorescence.

*A. buxifolia* and *A. lacei* have thinner-walled,
easily-collapsing spongy mesophyll cells and a fasciculate
inflorescence. *A. buxifolia*, as well as *A. miranda* of the
previous group, have somewhat longer (but still stout) filaments
than the other species of the subseries. *A. obovata* of series *Longifiles*, has stamens similar to those of *A. miranda*, although
they are shortly spurred (Fig. 87). *A. lacei* has very long and
slender filaments and the stamens are very like those of *A. wardii
(Longifiles)* which has short spurs (Fig. 87). In series
*Robustae* there is infraspecific variation in the presence of
anther spurs (e.g. *A. variegata*) and it seems probable that
*A. lacei* is misplaced in the *Graciles*. Both it and *A. buxifolia*
have abaxial calyx stomata, otherwise not yet found in subseries
*Parvifoliaceae*, and larger, more campanulate corollas. They are
not very close to one another.
Series Longifiles. The two species of subseries *Racemosae* studied are very alike; both have large bracts and a racemose inflorescence, a deeply-lobed campanulate corolla with stomata and gland-headed hairs on the abaxial surface. These hairs are rare outside the Longifiles and have been seen only on *A. setigera*, *A. serpens* and *A. variegata*. Despite the relatively large size of the leaves the midrib bundle is of the *Pieris*-type.

*A. pilifera*, of the monotypic subseries *Piliferae*, is provisionally included here *faute de mieux*. Its stamens have rather short filaments and the anthers are shortly spurred (Fig. 87). Although its leaves seem to be like those of subseries *Racemosae*, the midrib bundle is of the *Lyonia*-type (Fig. 86). If excluded from Agapetes it will probably have to be placed in a monotypic section of *Vaccinium* (c.f. Sleumer, who included it in section *Galeopetalum*).

*A. oblonga*, one of the two species in subseries *Oblongae*, has the largest bud scales in the genus (6.5 mm.), chartaceous leaves of a moderate size, and with a *Lyonia*-type midrib bundle, and a fasciculate inflorescence with up to seven flowers. These flowers are very like those of subseries *Subsessiles*, as is the gland-headed indumentum. There are abaxial calyx stomata.

*A. fasciculiflora*, the only member of subseries *Fasciculiflorae*, has not been studied.

Subseries *Cuneatae* were characterised by having at most
puberulous flowers (gland-headed hairs have been seen on the corolla of *A. wardii*) and entire leaves with cuneate bases. *A. wardii* tends to have a Lyonia-type midrib bundle, the other three species studied had Pieris-type bundles. All species have abaxial calyx stomata, *A. obovata* has abaxial corolla stomata as well. In stamen type and corolla shape it is misplaced here, and links on to the anomalous members of *Vaccinium* section Conchophyllum. *A. kanjilali*, with flowers almost 4 cm. long and leaves 2.6 cm. long, would repay detailed study.

The last subseries, Subsessiles, is distinguished from the others in having ± sessile flowers which are densely covered with gland-headed hairs on the outside. *A. spissa* looks very much like *A. smithiana* (section Pteryganthe) in leaf, and both *A. spissa* and *A. brachypoda* have Pieris-type midrib bundles. Abaxial calyx stomata are of variable occurrence; corolla stomata have not been seen. The corolla of all species is thin and has a distinctive appearance; the stamens are "typical" Longifiles-type stamens with long filaments and spurred anthers connate via their thecae.


Epiphytic or terrestrial shrubs or lianes; leaves large, evergreen and coriaceous, margin entire or serrulate, convolute in
bud, venation often ± Melastomataceous. Indumentum of small, clavate, glandular hairs on the leaf surface, and larger ones on the leaf margin. Inflorescence axillary, racemose or fasciculate, usually with deciduous perulae, often ramiflorous; bracts and bracteoles small, the latter opposite to alternate, usually near the bottom of the pedicel; pedicel articulate with the calyx. Flowers 5-merous. Calyx tube usually smooth, apparently sometimes ribbed or winged, the limb small to large, lobes free or fused. Corolla tubular or campanulate, usually large, lobes small to \( \frac{1}{2} \) the length of the corolla; tube thick and fleshy, sometimes apparently two-layered. Stamens 10, apparently always free; filaments flattened, castaneous, hairy or not; anthers rigid, with flaring tubules about half their total length, tubules dehiscing by introrse slits or pores, spurs paired, single or absent, very dimorphic in size of anther and filament, also often in the number and occurrence of spurs and the number of pores, thecae ± smooth or with sparse hairs. Ovary inferior, 5-locular, with many ovules, crowned by the disc; style slender and sometimes curved, impressed, stigma truncate. Fruit apparently a fleshy berry.

There are ca. 70 species in this genus, of which only 12 or 13 have been intensively studied. The type species is *D. moorhousiana*.

This genus is separable from all other S.E. Asian Vaccinieae
because of its very dimorphic stamens with rigid, thick-walled anthers which have diverging, flaring tubules (Fig. 38).

The name *Dimorphanthera* was first applied by von Mueller to three species previously placed in *Agapetes* which had dimorphic anthers. He did not describe the genus fully, but there is no doubt as to the identity of the plants to which he was referring, even though he described the type species as "*Agapetes moorhousiana - Dimorphanthera moorhousiana*". I follow Sleumer (1961) in the nomenclature of this genus.

The problem of Vaccinium section Pachyanthum.

*Vaccinium* section *Pachyanthum* (Sleumer, 1941; type *V. macbainii*) is here transferred to *Dimorphanthera*. The new combinations necessary are to be found in Appendix 1.

In general facies this section differs from all other sections of *Vaccinium* and agrees with *Dimorphanthera*. It blackens easily on drying and has very coarse-looking, coriaceous leaves; its flowers also blacken, unlike those of *Vaccinium*. I have been unable to find any difference in indumentum, although the material studied was not ideal for the examination of hairs. A cultivated plant named *V. keysseri* has very remarkable hairs (Fig. 21), but these have not been seen in other plants of the section, or even of the same species.

Florally section *Pachyantha* is very close to *Dimorphanthera*. Their stamens are almost identical, the similarity between
FIG. 88: VACCINIEAE - STAMENS OF DIMORPHANTHERA AND SATYRIA.

1. Dimorphanthera kempteriana - a & b major stamens from side and rear, c & d minor stamen from front and side; 2. D. amoena; 3. D. dekockii; 4. Vaccinium (= Dimorphanthera) macbainii; 5. Satyria panureensis - a from rear, x5, b from front, note connate filaments; 6. V. (=D.) c.f. amplifolium.
FIG. 89: VACCINIEAE - DIMORPHANTHERA
AND SATYRIA, ANATOMY AND COROLLA.

1. Vaccinium (= Dimorphanthera) macbainii, x50; 2. V. (= D.) ingens, x33;
3. D. apoane, x66; 4. Satyria warszowiczii, x25; 5. V. (= D.) c.f. amplifolium -
part of corolla showing two layers; 6. D. dekockii - the same; 7. D. lancifolia
- the same, all x5.
V. c.f. amplifolium and D. dekockii being especially close (Fig. 88). The anthers of both groups are thick-walled and rigid, the differentiation between tubule and theca is slight and papillae are ± non-existent. Spurs are absent from species in section Pachyantha, but they are also absent in several species of Dimorphanthera. The small campanulate corolla has very thick walls which appear to be bistratose (Fig. 89; see also p. 40). A number of species of Dimorphanthera have slightly bistratose corollas, e.g. D. womersleyi, D. dekockii, D. lancifolia (Fig. 89); one would not expect this peculiarity to be so well developed in Dimorphanthera since the corollas are generally thinner than in section Pachyantha. The size difference in corolla is not very great, since D. brachyantha has a corolla only 1.0-1.3 cm. long; those of section Pachyantha are ca. 0.5-0.9 cm. long (see Table 20).

Section Pachyantha is much more similar in its anatomy to Dimorphanthera than to Vaccinium. Its pith cells are notably thick-walled, the medullary rays are very prominent and the vessels large in diameter. Vaccinium differs in these characters (Table 20). There are what are probably fibres in the phloem in section Pachyantha and Dimorphanthera, the stem and petiole cortex have numerous sclereids. Although this last set of characters is not very restricted in its occurrence, it is a further point of agreement between the two groups. Section
Pachyantha, unlike all the S.E. Asian species of Agapetes and Vaccinium, has pericyclic phellogen and in this it agrees with Dimorphanthera and the other Vaccinieae. All species examined, apart from V. amplifolium, have a 2-3-layered hypodermis and a layer of lignified spongy mesophyll next to the abaxial epidermis (Fig. 89). This combination of characters is very rare outside the S. American Vaccinieae, Costera, Dimorphanthera and Paphia. Although Vaccinium sections Cinctosandra and Pyxothamnus tend to have these characters, they are not similar in other respects, and the four other sections of Vaccinium with similar lamina anatomy are probably wrongly included in Vaccinium (p. 494).

In some species of section Pachyantha the hypodermis is lignified, as in V. macbrainii, where the walls are up to 20μ thick. However, in both section Pachyantha and Dimorphanthera the hypodermis is usually thin-walled and un lignified. Garden-grown material of Vaccinium c.f. amplifolium has a 1-2-layered hypodermis and seems to lack the abaxial layer of lignified cells.

Section Pachyantha is maintained at the sectional level in Dimorphanthera because its inflorescences are very often borne on wood a single season old, as distinct from often being ramiflorous. Its small, very bistratose corolla is distinct from the normal corolla of Dimorphanthera. Further work may result in the rank of this section being changed, since neither of the species placed in section Pteridosiphon has been seen and some of the
small-flowered species of section *Dimorphanthera* may be similar to the species of section *Pachyantha*.

The relationships of *Dimorphanthera*.

Mueller, in his original mention of the genus, compared it to the S. American genus *Macleania*. Although not dissimilar anatomically, the two genera are rather different in corolla and anther.

*Dimorphanthera* is very close to the predominantly Central American genus *Satyria*, a relationship which does not seem to have been mentioned before. In general facies and inflorescence the two genera are very similar; both have coriaceous, palmately-nerved leaves with clavate hairs and a racemose/fasciculate inflorescence. According to Smith (1932), *Satyria* has deciduous bracts at the base of the inflorescence which may be the same as the perulae found in a number of species of *Dimorphanthera*. There is a remarkable similarity in stamen type (Fig. 88). Although all 7 species of *Satyria* seen have fused filaments they are flattened and castaneous as in *Dimorphanthera*. As has been mentioned, fusion of filaments (in contrast to non-fusion) is not a very great difference. Both genera have almost identical anthers.

Anatomically, too, there is considerable similarity (see Table 20). Both genera have large vessels and prominent medullary rays. The hypodermis in the 3 species of *Satyria* examined anatomically is 1-3-layered and un lignified, and *S. warszewiczii* has a layer
<table>
<thead>
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<th>Character</th>
<th>Vaccinium</th>
<th>Pachyantha</th>
<th>Dimorphantha</th>
<th>Satyria</th>
<th>Agapetes</th>
<th>Paphia</th>
<th>&quot;A. neo-caledonensis&quot;</th>
<th>&quot;A. scortechinii&quot;</th>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
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<td>+</td>
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<tr>
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<td>−, (+)</td>
<td>+, −</td>
<td>+, −</td>
<td>+, −</td>
<td>+</td>
<td>+ (&lt;5)</td>
<td>−</td>
</tr>
<tr>
<td>Corolla size (cm.)</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>1.3—4</td>
<td>1.3—5</td>
<td>(1.3—1—5)</td>
<td>1—4</td>
<td>2.5</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

**TABLE 20A** VARIATION OF SOME CHARACTERS IN THE S.E. ASIAN VACCINIACEAE
<table>
<thead>
<tr>
<th>Character</th>
<th>Vaccinium</th>
<th>Dimorphanthera</th>
<th>Satyria</th>
<th>Agepetes</th>
<th>Paphia</th>
<th>&quot;A&quot; sectotechnii and neo-caladenia</th>
<th>Costera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corolla walls</td>
<td>-</td>
<td>++</td>
<td>+, +</td>
<td>+, +</td>
<td>+, +</td>
<td>+, + (sect)</td>
<td></td>
</tr>
<tr>
<td>Corolla bistratose</td>
<td>-</td>
<td>++</td>
<td>+, +</td>
<td>+, +</td>
<td>+, +</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Hypodermal layers</td>
<td>0 - 1 (2 once)</td>
<td>(1-)2(-3)</td>
<td>2 - 4</td>
<td>1 - 4</td>
<td>0</td>
<td>2, 1</td>
<td>1</td>
</tr>
<tr>
<td>Hypodermis lignified</td>
<td>- (once)</td>
<td>+ or -</td>
<td>+ or -</td>
<td>+ or -</td>
<td>+ or -</td>
<td>+</td>
<td>+ (once)</td>
</tr>
<tr>
<td>Spongy tissue lignified</td>
<td>- (once)</td>
<td>+ (or -)</td>
<td>+ or -</td>
<td>+ or -</td>
<td>-</td>
<td>+</td>
<td>+ (once)</td>
</tr>
<tr>
<td>Midrib bundle</td>
<td>Pieris (Lyonia)</td>
<td>Pieris</td>
<td>Pieris</td>
<td>Lyonia</td>
<td>Lyonia or Pieris</td>
<td>Pieris</td>
<td>Pieris (Lyonia?)</td>
</tr>
<tr>
<td>Petiole bundle</td>
<td>often open</td>
<td>circular</td>
<td>circular</td>
<td>circular</td>
<td>variable</td>
<td>circular</td>
<td>circular</td>
</tr>
<tr>
<td>Phellogen hypodermal</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Broad multiseriate rays</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Average vessel size (μm)</td>
<td>20.2</td>
<td>29</td>
<td>33</td>
<td>36</td>
<td>20.5</td>
<td>32, 29</td>
<td>27 (1 sp.)</td>
</tr>
<tr>
<td>Pith lignification</td>
<td>thin</td>
<td>thick</td>
<td>thick</td>
<td>thin</td>
<td>thick</td>
<td>thick</td>
<td>thin</td>
</tr>
</tbody>
</table>

**TABLE 20B VARIATION OF SOME CHARACTERS IN THE S.E. ASIAN VACCINIACE**
of lignified spongy mesophyll next to the abaxial epidermis. Much more material must be studied. *S. ovata* and *S. warszewiczii* have a very curious petiole bundle structure (Fig. 25), but the other species, *S. panurensis*, has a circular petiole bundle like species of *Dimorphanthera*.

The differences between the genera are not great. *Satyria* has a circular or *Lyonia*-type midrib bundle (Fig. 89); this has not been seen in *Dimorphanthera*. The corolla of *Satyria* is narrow and tubular, but somewhat expanded at the base where the stamens lie. A comparable corolla has not been seen in *Dimorphanthera*, which in addition has free filaments. Data on stomatal distribution for the flowers are inadequate for comparison.

The great similarities between the two genera are thought to be indicative of a real relationship, and are not due to convergence.

**PAPHIA** Seem., *J. Bot.*, Lond. 2: 77 (1864).

Epiphytic or terrestrial evergreen shrubs or lianes with scattered, entire or serrulate, coriaceous leaves, venation palmate-opinate. Indumentum of clavate glandular hairs on the leaf surface and larger ones on the leaf margin; also unicellular hairs. Inflorescence axillary, fasciculate or subfasciculate, 1-3-flowered, apparently without prominent perulae;
sometimes ramiflorous, with a bract at the base and small, alternate or sub-opposite bracteoles at the base or up to $\frac{1}{2}$ up the pedicel; pedicel often rather long, articulate with the calyx. Flowers 5-merous. Calyx tube smooth or ribbed, ribs alternate to the small, ± fused calyx lobes. Corolla tubular or urceolate, often large, sometimes curved; lobes small. Stamens 10; filaments castaneous, fused at the base, hairy or not; anthers without spurs, ± granulate, usually longer than the filaments, tubules only slightly differentiated from the thecae and dehiscing by long, introrse slits. Ovary 5(-6) locular, inferior, surmounted by the nectary, ovules numerous; style impressed, slender, stigma ± truncate. Fruit apparently fleshy.

Some 13 species are considered to belong definitely to this genus, of which 7 have been studied. The type species is *P. vitiensis*.

Seeman separated *Paphia* (*P. vitiensis* was the only species in the original description) from *Pentapterygium* because its calyx tube was not angled, and from both *Pentapterygium* and *Epigynium* (*sic, = Vaccinium*) because its corolla was more tubular than that of the other two genera. He noticed the prominently hooked (beaked) anthers of *Paphia*. *P. vitiensis* has the most beaked anthers of the genus, but this difference is only one of degree (Fig. 90), and it agrees well with the other species here included in *Paphia* in all external characters; it would be
surprising if it differed much in anatomy.

Separation of Paphia from other Vaccinioeae.

Detailed discussion of "Agapetes" scortechinii and "A.," neo-caledonica will be deferred until a special section at the end.

The species placed in Paphia have been considered to belong to Agapetes by the latest worker on this group (Sleumer, 1939, 1960, 1967b, etc.). Copeland (1931) and Airy Shaw (1959) both thought that differences would be found between Paphia and Agapetes sensu stricto. Airy Shaw thought that A. scortechinii was a link between the mainland S.E. Asian species of Agapetes and the species of Paphia growing on the islands off S.E. Asia and in N. Australia. My work has shown that Copeland and Airy Shaw were justified in their hopes.

In general facies and indumentum Paphia and Agapetes are quite distinct. Paphia, like Dimorphanthera section Pachyantha, often dries blackish, and its coriaceous leaves with marginal, black, clavate hairs are unlike those of Agapetes. Also there are small clavate hairs on the leaf surface, which are, at best, of rare occurrence in Agapetes. The fasciculate inflorescence is very like that of Agapetes series Gracilea and Longifiles, into which Sleumer put the species now placed in Paphia, but such an inflorescence is of very widespread occurrence in the Vaccinioeae.

Florally Paphia is only superficially like Agapetes.
FIG. 90: VACCINIEAE - STAMENS AND HAIRS OF PAPHIA.

FIG. 91: VACCINIACEAE - PAPHIA AND COSTERA, FLOWER.

1. <i>Agapetes</i> (= <i>Paphia</i>) c.f. brassii; 2. Costera ovalifolia; 3. C. cyclophylia;
4-8. "Agapetes" scortechinii, 4. stamen; 5. abaxial corolla hair; 6-8 T.S. ovary-base, middle and apex (1-4, x10; 6-8 x6).
Apparently in *Paphia* the corollas are always plain coloured, not banded as they often are in the larger-flowered species of *Agapetes*. The corolla tube in *Paphia* is rather thick. The stamens are not particularly close to those of *Agapetes* (c.f. Figs. 87 & 90). The demarcation between fertile theca and sterile tubule is very indistinct: the thecae and tubules are approximately equal in length. The tubules dehisce by very long slits. The fused castaneous filaments are quite unlike those of *Agapetes*, which are free and not dark in colour. The ovary is 5-locular in *Paphia*, pseudo-10-locular in *Agapetes* and its close relatives. Species of both genera have abaxial calyx stomata. Thus the floral similarity between the two genera is more apparent than real.

Anatomically the differences are just as marked, and of the same order as those supporting the transfer of *Vaccinium* section *Pachyanthum* to *Dimorphanthera*. All species examined have a 2(-3) layered hypodermis whose innermost layer is slightly lignified; in *"A." alberti-eduardii* the most interior layer has 15μ thick lignified walls. All species have at least a single layer of lignified spongy mesophyll adjacent to the abaxial epidermis, but in *"A." sclerophylla* and even more in *"A." vitis-idaea* the whole spongy tissue becomes slightly lignified. The vein endings are large (ca. 60μ-120μ) in the species in which they were seen; they are smaller in *Vaccinium*. The midrib
bundle is of the Pieris type, although transiently Lyonia type at the base of the lamina. Agapetes is quite devoid of any hypodermis or of leaf lignification unassociated with the vascular bundles. In the stem of Paphia the pith is often irregularly thick-walled, the phellogen is pericyclic and the xylem has broad vessels and medullary rays. In Agapetes the pith lignification is less and evenly distributed, the phellogen is hypodermal and the xylem has narrower vessels and medullary rays (see Table 20).

As a result of the reinstatement of Paphia several new combinations have to be made; they are to be found in Appendix 1.

All the characters noted above link Paphia to the new world genera previously put in the Thibaudieae and also with Dimorphanthera. In anatomy they are all very similar (see above), and Paphia is closest in stamen type to genera like Thibaudia, Cavendishia, etc. More work is needed to establish its exact relationships.

The problem of "Agapetes" scortechinii and "A." neo-caledonica.

The two above-mentioned species must be excluded from Agapetes for the same reason as Paphia itself is excluded, although they are not yet formally placed in Paphia.

Both species have an hypodermis which has only a single layer but which is quite well lignified. In all other anatomical details agreement with Paphia is good.
The flowers of "A." scortechinii are different from other species of Paphila. The calyx tube and the pedicel are continuous; the former is slightly angled. The calyx limb is very large (some 14 mm., as compared to <3,5 mm. in Paphila). The stamens are different to the other species of the genus, although those of P. sclerophylla are somewhat similar. They are curved at the theca/tubule junction and dehisce by an oval pore (Fig. 91), P. sclerophylla dehisces by a slit (Fig. 90). The thecae are very granular and the filaments are connate.

The ovary of "A." scortechinii is 10-locular at the very apex (Fig. 91) and the placentae are slightly bilobed, but the significance of this is obscure. No other genera in the Vaccinieae is known to have such an ovary, but it is not easily observable. There are long-stalked, gland-headed hairs on the corolla and vegetative parts of the plant; these are unusual in this part of the Vaccinieae. The cells of the testa are very incrassate, the walls being ca. 35 μ thick.

In general, "A." scortechinii is very similar to Macleania. Comparable hairs have not been seen in the species of Macleania examined, nor are the pedicels continuous with the calyx. The calyx lobes of Macleania do not seem to exceed 8 mm. (M. salapa), but the similarity in stamens is especially remarkable. It may be that "A." scortechinii will have to be placed in a monotypic genus, but until the S.American genera are studied further it is
unwise to be more definite. It certainly does not seem to belong to *Paphia*.

*A. neo-caledonica* also has its calyx tube continuous with the pedicel, but its calyx limb is the size of the other species of *Paphia*. According to the original description (Guillamin, Bull. Mus. Nat. Hist. Paris, Ser. 2: 31: 178 (1959)), the filaments are the same length as the anther. Thus it does not seem to be close to "*A." scortechinii* florally, but I hesitate to refer it to *Paphia* until I can see its flowers.


Usually epiphytic shrubs with entire, coriaceous leaves with palmate venation and often with paired petiole glands. Indumentum of unicellular hairs and gland-headed hairs; the latter seen only on the stem. Inflorescence a few-flowered axillary fascicle; bracts and bracteoles small, the latter basal and sometimes connate; calyx and pedicel continuous. Flowers 4- or 5-merous. Calyx limb small, lobes ± free. Corolla campanulate, small, deeply (to over ¼) lobed. Stamens 5, 8 or 10; filaments rather flattened, free, hairy; anthers slightly granular, without appendages, tubules about equal in length to the thecae, dehiscing by slits. Ovary 4-5-locular, inferior; slender style impressed,
stigma truncate. Fruit fleshy; seeds rather few, large, ovoid; cells of the testa ± hexagonal, walls incrassate.

There are 9 species in this genus, of which 4 have been studied. The type species is *C. ovalifolia*.

**Synonymy.**

*Aere* was based on the single species *I. lanaense*. This species is very similar in anatomy and testa structure to *C. ovalifolia*; both species have a lignified hypodermis and a lignified layer of spongy tissue next to the abaxial epidermis, they also have very little, if any, thickening of the periclinal walls of the testa cells (Fig. 16). *Aere* was separated from Costera because it had a 5-locular ovary (usually 4-locular) and also because it was haploestemonous. These differences are not very significant and in view of the similarities in anatomy, testa structure, inflorescence, pedicel type, etc. the two are considered to be congeneric, see also Sleumer (1967b).

*Cymothoe* (only species, *C. cyclophylla*) has very different leaves to the other species (in *Cymothoe* they are ± orbicular, with a cordate base), it lacks petiole glands and there are more seeds per loculus in the fruit. The material seen resuscitated very badly, but although there was an adaxial hypodermis, it was un lignified, and the spongy mesophyll seemed to be entirely un lignified. The bast and libriform tissue around the midrib bundle was much better developed than in the other species, and
the bundle itself tends to be the *Lyonia* type (Fig. 80). The flowers and stamens are very similar to *C. ovalifolia* (Fig. 91), but the inner periclinal walls of the testa are thickened, as well as the anticlinal walls. It is obviously a very distinct species, but more work is needed to see just how far, if at all, these differences between it and other members of the genus are bridged by the unstudied species.

**Relationships of Costera.**

Although Sleumer (1967b) found few characters to separate Costera from the species of *Vaccinium* in S.E. Asia, these studies have provided several additional features. The ovary is simply 4- or 5-locular, never pseudo-10-locular as in the other S.E. Asian species of *Vaccinium* (although simply 5-locular ovaries are common in *Vaccinium* elsewhere). The fasciculate inflorescence in *Vaccinium* is practically restricted to those sections which are most doubtfully included in *Vaccinium*, i.e. sections *Disterigmopsis* and *Brachyceratum*. The anatomy of Costera is as different from *Vaccinium* as is that of *Paphia* and *Dimorphanthera*: the phellogen is pericyclic and *C. loheri*, *C. ovalifolia* and *C. lanaense* have lignified hypoderms and lignified spongy mesophyll cells. *C. cyclophylla* differs in these respects (see above), but it has very large vein endings (ca. 160) and this suggests a relationship with genera other than *Vaccinium*. All four species have circular vascular bundles
in the petiole although in *C. loheri*, the smallest-leaved species, this is only a very transient condition.

Sleumer (1967b) noted the vegetative similarity between *C. loheri* and *V. microphyllum*. This latter species is the only S.E. Asian species of *Vaccinium* with an abaxial layer of lignified mesophyll tissue (the spongy mesophyll was generally lignified in one collection seen, but in the other three there was only a single layer), but in all other details it differs from *C. loheri*. Possibly other species of *Vaccinium* section *Garianthe* also have lignified mesophyll tissue, but even so phellogen position, lignified hypodermis, petiole bundle type, etc. should serve to separate them anatomically.

Airy Shaw, when describing *Cymothoe*, suggested that in inflorescence, calyx, habit, etc. it was similar to S. American genera like *Sphyrosperrum*. The three species in which palisade tissue was well resuscitated have very tall, broad palisade cells which easily collapse like bellows and which may have thin bands of thickening, i.e. rather similar to the palisade cells of *Sphyrosperrum*, etc. The general anatomy of *Costera* certainly suggests relationships with S. American genera.

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Lasiococcus Small, Man. S. E. Flora 1008 (1933).

Buxella Small, Man. S. E. Flora 1009 (1933).

Evergreen or deciduous shrubs with entire or serrulate leaves convolute in bud, indumentum of large-headed, small-stalked or small-headed, long-stalked gland-headed hairs and/or unicellular hairs. Inflorescence of axillary, eperulate racemes borne on the wood of the previous season; bracts and paired bracteoles present, the latter variable in position; calyx articulate with the pedicel. Flowers usually 5-merous. Calyx lobes small, free. Corolla urceolate to campanulate, small (<1 cm.), lobes small. Stamens 8 or 10; filaments free, glabrous or hairy; anthers slightly granular, without spurs, tubules of varying length and dehiscing by introrse slits. Ovary 8- or 10-locular, inferior; style impressed, slender, stigma ± truncate. Fruit fleshy; seeds one per loculus, surrounded by a stony layer; cells of the testa ± elongated.

There are ca. 50 species in this genus, of which 15 have been studied. The type species is G. buxifolia.

Nomenclature.

Lussacia is a nomenclatural synonym of Gaylussacia.

Decachaena is a nomenclatural synonym of Decamerium as is also, it would seem, Lasiococcus. Decamerium was separated as a genus from Vaccinium on its fruit type, but Nuttall recognised that it was close to Gaylussacia although he thought that they
could be separated by the deciduous habit, geographic range and having a fruit not grooved, nor truly 10-celled, but with 10 distinct pyrenes. Nuttall included *D. frondosum*, *D. resinosum*, *D. hirtellum* and *D. dumosum* in his genus, Gray mentioned all but the first in his, and Small mentioned *L. dumosum*, *L. mosieri* and *L. orocola*. None of the segregates can be maintained, because although most of the species concerned seem to have very distinctive hairs (Fig. 19) which are almost like glandular scales, the evergreen habit is variable both in some N. and some S. American species. I did not notice a difference in fruits and there is no difference in anatomy.

The relationship between some of the N. and S. American species seems to be close, see Camp (1941) and Sleumer (1967a). This work supports this relationship.

*Buxella* (*B. brachycera*) is a distinct species, entirely without glandular hairs, and its stamens have long filaments (Fig. 79). In anatomy, inflorescence and fruit it is similar to the other species, and so is not considered generically distinguishable.

**Relationships of Gaylussacia.**

Sleumer (1941) suggested that *Gaylussacia* was tribally distinguishable from all other Vaccinioidae. The only distinguishing features between *Gaylussacia* and *Vaccinium* are that the former always has 8- or 10-locular ovaries and a seed
enclosed by a stony/fibrous layer of lignified cells. In inflorescence, stamens (Fig. 79) and anatomy it is very similar to Vaccinium, and it is by no means the most distinct genus within the Vaccinieae as here recognised.

5.6. THE PYROLOIDEAE AND MONOTROPOIDEAE.

I follow Henderson (1919) and Copeland (1941 & 1947) in considering these plants to be members of the Ericaceae. Henderson showed very convincingly that they were not distinguishable from the Ericaceae by any clear-cut differences, but rather that they represented a gradual trend towards increased dependance on the fungal symbiont. The characters used by Drude (1897) to separate his Pyrolaceae (= Monotropoideae + Pyroloideae) from the Ericaceae are not good ones. The "uniform seed type" he mentions for the family is similar to that of Ledum and other Rhodoreae, the placentation difference (approaching parietal in some genera) is only a difference of degree, since some of the Rhododendroideae have placentation as parietal as the Pyroloideae, single pollen grains are found in all the Monotropoideae but in only some of the Pyroloideae, and finally the disc, which is supposed to be lacking, is found in genera from both subfamilies.

Embryologically there are no great differences, as Samuelsson (1913) first showed. Although the embryo is smaller and the planes of the early divisions of the embryo may be
different (section 2.3.3.), these differences also seem to be due to the reduced size and increased number of seeds consequent to increasing dependance on the fungus. The stamens too are basically Ericaceous in type; those of the four genera of the Pyroloideae are all very similar, inverting late in development and dehiscing by terminal pores, but those of the Monotropoideae are variable. The anthers of Sarcodes dehisce dorsally (Fig. 92), rather like those of Notopora, those of Pterospora are spurred, whilst the stamens of Monotropa are superficially different from all other Ericaceae.

Both subfamilies have unilacunar nodes and at least some species in both have homogenous pith. This seems to be the case in all the Monotropoideae, but in Chimaphila the pith is heterogenous and it approaches the Calluna type in P. asarifolia and Orthilia secunda. Other details of the anatomy are those of a group placing less and less dependance on photosynthesis, as Henderson (1919) noted. There is never any bast or libriform tissue in the leaf, and the palisade tissue is usually poorly differentiated from the spongy mesophyll (Fig. 92). Stomata often occur on both sides of the leaf in the Pyroloideae and they are always anomocytic and unorientated; in the Monotropoideae they are rare.

Floral stomata show interesting distribution. In the Pyroloideae they nearly always occur on both surfaces of the
calyx and corolla (personal data; Pyykkö, 1968). Adaxial calyx stomata are lacking in *Orthilia secunda* and *P. aphylla*, *P. minor* lacks adaxial corolla stomata. No floral stomata have been found in the few Monotropoideae examined apart from one seen on a "calyx" lobe of *Hemitomes*, but this may not really be a calyx lobe at all. There were none in well preserved specimens of *Sarcodes* and *Pterospora*, and they were also lacking in less well preserved specimens of *Monotropa*.

None of the rather scanty additional data obtained suggests that the two groups are other than subfamilies of the Ericaceae. The Pyroloideae are a very homogenous group whose four genera are close to one another. The Monotropoideae are florally very diverse, and more work is needed to establish their interrelationship (see Copeland, 1941).

5.7. THE WITTSTEINIOIDEAE.

WITTSTEINIOIDEAE, SUBFAM. NOV.


Evergreen rhizomatous shrublet with rather thick serrate leaves convolute in bud. Indumentum of uniseriate hairs in the leaf axils and unicellular hairs. Inflorescence axillary on the previous season's growth, one or two flowered, shortly racemose; bracts and 2-5 bracteoles deciduous; calyx articulate with the pedicel. Flower basically 5-merous. Calyx lobes 5,
quite free. Corolla tubular/urceolate, lobes small, toothed. Stamens 5, antisepalous; filaments slightly adnate to the corolla, glabrous; anthers dehiscing by two long, introrse slits; pollen grains single. Ovary inferior, crowned by the nectary; usually three-locular with rather few, large ovules borne in two ranks on small placentae; style impressed, slender, stigma 3-lobed. Fruit fleshy; seeds few, ovoid; cells of the testa with sinuous, thickened, anticlinal walls.

There is only a single, monotypic genus in this subfamily. For a Latin description, see Appendix 1.


The only species described, *W. vacciniacea*, has been studied. Taxonomic History.

Wittsteinia has had a rather chequered history. Mueller thought that it was intermediate between the Ericaceae and the Vaccinaceae (sic), but included it in the latter. He compared the type of dehiscence of the anther to that found in Diplarche and he also noted that *Sphyrospermum* had the same number of stamens. When he obtained ripe fruit he compared the small embryo to that of the Pyrolaceae (Mueller, 1863). Hooker (1876) followed him in including it in his Vaccinaceae, although he noted that it differed from all other members of that family in its anthers, placenta and small embryo. Drude (1897) included
FIG. 92: PYROLOIDEAE, MONOTROPOTOIDEAE AND WITTSTEINIOIDEAE.

Wittsteinia in the Arbutoideae-Gaultherioideae without comment, apart from recording the fact that some workers had placed it in the Vaccinioideae. Sleumer (1941) included it in the Vaccinioideae as an ancient, isolated and deviant genus.

Burtt (1948) transferred Wittsteinia to the Epacridaceae, tribe Prionoteae, but it was shown in section 4.3.3. that it has little in common with other members of the Prionoteae or the Epacridaceae as a whole, and is best placed in the Ericaceae. Reasons for proposing a new subfamily.

Although Wittsteinia is more similar to the Ericaceae than to the Epacridaceae (see Table 2 for the variation of some of the characters), on many counts it is the most distinct genus in the Ericaceae.

It is similar to the Ericaceae in general habit and is especially close to Chimaphila umbellata in this respect. Anatomy and indumentum distinguish it clearly from that plant and all other Ericaceae. The tufts of uniseriate hairs in the leaf axils (Fig. 92) are unknown elsewhere, although uniseriate hairs, most often apparently the end point in a reduction series from multiseriate hairs, occur sporadically elsewhere. Very similar hairs have been found only on the flowers of Epigaea. Simply trilacunar nodes (Fig. 24) have not been reported before for leaves in the Ericaceae, although complex trilacunar nodes are found in Rhododendron. The midrib and other veins of the leaf
have a **Pieris**-type bundle without associated fibres (Fig. 40) and the fibrous pericyclic sheath in the stem is poorly developed. The opaque epidermal cells with numerous small droplets are another notable feature. Such an epidermis is not known elsewhere; the lack of leaf bundle fibres is of restricted occurrence. Phellogen has not been seen; it is, at best, tardily developed. In at least some details of wood anatomy *Wittsteinia* is very similar to the *Gaultheria* group of genera (Cox, 1948b).

The inflorescence is not always a single, axillary, multibracteolate flower as reported by Burtt (1948); there are often two flowers per axil borne on a short peduncle which may be up to 6 mm. long. There may be only two bracts per flower, but since both bracts and bracteoles are deciduous this point could not be established. Thus the inflorescence may be different to that of *Prionotes* and *Lebetanthus* (see section 4.3.3.).

The flower has free, very prominent, calyx lobes, which Sleumer (1941) compared to those of *Vaccinium* section *Macropelma*. There are abaxial calyx stomata, but none on the corolla. The greenish-yellow corolla is very Ericaceous in appearance, but until recently it does not seem to have been realised that the corolla lobes are serrate (Fig. 92; see also Jackes, 1967). This is a very rare character within the Ericaceae.

The five, antisepalous stamens have anthers which dehisce by two introrse slits which extend the length of the thecae.
An endothecium, if present, is not prominent and the anther vascular bundle is hooked (see section 2.3.2.). The pollen grains are single and tricolporate; the latter character is common to most of the Ericaceae, but the former is restricted in occurrence. There is no trace of three abortive cells persisting along with a single, mature grain, so it is presumed that the grains are truly single, and not reduced tetrads. The filaments are definitely slightly epipetalous; they are more so than any other genus of the family apart from Diplarche.

The inferior, 3-locular ovary is without parallel apart from a single specimen (unidentified) in the Vaccinieae (Spruce 5897), which also has 5 stamens and single pollen grains. In stamen, anatomy, etc., this specimen is a typical member of the Vaccinieae, so it is thought that the similarities are coincidental. The rather small placenta with ovules borne in 1-3 ranks and the prominently three-lobed stigma make the gynaeicum without parallel in the family. The style, as would be expected, is hollow; pollen tubes have been observed growing down it.

The testa, with its wavy anticlinal walls and unthickened periclinal walls (Fig. 92), differs in the first respect from all other Ericaceae seen, in the second it is similar to Costera ovalifolia and possibly other species as well.
The Wittsteinioideae is an isolated subfamily. Although the inferior ovary immediately invites comparison with the Vaccinieae there is otherwise little similarity to that tribe, apart perhaps from the testa structure. Its anthers dehiscing by slits might suggest a relationship with the Rhododendroideae, but there are no other important points of similarity. Wittsteinia shows no close relationship to any extant member of the Ericaceae.
6. GEOGRAPHICAL DISTRIBUTION

"What heathers tell bees, but the learned ones fail to understand" Croizat, (1968a), on the importance of the Ericaceae to Phytogeography.

6.1. INTRODUCTION.

The Ericaceae are a very interesting family in the distribution patterns which they show at all taxonomic levels, even if one does not agree with the explanations advanced by Croizat. Before one can fully assess these distributional patterns one has to have the taxonomy fully sorted out, and it is obvious from the preceding chapter that this situation does not obtain in many parts of the Ericaceae. Also the implications of a given pattern depend very much on the taxonomic level at which the problem is considered (see also Hepper, 1965). A section may show affinities in one direction whilst the genus as a whole has affinities in quite a different direction. One has to be careful to avoid using distributional patterns as reasons for separating taxa, and then using these taxa in a phytogeographical analysis. Distribution patterns occurring elsewhere in the group may suggest areas where relatives may occur, but they cannot be used as primary evidence that plants in these areas are relatives.
Often the patterns themselves are clear enough and occur in a large number of cases, but the reasons for the patterns are obscure. This sort of problem becomes more serious as one gets nearer the equator when one deals with plants at the continental level, partly because the continents themselves are farther apart at lower latitudes and so explanations are likely to be more tenuous, and partly because even now much less is known about the history of these continents. One has to be a geologist, geophysicist, palaeobotanist and taxonomist to evaluate the relevant data correctly.

In the following discussion little attempt has been made to tie up the different types of pattern in a detailed evolutionary sequence (but see section 6.3), either within the Ericaceae or from the point of view of Angiosperm evolution as a whole. The subject is too vast for facile statements. The discussion is based on the different patterns of distribution shown by the Ericaceae at various levels (sectional and above), rather than dealing with each tribe separately, since genera from different tribes have the same patterns. Since not all groups have evolved at the same rate, sections may show the same pattern of distribution as genera, and for the same causes. It is also realised that the same pattern of distribution may have different causes. Each pattern must be considered as a unique case, at least at first (see also section 6.3.)
The maps are all original, and are based on those made by other authors (acknowledgments are given where necessary), literature records (where these are dependable), and herbarium specimens. Owing to the small scale of the maps, the distributions have been generalised.

6.2. THE DISTRIBUTION PATTERNS FOUND.

6.2.1. GENERAL.

The distribution of the Ericaceae at the tribal level is summarised in Table 21. Apart from the Antarctic, all continents are inhabited by at least two subfamilies. The Ericaceae do not favour moist, lowland tropical habitats or very arid regions, so they are absent from much of central Africa and S. America, and apart from the north cool temperate region, the genera do not have very wide distributions (exceptions are Vaccinium and Gaultheria). The only continent really poor in Ericaceae is Australia, but this is the centre of diversity of the closely related Epacridaceae. In the tropics the Ericaceae ascend the hills, as Bader (1960 & 1965) has shown. In this way the climate is ameliorated, and often the precipitation increases. In Africa Vaccinium grows at 3,500 m. on Ruwenzori but at only 1,680 m. in the Transvaal (Bader, 1965). The ascent of the hills enables the Ericaceae (and other groups) to migrate through otherwise unfavourable tropical areas (see below).
<table>
<thead>
<tr>
<th>Tribe</th>
<th>S. America</th>
<th>N. America (的能力)</th>
<th>Asia (包括新几内亚)</th>
<th>India</th>
<th>Europe</th>
<th>Australia</th>
<th>Africa</th>
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<td>+</td>
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</table>

Table 21: DISTRIBUTION OF THE RHODODENDRONEAE BY TRIBES.
The Ericaceae are basically plants of subtropical/warm temperate montane forests which have locally adapted to more xeric habitats (e.g. the Arbutoideae in S.W. N. America and the Ericoideae in the Cape region), to moist, tropical lowland, mangrove swamp habitats (on the Equator in west S. America; see Smith, 1946), and to high Arctic climates (Cassiope, etc.). In crude terms the centre of diversity of the Ericoideae is the Cape region, with extensions up the E. African mountains and also in the Mediterranean; of the Rhododendroideae, S.E. Asia, but also N. America and partly in S. America; of the Arbutoideae, in California and Mexico; of the Vaccinioideae is E. and S.E. Asia, and for some of the Vaccinieae in S. America. The Pyroloideae and the Monotropoideae are N. Temperate subfamilies, also with considerable variation in N. America and S.E. Asia; they will be little considered in the following discussion.

6.2.2. CIRCUM-BOREAL/COLD TEMPERATE GROUPS.

This group is comprised of Loiseleuria, Arctuous (Map 1), the Cassiopeae (Map 2), Phyllodoce, Rhododendron subsection Lapponicum, Ledum, Chamaedaphne, Andromeda, Vaccinium sections Vitis-Idaea (Map 7), Myrtillus, Oxycoccus and Ulliginosa, and Arctostaphylos uva-ursi (Map 1).

All these groups are small in size, and even in the oligotypic genera usually only one species is circumboreal, the others live in less severe climates. The only circumboreal
species are *Loiseleuria procumbens*, *Arctoës alpina*, *Cassiope tetragona*, *Phyllodoce coerules* (Map 6), *Rhododendron lapponicum*, *Ledum palustre*, *Chamaedaphne calyculata*, *Andromeda polifolia*, *V. vitis-idaea*, *V. myrtillus*, *V. uliginosum*, *V. oxycoccus* and *V. microcarpum*. There is often a break in these species' range somewhere in Central Asia, and to the south they may reach fairly low latitudes by growing high up on mountain chains; e.g. especially *Arctostaphylos cratericola*, which is very close to *A. uva-ursi*, and which grows on the volcanoes of Guatemala inside the tropics (Map 1). *Loiseleuria* and *Phyllodoce* have disjunct localities in the Alps and many of the species have disjunct southern localities which may perhaps be explained by distributional changes in the Holocene/Pleistocene (see also Hultén, 1962). The species have probably attained their circumpolar areas by migration over the Behring land bridge, since this has been emergent at intervals all through the Tertiary, and even now the climatic tolerances of these species are such that they could use the bridge during the glacial periods. *Cassiope tetragona* reaches 82°N. in Greenland; this and some other species may have migrated over the N. Atlantic as well.

It can be seen that the genera and sections involved are mostly very distinct and are placed in several tribes. They presumably have been in existence for a considerable time (see
MAP1: DISTRIBUTION OF SOME OF THE ARBUTOIDEAE.

— = Arctostaphylos uva-ursi,  --- = Arctoïs (both from Hultén, 1968),
■ = Arbutus,  . . . . = Comarostaphylis,  o = Ornithostaphylis,  x = Xylococcus,
c = Arctostaphylos cratericola.
MAP 2: DISTRIBUTION OF THE CASSIOPEAE AND BEJARIEAE.

— = Cassiope (partly after Hultén, 1968 and Good, 1926), ■ = Harrimanella (after Hultén, 1958 and 1968), ◯ = Bejaria.
section 6.3.). Cassiope and Andromeda have been reported as fossils (leaf and fruit respectively) from the Eocene in Europe (Conwentz, 1886), and Andromeda is reported from the Cretaceous (Emberger, 1968; the original reference has not been checked). Most of the groups involved are related to more thermophilous plants from which they probably evolved. However, the Cassiopeae as a whole is not close to any extant group. It has its greatest variability in cold temperate E. Asia and to a rather lesser extent in W. N. America; there is a (more recent?) group of closely related species in the Himalayas (C. wardii, etc; Good, 1926). Phyllodoce is also centred on the N. Pacific; perhaps the greatest variation here is found in western N. America. Aretous, Vaccinium sections Myrtillus, Oxyccoccus, and Uliginosum are also most variable in this general region; Vaccinium section Myrtillus has one species (V. gerniniflorum) which reaches Mexico. It is a sub-evergreen shrublet which lives at high altitudes on the mountains, as might be expected.

6.2.3. MID-LATITUDE GROUPS WITH LARGE DISJUNCTIONS.

This is a very interesting group which has a relatively large number of representatives in the Ericaceae. It can be subdivided as follows:-

1). Occurring in Europe, Asia and, usually, America.

Vaccinium section Hemimyrtillus grows in the Azores (dealt with in section 6.2.5.) the Madeira Islands and north Turkey;
there are also similar species in E. Asia, (the V. hirtum group; Map 3). Section Cyanococcus may be the N. American representative of this group; it is common over most of that continent. Rhododendron subsection Hymenanthes occurs in the Iberian peninsula and Turkey (the same species), another closely related species occurs in western N. America and a further one in the Alleghanies (eastern N. America). Other species of this subsection are found in N.E. Turkey, the Caucasus, N.E. Asia and several in Japan. Subgenus Azalea has a similar distribution, although it does not occur on the Iberian peninsula. It too has a single species on the W. coast of N. America (R. occidentale); there are several species in eastern N. America.

Corema (Empetraceae) grows on the Iberian peninsula and in eastern N. America, but no genera of the Ericaceae have this distribution. None of the Eriicoideae occur in N. America, and although much has been written on the status of Calluna in the New World it is best considered to be adventive there (for references, see le Gallo, 1945; Emerson, 1967).

2). Occurring in N.E. and E. Asia and in eastern N. America.

Fieris, Lyonia, (Map 4), Gaultheria series Hispidulae and Vaccinium section Oxycoccoides are examples in the Ericaceae; in the Diapensiaceae Shortia and Berneuxia/Galax. In E. Asia these groups are usually restricted to the Himalayas and regions to the east and north; in N. America to the Alleghany and Appalachian
MAP 3: HIGHLY DISJUNCT TEMPERATE GROUPS.

— = Vaccinium section Hemimyrtillus, ---- = Epigaea, ------ = Cladothamneae
(E = Elliottia).
MAP 4: DISTRIBUTION OF THE LYONIA GROUP OF GENERA.

— = Lyonia, — = Pieris, • = Craibiodendron, —— = Arcteria
(• = isolated locality of Lyonia).
mountain systems. They are not usually plants of the Atlantic coastal plain. *Ghispidula* itself has quite a wide distribution in the northern part of N. America. Clethra section Clethra has a basically similar distribution, but in Asia it gets into Malaysia.

3). Occurring in E. Asia and W. and eastern N. America.

The Cladothamneae (Map 3), *Menziesia* and *Leucothoe* belong to this group. Again, in E. America the plants involved are usually restricted to the relatively humid, montane areas, in the west they occur on the mountains from N. California northwards. *Menziesia ferruginea* reaches 63°N. on the west coast; it is the only species of the genus there. There is also only one species of *Leucothoe* in the west (*L. davisiae*). All the American species are very distinct when compared to the Asiatic ones, but in America the west and east coast species may be very similar (*Menziesia*) or separable at the sectional level (*Leucothoe*).

4). Occurring in E. Asia and western N. America.

*Gaultheria* section *Ambylandra* (1 species in Japan, 2 in west N. America; see Map 5) and *Rhododendron* subgenus *Azaleastrum* (a single American species placed in section *Candidastrum*, a monotypic section, *Mumeazalea*, in Japan, a N.E. Asian section (Azaleastrum) and finally section *Choniastrum*, which is probably best removed, living rather more to the south in Asia), are the main examples in the Ericaceae. Obviously the taxa involved
are not at the same level, but even the species of Gaultheria section Amblyandra are very different from the Japanese species, so both examples are probably old patterns.

Occurring in Europe and W. America only.

Arbutus (Map 1) is the only member of this group. It has a rather more southerly distribution, particularly in America, than other members of the mid-latitude disjunct groups.

These disjunctions are in genera which are predominantly temperate and mesophytic. Their stations today are in areas which are often considered to be climatically similar to the warm temperate Tertiary where there are a number of other species and genera which are also relicts of the temperate Tertiary flora. The areas concerned have moderate to considerable relief, but have not been isolated by water or climatic barriers since early Tertiary times (the seas separating Japan from the land to the north are less than 200 m. deep, and Japan was connected to the mainland of Asia in the Tertiary). Fernald (1931) noted that the Appalachian region had been emergent for a long time, although the present mountains are Tertiary (following the lines laid down by earlier orogenies); the earlier mountains had been peneplained by late Mesozoic times. Li (1952) compared the climate of the Yangtze valley to that of early Tertiary times. There are many other examples of similarly disjunct groups known from both higher and lower plants (see also Gray, 1859;
Yoshimura, 1968; Abramov & Abramova, 1969). It can be seen from the maps in Jager (1968) that the areas in which these groups are to be found at present have a high degree of "oceanity". These areas are characterised by the occurrence of many plants with a preference for an equable climate.

There is considerable evidence that many genera now restricted to areas of equable climate in the (warm) temperate zone have been far more widespread in the past, and that their present day, rather restricted, localities are the result of post-Eocene climatic deterioration (e.g. Stebbins, 1940; Tralau, 1963; Samylina, 1968). As Reid (1920) noted, the Pliocene European flora which had Asiatic affinities now grows at 1,500 - 2,000 m. in the Himalayas and W. China. *Rhododendron ponticum* is reported from Ireland as late as the Pleistocene interglacials (Jessen, 1918), and it seems to have been fairly widespread in southern Europe at this time (for map see Cain, 1948). *Orphanidesites primaevus* is less reliably reported from the Eocene European Amber flora (Conwentz, 1886). Although *Arbutus* may be a representative of a more xerophilous group, at least some of the European species live in areas of high humidity and rainfall, and this seems to be true of *A. menziesii* of N. America. Thus it may be necessary to include this in a group of Mediterranean taxa which got to (or came from) California via isolated pockets of xerophilous vegetation (Stebbins and Day, 1967).
In the early Tertiary the Behring land bridge was emergent, and since the fossil floras of that latitude are not microthermal it is probable that the taxa concerned achieved a ± circumpolar distribution in these times and then became restricted in their range. Migration over lands around the north Atlantic is less probable. Although nearly all the examples mentioned fit into the same general pattern, it does not follow that they are all of the same age. It is probable that these disjunctions occurred at various times during the Tertiary.

Although the W. coast of America is not so rich in Tertiary relict species several are to be found there, e.g. *Sequoia sempervirens*. *Menziesia ferruginea* is not similar to the Japanese species of *Menziesia* but is similar to the east American species of the genus and hence is not to be regarded as a recent immigrant. Other species on the west coast are also very distinct, e.g. *Cladothamnus pyroliflorus*, but some of the species belonging to *Rhododendron* subsection *Hymenanthes* may be closer to the E. Asian species and represent a later immigration. At present *Therorhodion* just enters N. America; one can envisage conditions which would push it farther into America and make it disjunct with regard to its Asian stations. This would give a pattern similar to that of many amphi- N. Pacific plants which have closely similar or identical species on both sides, often as a result of Pleistocene climatic changes.
It must also be remembered that some of the Appalachian and Alleghany plants show affinities to more megathermic plants. Thus the disjunctions may not be caused by retraction of a range which was more to the North, but to evolution of more microtherm taxa from a megatherm group. This is especially important for Pieris and Lyonia, both of which have stations in the Caribbean.

62.4. GROUPS WITH LOCALISED AREAS OF DISTRIBUTION IN ONE CONTINENT.

Continental S.E. Asia. This area comprises the Tertiary mountain chains of the Himalayas and associated mountains, together with the more stable areas of Tibet, China (which does include some older mountains) and India.

Around Japan there is a notable centre of endemic groups. Arcteac (Map 4), Tsusiphyllum (Japan only) and Bryanthus (Map 6) are the genera concerned, and there are several infrageneric groups belonging to the middle latitude disjunct groups just considered found here, e.g. Leucothoe section Paraleucothoe, Epigaea asiatica, two species of Cladothamnus as well as several sections, etc. of Rhododendron. Therorhodion is centred on countries bordering the N. Pacific; Vaccinium sections Praestans and Ciliata are rather more continental, but in the same general region as is Rhododendron subgenus Tsutsia, sensu Seithe (1960).

In the more unstable mountainous region of the Himalayas
are to be found several genera and sections. **Rhododendron** *Hymenanthes* group is most diverse here (see Hutchinson, 1947), and there are many other sections and subgenera of *Rhododendron*. *Diplarche* (Map 6) is found only at very high altitudes in this region, as are *Vaccinium* section *Cyanophthalmus* and the *Cassione wardii* group of species. *Lyonia* section *Pieridopsis*, several species of *Pieris*, *Craibiodendron* (Map 4), *Leucothoë* section *Oligarista*, and the genus *Enkianthus* occur here. The last named, as well as *Lyonia* and *Pieris* (Map 4), have several localities elsewhere in S.E. Asia; *Enkianthus* and *Lyonia* get into Japan. *Gaultheria* has a notable centre of diversity in this region, with several restricted groups. *Agapetes* and other sections of *Vaccinium* are dealt with immediately below.

**Malaysia.** On the mountains of the Malay peninsula there are several isolated taxa which are probably rather old groups. These are "*Agapetes* s. cortechnii", *Gaultheria malayana* and *Pernettyopsis* (Map 5), also found in Sumatra. As van Steenis (1967) shows, the age of such species may exceed that of the mountains on which they presently grow. *Lyonia ovalifolia* has a station here; this is the most southerly locality for *Lyonia* in the Old World. The Ericaceae on the Western Ghats of south west India and in Ceylon (*Gaultheria* (Map 5), *Vaccinium* section *Bracteata* (Map 7) and *Rhododendron*) are very far from their Himalayan centres, yet the species concerned have not diverged much.

On the islands grow *Costera*, *Diplycosia* (Map 5), *Dimorphanthera* (Map 11) and *Paphia* (Map 10). *Diplycosia* alone just reaches the mainland. *Paphia* and *Dimorphanthera* are
MAP 5: DISTRIBUTION OF SOME OF THE GUALTHERIA GROUP OF GENERA.

= Gualtheria (very generalised, ↓ = isolated localities), --- = Gualtheria section Amblyandra, ---- = Diplycosia, P = Pernettyopsis, T = Tepuia.
practically restricted to New Guinea, with very few species elsewhere, Costera is similarly restricted to Borneo, but Diplycosia has many species on both islands, as well as elsewhere (see Sleumer, 1967b).

Both Rhododendron (Map 8) and Vaccinium (Map 7) have very important centres of diversity here. Although Rhododendron section Vireya hardly gets onto the mainland, the sections of Vaccinium with hypodermal phellogen (and Agapetes) are prominently represented there, the sections involved having little overlap with the island sections. Of the mainland sections, Conchophyllum and Epigynium are centred on the Himalayas, as is the whole of the genus Agapetes; this latter genus also follows the mountain ranges south into the tropics (Map 10). Section Bracteatum has a very wide distribution: from Japan, the Bonin Islands and Sumatra (the disjunct locality in the New Hebrides will be dealt with in section 6.2.6.) to Kashmir, Ceylon and the Western Ghats. Species of sections Bracteatum and Eococcus sensu Sleumer (1941) behave similarly in having this wide distribution. Section Galeopetalum is also centred on the mainland. One species of Rhododendron (R. lochae) and two of Paphia grow in N.E. Queensland; they are the only Ericaceae there. N.E. Queensland has considerable affinities with the New Guinea flora. Only one species of the Ericaceae grows on Timor (V. timorensis). This is possibly because its climate is drier
MAP 6: DISTRIBUTION OF THE DIPLARCHEAE, DABOECIEAE AND SOME OF THE PHYLLODOCEAE.

- = Phyllodoce (partly from Hultén, 1968), --- = Bryanthus, -- = Kalmia, ● = Kalmiopsis, == = Leiophyllum, ◊ = Diplarche, ☀ = Daboecia, R = Rhodothamnus, L = Ledothamnus.
MAP 7: DISTRIBUTION OF SOME SECTIONS OF VACCINIUM.

- = section Vitis-Idaea (from Hultén, 1968), p = section Macropelma,
= sections of Vaccinium with hypodermal phellogen, b = V. boninse,
m = V. macgillivravi, w = V. whirimaei (all members of sections with
hypodermal phellogen).
MAP 8: RHODODENDRON IN MALAYSIA; GAYLUSSACIA IN AMERICA.

- - - Rhododendron Hymenanthes group, — — = main concentration of section Vireya,
--- a few species of subsection Pseudovireya (after Sleumer, 1966);
= Gaylussacia section Gaylussacia, = = = = = section Decamerium, = = = = = = = = = section
Vitis-Idaea (partly after Sleumer, 1967a).
than other parts of Malaysia and approaches that of N.W. Australia (Good, 1953).

Within Malaysia itself there are interesting distributional parallels between Vaccinium and Rhododendron, and also with the genera mentioned above. Thus Vaccinium section Rizioletis and Rhododendron subsection Malayovireya are restricted to Borneo, V. section Neojunghuhnia and R. subsections Phaeovireya and Solenovireya almost exclusively to New Guinea. V. section Euenigynium and R. subsection Euvireya, etc. are widespread throughout the archipelago.

There is only slight overlap between the sections of Vaccinium with hypodermal phellogen and those without, and between Rhododendron section Vireya and the rest of Rhododendron. In the latter case, this overlap is due to the wide distribution of subsection Pseudovireya. Both Vaccinium and Rhododendron give the impression of being rather recent, aggressive groups which have evolved in situ, the number of taxa decreasing rapidly away from the Malaysian Archipelago ("equiformal progressional species numbers"), although Vaccinium behaves differently in S.E. Asia.

Europe. Europe is rather poor in Ericaceae. There are various representatives of the disjunct groups here; also Erica subgenus Pentapera (north east Mediterranean; 2 species), Rhodothamnus (2 species, disjunct by 2,400 km.; Map 6), Calluna (monotypic, with a wide distribution in Western Europe), Daboecia...
(Map 6) and Bruckenthalia (the north east Mediterranean region). Although Rhodothamnus may be a more megathermic relative of Phyllodoce and perhaps of early Tertiary age (the wide disjunction of the two species would support this), the taxonomically isolated genera Calluna and Daboecia are perhaps even older. Both of them show at least some similarity to the predominantly (S.) African Ericoideae.

**Africa.** Here are found many of the genera of the Ericoideae, which are centred on the Cape region and the Drakensberg. They occur sporadically farther north, but the fossil evidence suggests that at least some of them were formerly more widespread here than at present. Agauria (Map 9) is an endemic genus; its distribution off the African mainland is almost the same as that of Philippia - see section 6.2.6. Both these genera, as well as Vaccinium section Cinctosandra are montane groups most variable in the east; in the case of Agauria and section Cinctosandra on Madagascar. It is unlikely that all these groups are the same age; the Ericoideae seem to be a very old group which has evolved in Africa itself, the others are probably later immigrants.

**N. America.** As mentioned above, there are a number of temperate disjunct taxa centred on the Appalachians and the Alleghanies. There are other taxonomically isolated groups to be found here: Leiophyllum (Map. 6) and Oxydendrum; with Zenobia rather more to the South. Vaccinium sections Pseudocyanococcus
and *Herpothammus* and the very isolated species of *Gaultheria*, *G. procumbens*, also occur in this general region. Only one species of *Kalmia* grows on the west of the continent; this species, *K. polifolia*, also grows with the several others centred on (south) east U.S.A. One species of the *Kalmiella* group has a few localities around the N. Caribbean. *Gavluussacia* sections *Vitis-Idaea* and *Decamerium* are endemic to eastern N. America (Map 8), and this is where species belonging to the otherwise S. American section *Gavluussacia* are found. *Bejaria* section *Racemosae* is restricted to Florida and immediately adjacent regions; both it, *Gavluussacia* and the various localities of *Agarista*, *Lyonia* section *Lyonia* and the *Kalmiella* group in south east U.S.A. are mostly away from the mountains; they give the impression of being more recent groups in that part of America (see Fernald, 1931).

*Kalmiopsis* (Map 6) is found in the mountains of N. California, which Stebbins and Major (1965) recognise as a notable centre for relict mesophytic species. There are representatives of some of the mid latitude disjunct groups in the west of America in the coastal Rockies. California and adjacent Mexico are very definitely the centre of diversity of the *Arbutoideae* (Map 1), which seem to have undergone much of their evolution there as members of the xerophytic Madro-Tertiary flora. *Arbutus* and *Comarostaphylis* are most diverse in Mexico, although the former
genus has other disjunct species (see above). *Xylococcus* and *Ornithostaphylis* are monotypic genera found in S. California and the northern part of Baja California. *Arctostaphylos* itself is most diverse in California, but a few species (apart from *A. uva-ursi*) are found in adjacent states and in Mexico. Fossils of *Arbutus* are known from this area in the middle Miocene, and *Arctostaphylos* is found in the lower Pliocene (Axelrod, 1938), but the evolution of the Madro-Tertiary flora, of which these genera are members, probably started around the middle Eocene (Weberling, 1968).

**The Caribbean.** Western Cuba is the centre of a number of distinct groups: *Lyonia* section *Lyonia* (which also occurs elsewhere on the Greater Antilles), *Pieris cubensis*, two species of the *Kalmiella* group and *B. cubensis*, the only species of *Bejaria* in the Caribbean. Elsewhere there are fewer species; *Gaultheria sphagnicola* and *G. domingensis* grow on the Greater Antilles, as do a few Vaccinieae closely related to C. and S. American groups, also *Clethra* section *Cuellaria*, which shows relationships in the same direction. There are practically no Ericaceae on the Lesser Antilles, although there are some on Trinidad, which is geologically part of S. America. Here grows the rather curious genus *Findlaya* (Map 10). *Hornemannia* is found on several islands of both the Greater and Lesser Antilles. The distinctness of many of these taxa suggests that they have been isolated since the earlier part of the Tertiary; others again
may be more recent immigrants.

**S. America.** Many of the genera of the Vaccinieae are endemic to S. America (including C. America), and *Clethra* section *Cuellaria* is centred here, but with one species very remarkably occurring on the Madeira Islands. The genera concerned can roughly be divided into four groups

1. Common on the Andes, with few stations in Venezuela and Brazil, but relatively more in C. America (Maps 10 & II). They do not live on the Antilles. In the Andes they do not get farther than 18°S.; at this point the rainfall gets markedly less and even further north the belt of heavier precipitation veers away from the coast and there the Vaccinieae are found farther away from the coast. The sections of *Vaccinium* close to other S. American genera live in this area, i.e. the Andes and C. America; another section, *Pyxothamnus*, is common in this area but also has a single species, *V. ovatum*, in the mountains of western N. America. Smith (1932) noted that the species of several genera growing in N. W. Colombia tended to be very distinct and isolated.

2. There are several taxonomically very isolated groups found on the sandstone Tepuis of Venezuela and N. Brazil. These include *Ledothamnus* (Map 6), *Tepuia* (Map 5), *Notopora* and *Findlaya* (Map 10). *Vaccinium* section *Neurodesia* is also well represented here. The anatomy of the members of these groups
which have been studied is rather xeromorphic (the rainfall is not great), and they give the impression of being long isolated genera. The species of the Andean-centred genera do not seem to be particularly noteworthy and are probably more recent in their evolution.

3). Gaylussacia (Map 8) and Agarista (Map 9) are two genera which are centred on the coastal highlands of Brazil, from Santa Catalina to Minas Geraes. Both genera have isolated localities elsewhere, and of course Gaylussacia has several (derived?) species in N. America - see also Sleumer, 1967a.

4). Gaultheria in S. America has species in all three areas (Map 5), but since their relationships are poorly known it is not possible to analyse its distribution further. Interestingly it is not found in the Andes in the area where the rainfall is low, but occurs both to the north and the south of this. Bejaria (Map 2) is predominantly to be found in the Andes, but it has a relatively large number of stations on the Coast Range of Venezuela, the Sierra de Santa Marta, the Cordillera Merida and the Sierra de Perija. Clethra section Cuellaria has species growing in Brazil and in the central Andes (for map, see Sleumer, 1967c).

Harrington (1962) recognises three main old blocks in S. America corresponding to the Guiana Shield (Venezuela, N. Brazil), the Central Brazilian Shield and the Coastal Brazilian
Shield. Other areas show moderate stability (parts of Chile and Argentina), whilst the Andes are a highly unstable region. Thus the genera of groups 2 and 3 (above) are living on areas which have been stable and emergent for a long time, and the others are on a geologically more recent area. The age of the Santa Marta massif is doubtful; Schuchert (1935) thought that it was probably rather old. Certainly the Vaccinieae growing on the Andes present a very confused picture taxonomically and this may be due in part to a recent origin, perhaps correlated with the block-faulting which produced the Andes (mostly post Oligocene in age). They may also have been ± differentiated prior to this and simply have been able to take advantage of the new conditions; as with most problems of this nature, one just cannot say (see section 6.3.)

South East Australia and New Zealand. The very isolated genus Wittsteinia lives in the very south east of Australia (Map 10), but it overlaps with Gaultheria in distribution; they may even grow on the same mountain. The few species of Gaultheria itself in south east Australia, Tasmania and New Zealand, have very interesting affinities. G. appressa and G. hispida seem to be very close to the S.E. Asian species of section Leucothoides; G. antipoda, G. depressa and G. rupestris to the Malaysian G. mundula. These relationships may become more comprehensible when the taxonomy of Gaultheria is better known. The
baccate-fruited species seem to have a close relationship with some of the S. American species, and this raises the problem as to the role of Antarctica in the evolution and dispersal of the angiosperms. At the very least it seems to have acted as a bridge for some angiosperms in the early Tertiary; Gaultheria may have used it. There are a number of groups with very close relationships between S. America and New Zealand, S.E. Australia and Tasmania, e.g. Ranunculus, Hebe, Euphrasia, Nothofagus, Cyttaria, but they may owe their present distribution patterns to a variety of causes. Camp (1947) was not justified in saying that Gaultheria and "Pernettya" had a concentration of diploid species in the far south, and that that was where the most primitive species were to be found. Even now very few chromosome counts are known from Gaultheria, and in morphology and life form the baccate-fruited species give the appearance of being a derived, and not primitive, group.

6.2.5. THE ISLAND ERICACEAE.

The occurrence of Ericaceae on islands of the continental shelf such as Great Britain poses no great problem to the plant geographer seeking to explain how the plants arrived, and the plants themselves are usually little differentiated from those growing on the mainland. The same applies to those Ericaceae on the Malaysian archipelagos; there is good evidence that the islands there were formerly more extensive, and that there have been islands where now there are none. Likewise Fernando Po
(in the Bight of Biafra), Greenland and Iceland are, or have been in the Pleistocene, very close to the areas from which they derived their floras, at least no farther away than a small amount of long distance dispersal would easily cover. Other Ericaceae live on islands which are far more isolated, and they, like the other plants on such islands which are not strand plants, pose a much greater problem.

**Madagascar and Reunion.** Both Agauria and Philippia are found on these islands, and Agauria is also found on Mauritius; indeed the greatest variation in Agauria occurs on Madagascar (Sleumer, 1933). Although Madagascar is quite close to Africa, (ca. 400 km.) and separated by a relatively shallow water channel, its flora has a very high proportion of endemic species and genera and has a remarkably strong affinity to that of India. In the case of the Ericaceae the affinity is with Africa. Reunion and Mauritius are 700 km. farther east and at the southern end of the Seychelles ridge, which geophysical studies have shown to have a sub-continental structure. It is probable that this ridge was close to India (the Bombay region), perhaps as late as the early Tertiary; both it and Madagascar had a different relationship to the coast of Africa at that time (Davies, 1968; le Pichon and Hiertzler, 1968). Possibly Agauria was on Madagascar by this time; both genera may be later immigrants onto Reunion and Mauritius.
Hawaii and the S. Pacific. A few species of *Vaccinium* grow on Hawaii; they are all related to one another (Map 7, section Macropelma). At present Hawaii is a very isolated island, but there is a chain of islands and seamounts trending W.N.W. to 33°N., and the Emperor seamounts strike almost due north to join Kamtschatka. Islands in the first mentioned chain are Cretaceous in age, the others are possibly even older. The relatives of the species on Hawaii are all around the N. Pacific, so at present it is anybody's guess as to how they got there.

Some 4,200 km. separate these Hawaiian species from *V. cereum* and *V. rapa*, which have been placed in the same section. Since their affinities are obscure, it will only be mentioned that whatever their final position within *Vaccinium*, it is going to provide problems for the phytogeographer.

The Islands of the W. Pacific. *Vaccinium macgillivrayi* grows near sea level in New Caledonia, separated by some 5,500 km. from its nearest relatives, *V. whitmeii* grows on Samoa (Map 7), "Agapetes" *neo caledonica* on New Caledonia and *Paphia vitiensis* on Fiji (Map 10), all less, but still considerable distances from their nearest relatives. "Agapetes" *neo claedonica* especially is a very distinct species; but they are not particularly remarkable plants. All four live in an area noted for its numerous islands, which could provide stepping stones if the idea of long distance dispersal is not appealing.
Furthermore, all except V. whitmei are on islands inside the "andesite line". This is a line to the west of which a type of lava is erupted which is characteristic of continental areas, and the crust in this area does seem to be sub-continental. The depth of the sea is not great, and not impossible raisings of the sea floor would very much increase the extent of the islands in this region. Samoa itself is only just to the east of the Andesite line. Fiji is just inside on the extreme east, and Smith (1955) notes that Paphia is one of the 101/445 genera native to the islands whose distribution in an easterly direction ends here.

The Islands of the E. Pacific. Pernettyoid Gaultherias occur on the Galapagos and Juan Fernandez islands (Map 5). Croizat (1952) uncritically uses the former station as prima facie evidence that the Galapagos are continental. In fact the Galapagos Islands are joined to the American mainland by the Cocos and Carnegie ridges, both less than 1,100 m. deep. The Juan Fernandez islands are no farther from the S. American mainland, but do not have any particular shallow water connection to it. The species concerned are baccate and do not seem to be markedly different from mainland species of the "P." mucronata/"P." buxifolia alliance.

The Atlantic Islands. Empetrum rubrum is to be found on Tristan da Cunha, a young, very isolated, volcanic island of the
S. Atlantic, whilst in the N. Atlantic the Azores, likewise a very young island group, have several members of the Ericaceae (Vaccinium cylindraceum, Daboecia azorica, Erica azorica and Calluna vulgaris), as well as Corema album of the Empetraceae.

Some degree of long distance dispersal was probably necessary for the arrival of these plants on the islands (see Guppy, 1917), and in their relationships these plants are similar to the rest of the flora. The forest trees and shrubs on the Azores are related to other Macaronesian plants (Erica arborea and Vaccinium padifolium grow on Madeira) whilst the other Ericaceae are plants of the higher moors and have relatives more to the north in Europe. Vaccinium padifolium and Arbutus andrachne are to be found in the Madeiras, but these islands have a notable old (Tertiary) element in their flora (Guppy, 1917). Just how Clethra arborea reached the Madeiras must remain a matter for conjecture; it is possible that it is a member of a group which achieved wide dispersal prior, or immediately consequent, to the opening of the Atlantic ocean (see below).

6.2.6. TROPICAL TRANSPACIFIC AND TRANSATLANTIC CONNECTIONS.

Previously unrecognised affinities lie between some of the Vaccinieae of Malaysia and those from S. America. Dimorphanthera (New Guinea) is very close to Satyria (mainly S. America; Map 11), and Paphia and Costera are also fairly close to S. American genera (Map 10). Van Steenis (1962) listed all
the tropical amphi-transpacific connections known to him, and suggested that they were the result of migration over a land bridge or island stepping stones across the central Pacific. There are a number of seamounts in the W. Pacific, trending E.S.E., and these mark the site of the Darwin Rise. This is believed to have been a structure not dissimilar to the mid-Atlantic ridge and to have been active in Cretaceous times (Menard, 1964). At this time the sea mounts would have been islands, since the whole ocean bottom in the area was raised, and there was marked volcanicity in the region. However, it is usually forgotten that at the time the Darwin Rise was active, S. America would have been farther east than it is now. There is no evidence at present that the Darwin Rise reached farther than the present centre of the Pacific, although traces of it further east may have been obscured by the activity of the present day E. Pacific ridge. If one follows Croizat's views on evolution, then the problem would be easily solved by assuming parallel evolution of a previously widely distributed ancestral taxon (Croizat, 1968b, and references therein), but this does not seem to be a satisfactory explanation for the type and level of disjunctions to be found in the Ericaceae. A trans-Pacific bridge of any sort seems to be geologically improbable, so no explanation can be offered for this disjunction which is less than pure hypothesis. Reduction in range of a pan-tropical genus,
MAP 9: A TROPICAL AMPHI-TRANSATLANTIC DISJUNCTION.

In Africa - Agauria (from Sleumer 1938b, modified), ↓ = isolated localities.
In America - Agarista. F = fossil records of "Leucothoe protogaea" (see text for references).
MAP 10: DISTRIBUTION OF SOME OF THE VACCINIEAE AND OF WITTSTEINIA.

Ø = Agapetes,   Ø = Paphia (both after Sleumer, 1967b),   • = Cavendishia,
S = "Agapetes" scortechinii, N = "A." neo-caledonica, V = Paphia vitiensis,
F = Findlaya, No = Notopora, W = Wittsteinia.
MAP 11: A TROPICAL AMPHI-TRANS PACIFIC DISJUNCTION.

• = Satyria, --- = Dimorphanthera, *** = Dimorphanthera section Pachyantha
(the last two from Sleumer, 1967b).
migration around the N. Pacific and long distance dispersal all seem equally improbable, so Occam's razor is of no help either.

The demonstration that Agauria and Agarista are closely related results in one of the most infrequent of distribution patterns, a close relationship between tropical America and tropical Africa (Map 9). Hepper (1965) lists a number of examples known to him, and Iltis (1967) adds some more. The latter author favours long-distance transport, at least for several of the groups favouring open habitats (in his case it was Cleome). Although the present position of the continents would appear to preclude easy exchange of their flora, it has been conclusively shown that there is a remarkable fit between the two continents both in many geological details and also bathymetrically (for references, see Funnell and Smith, 1968). Estimates of the time of drift vary, but they are rather later than was originally thought. Funnel and Smith (1968) estimate that drifting started in the late Triassic, but was only 25% completed by the mid-Cretaceous. Hallam (1967) dismisses the Jurassic Cape Verde sediments as neritic and thought that the formation of the Atlantic started in the early Cretaceous; le Pichon (1968) suggests a similar time scale.

In the absence of reliable fossil evidence it is hard to say just how this disjunction arose. It is conceivable that the ancestors of the genera in question arrived from, or via, India via the Seychelles ridge and Madagascar; this would put the time
of their arrival in Africa at the early Tertiary and in America rather later and only after long distance dispersal across the S. Atlantic. Fossils of "Leucothoe protogaea" are known from several localities in Europe, and this species is compared to Leucothoe (= Agarista) oleifolia and other species from S. America. According to Takhtajan (1969), they form 30% of the fossil leaf flora in parts of the Urals (Map 9). Fossils of L. protogaea from Roumania (illustrations in Petruscu, 1968, also in litt.) are like those on many angiosperms in general appearance; the identification of most such fossils has been based on general appearance. Ferguson (in litt.) found that some of the material from Germany referred to L. protogaea was very similar to Myrica both in gross morphology and cuticle type. If fossils referrable to Agauria and Agarista are confirmed from the Northern Hemisphere it will add another dimension to the hypotheses explaining their present day restriction to Africa and S. America.

At present both genera are restricted to montane areas hardly extending beyond the tropics, yet Agarista in S. America is not very successful on the Andes. This preference may partly explain their present, rather peculiar, distribution where each genus has its greatest variability on the east of the continents and not on the east of S. America and the adjacent west of Africa.
6.3. CONCLUSIONS.

Distribution patterns make rather more sense when considered from the point of view of the evolution and ecology of the whole family. Many of the Ericaceae are associated very strongly with mountain ranges in the middle or subtropical latitudes. Rainfall is moderate to high, and the climate generally is not too extreme. On the whole they are heliophilous plants, and even many of the epiphytes in the tropics live in the open at higher altitudes. Perhaps the epiphytic habitat is a way of remaining heliophilous in a more closed vegetation system. Epiphytes do not give the impression of being primitive in the Ericaceae; in Rhododendron they are associated with an advanced indumentum and seed, in the Vaccinieae with advanced floral characters, and in Agapetes and S.E. Asian species of Vaccinium with a probably derived hypodermal phellogen. The sub-tropical, montane habitat mentioned above is that in which the early Angiosperms are sometimes thought to have evolved (e.g. Axelrod, 1952; Takhtajan, 1969).

The Ericaceae, on the whole, does not give the impression of being an advanced family. The very variable development of sympetalary, the relatively large number of floral parts (usually 10 stamens and a 5-locular ovary, with many ovules per loculus), weak development of zygomorphy and adnation and connation of parts, and the woody habit are all characters which are not
advanced in most schemes of evolution. It seems a reasonable
assumption that the Ericaceae is one of the older sympetalous
families because it has this complex of characters although it
is not possible to give ages, owing to the lack of fossils.

It is thus not surprising that the Ericaceae have a number
of distribution patterns which seem to be indicative of considerable
age of the taxa involved, and which are explicable in terms of
events which occurred in the early Tertiary or even earlier.
The great taxonomic distinctness of many of the northern groups
of the Ericaceae (Section 6.2.2.) may also be due to ancient
evolution in very high latitudes which would be the only place
where the climate was suitable for such plants in the earlier
part of the Tertiary and before (Dorf, 1960). If Good's (1966)
estimate of 5% disjunct distributions for all Angiosperm genera
is correct, then the Ericaceae score very highly in this respect.
It is interesting that the two continents which on all evidence
seem to have been most effectively isolated at least from the
later part of the Mesozoic to the present, Australia and Africa,
have very distinct representatives of the Ericales (the
Ericoideae in Africa and the Epacridaceae and Wittsteinioideae
in Australia). The other, less remarkable, members of the
Ericales on those continents are probably more recent immigrants.
Even so, one has to be very careful in the interpretation of
these patterns. Some Epacridaceae are known from the London
clay flora (Chandler, 1964); they are supposed to have reached Britain by migration along the shores of the ancient Tethys. However, the fossil record is such that it does not preclude the Epacridaceae from being relict in Australia. Similar problems have arisen in palaeozoology, where the distribution of the marsupials has been interpreted as that of a group which always has been centred on the Southern continents, but which the fossil evidence suggests is in fact relict there (Simpson, 1966).

A number of the distribution patterns of the Ericaceae do seem interpretable in fairly definite terms, usually as Tertiary (or earlier) relicts. Within many genera there are several patterns. The only circum-boreal species of *Arctostaphylos*, *A. uva-ursi*, is probably more recent than some of the Californian species. Disjunctions occurring at the same time will be recognised at different taxonomic levels today, owing to the vagaries of evolution. As Fernald (1931) noted, *Leiophyllum* on the Atlantic Plain of N. America is rather different from its montane, and presumably older, stations; the same is true of *Leucothoe* (*L. racemosa* on the hills, *L. recurva* on the plains). Other genera, like *Oxydendrum*, have not taken advantage of this new habitat.

This emphasises the point that it is not youth per se which enables a taxon to take advantage of a new habitat, so one cannot estimate the age of a taxon from that of its habitat. The
ability to occupy a new habitat depends on many factors; the morphology, ecological tolerance and breeding system of the species, and also on just being at the right place at the right time. **Belaria** is often considered to be an old genus, and morphologically it is not advanced, yet it is mainly to be found on the geologically recent Andes. Smith (1932) thought that the monotypic genus *Lateropora* (Vaccinieae) was an old genus, yet it is to be found on Chiriqui volcano, in Panama, which is only Pliocene in age. Age does not necessarily prevent a group from becoming rejuvenated by entering geologically young, favourable habitats.

The penchant the Ericaceae have for montane habitats will obviously tend to make them a rather migratory group. As mentioned above, van Steenis' (1967) remarks on the age of taxa compared to the age of their montane habitats are applicable to the Ericaceae and so this too complicates explanations in terms of age and evolution. It is perhaps rather surprising that there is only one genus of the family to be found in temperate regions of both northern and southern hemispheres (*Gaultheria*), although the Empetraceae are a noted bipolar group.

Long distance dispersal is not favoured as an explanation of most of the disjunctions in continental areas, although for some of the island stations it is more likely. Latitudinal and longitudinal disjunctions on continental areas are probably due
to migration, extinction and evolution. The Ericaceae are not obviously adapted to long distance dispersal although, as van Steenis (1962) mentioned, the possession of means for wide dispersal seems often to have no correlation with the area inhabited by a plant. Despite this, most members of the Ericaceae do have several characters which would facilitate long distance dispersal. These are their usually small seeds dispersed by birds or wind, their liking for rather open vegetation, and also the fact that very often they are self compatible. Good seed has been set in the garden here in large-flowered species of Rhododendron, Macleania and Agapetes (grown as single specimens), and also in many, but not all, other species (Diplycosia heterophylla and Zenobia are two of the exceptions). As Baker (1959) notes, self compatibility is advantageous for long distance dispersal.

The field of plant geography is an adjunct of taxonomy which, perhaps even more than taxonomy itself, desperately needs the sensible synthesis of many different disciplines. The rewards are great, but the dangers of making meaningless or incorrect generalisations are likewise great. Data is especially needed from palaeoclimatology and palaeontology to help to comprehend the distribution of all such old, widely distributed groups.
This work would have been impossible without a grant from the Science Research Council, for which I am very grateful. I wish to thank my supervisors, Mr. B. L. Burtt and Dr. F. H. Davis, for their invaluable advice, Professor R. Brown, F.R.S. and Professor H. R. Fletcher for providing facilities for research, members of the staff at the Royal Botanic Garden and the Botany and Geology departments of Edinburgh University for helpful discussion and the Directors of Kew, Copenhagen and Melbourne Herbaria for the provision of material for study. I am also indebted to numerous individuals for providing fresh material of species of which otherwise herbarium material was all that was available. Last, but not least, I should like to thank my typist, Mrs. Paterson, who has coped successfully with a difficult manuscript, and Mrs. Brodie, who has typed the tables.
APPENDIX 1.

The following new combinations in the Vaccinieae are necessary as a result of the realignment of genera in Malaysia.

a) in *Dimorphanthera* (see p. 597).

*Dimorphanthera* section *Pachyantha* (Sleumer) Stevens, comb. nov.


*Dimorphanthera macbainii* (F. v M.) Stevens, comb. nov.


*D. amplifolia* (F. v M.) Stevens, comb. nov.


*D. keysseri* (Schltr. ex Diels) Stevens, comb. nov.


*D. fissiflora* (Sleumer) Stevens, comb. nov.


*D. ingens* (Sleumer) Stevens, comb. nov.


b) in *Paphia* (see p. 561).

*Paphia costata* (C. H. Wright) Stevens, comb. nov.

*Agapetes costata* C. H. Wright, Kew Bull. 102 (1889).

*P. alberti-eduardii* (Sleumer) Stevens, comb. nov.

P. rubrocalyx (Sleumer) Stevens, comb. nov.

P. brassii (Sleumer) Stevens, comb. nov.

P. carrii (Sleumer) Stevens, comb. nov.

P. sclerophylla (Sleumer) Stevens, comb. nov.

P. vitis-idaea (Sleumer) Stevens, comb. nov.

I do not know if Agapetes queenslandica Domin (Reprium nov. Spec. Regni veg. 12: 132 (1923)) is synonymous with Paphia meiniana (F. v M.) Schlt. (1919)., so a new combination has not been made for it.

As a result of the realignments of the generic limits in the Cladothamneae (p. 290) the following new combinations are necessary:

Cladothamnus paniculata (Siebold & Zuccarini) Stevens, comb. nov.
Elliotia paniculata (Siebold & Zuccarini) Hooker f., Genera Plantarum 2 (2): 598 (1876).
Cladothamnus bracteata (Maximowicz) Stevens, comb. nov.

Elliottia bracteata (Maximowicz) Hooker f., Genera Plantarum 2 (2): 598 (1876).

The following are the descriptions of the three new tribes and one new subfamily which are proposed as a result of this work.

**DABOECIEAE** Stevens, tribus nova (vide p. 331).

Frutices parvi, sempervirentes; folia parva, revoluta; infra pilis densis albis unicellularibus et ad marginem pilis glanduliferis praedita. Inflorescentia terminalis, eperulata, racemosa, pauciflora; bracteae adsunt sed bracteolae ut videtur nullae. Flores 4-5(-6)-meri, parvi, actinomorphi. Corolla urceolata, lobis parvis. Stamina plerumque 8; filamenta glabra; antherae sagittatae, granulares, texto resorbendo per rimas breves dehiscentes, filis viscinis nullis. Ovarium loculis 3-5(-6), pilis glandulis praeditum, in stylum angustatum. Capsula septicidalis. Semina ovoidea; testa uno principali strato, intus crassis parietibus, extus parietibus tenuibus, papillatis.

**Daboecia** D. Don genus solus typum tribus est.

**ENKIANTHEAE** Stevens, tribus nova (vide p. 374).

Frutices decidui vel sempervirentes, folia serrata, in gemma convoluta, pilis unicellularibus et multicellularibus, hic cellulis
moderate elongatis. Inflorescentia terminalis, perulata, umbellata vel corymbosa; pauciflora; bracteae decidueae, bracteolae plerunque nullae; pedicellus cum calyce articulatus. Corolla urceolata vel campanulata, lobis 5, parvis vel mediocribus. Stamina 10, amplitudine dimorpha; filamenta papillosa vel pubescentia, basi tumida; antherae aristis duobus, per rimas longas dehiscentes; pollinis grana singularia. Ovarium loculis 5, placentis apicalibus vel basalibus, in stylum angustatum, vel stylo impresso. Capsula loculicida, suturis + incrassatis. Semina ovoidea; laevia vel alata; testa uno principali strato, cellulis altis parvis incrassatis.

Enkianthus Lour. genus solus tribus typum est.

CASSIOPEAE Stevens, tribus nova (vide p. 384).

Frutices parvi, sempervirentes; folia parva aciforma et petiolata, vel epetiolata, vel epetiolata canale abaxiali, pilis unicellularibus vel parvis glanduliferis praedita. Inflorescentia terminalis vel axillaris, uniflora; bracteolae nullae vel 4; pedicellus cum calyce articulatus. Corolla campanulata, ad ¼-⅓ in lobis 5 fissa. Stamina 10; filaments glabra; antherae ovoidea, duobus calcaribus, per rimas latas apicales dehiscentes. Ovarium loculis 5; placentae ± apicales; stylum impressum. Capsula loculicida, parietibus tenuibus. Semina ovoidea; cellulae testae elongatae, parietibus tenuibus.
Cassiope D. Don tribus typum est. Genus alterum - Harrimanella Coville.

WITTSTEINIOIDEAE Stevens, subfamilia nova (vide p. 571).

Frutex, parvus, sempervirens, repens; folia serrata, crassa, in gemma convoluta, pilis unicellularibus et in axillis foliorum multicellularibus unisetiatis. Inflorescentia axillaris; flores 1-2; bracteolae minimae 2; pedicellum cum calycis tubo articulatis. Corolla urceolate, parva, lobis 5, dentatis. Stamina 5, imo corollae tubo inserta; filamenta glabra; antherae laeves, per rimas longes dehiscentes, pollinis grana singularia. Ovarium loculis 3; ovula paucha; stylum impressum. Fructus carnosus; semina oovoidea; cellulae testae sinuatae, spissecentibus anticlinalibus.

Wittsteinia F. v. M. genus solus subfamiliae typum est.
The following is a list of the species studied, with authorities. Representative specimens are cited. Unless otherwise mentioned all specimens are in the herbarium at the Royal Botanic Garden, Edinburgh; if there are no letters in parentheses after the cited specimen it indicates that leaf and stem anatomy have been studied from that specimen, as well as details of flowers (if present).

The symbols are:  se = seed and fruit only, st = stem anatomy only,  l = leaf anatomy only,  f = details of flower only;  K = specimen from Kew Herbarium, BM from the British Museum (Natural History), CH from Copenhagen and MEL from Melbourne.

**DIAPENSIACEAE**

Berneuxia tibetica Decne.: E.H. Wilson 3392.

Shortia uniflora Maxim.: Cult. Ed.

Schizocodon soldanelloides Sieb. & Zucc.: Cult. Ed.

Galax aphylla L.: Cult. Ed.

Diapensia wardii W. E. Evans: Ludlow, Sherriff & Taylor 5227.

Diapensia purpurea Diels f. bulleyana (Forr.) W. E. Evans: Farrer 1584.

Pyxidanthera barbulata Michx.: Shreve & Muller - New Jersey, 1/6/1907.

Pyxidanthera brevifolia Walls: Ahlen & Jackson 53164.

**EMPETRACEAE**

Ceratiola ericoides Michx.: Ahles & Haeasloop 53100 & 53100A.


Empetrum hermaphroditicum (Lge.) Hagerup: Alm 1367


**CLETHRACEAE**

Clethra alnifolia L.: McKenzie 321 (f); Heller 746 (l, st).

C. aloceri Greesm.: Pringle 8923.

C. arborea Ait.: Mandon 170 (f, l, st); Cult. Ed. C1825 (se).

C. cuneata Rusby: Bang 717.
C. elongata Rusby; Steinbach 9097.
C. faberi Hance; H. T. Tsai 51447 (l, st); W. T. Tsang 26761 (se); R. C. Ching 6854 (f).
C. occidentalis (L.) Kuntze; McNab - Jamaica, August 1839.
C. ovalifolia Turcz.; Spruce 5150 (l, st); Mathews 1477 (f).
C. papuana J. J. Smith; Sleumer & Vink 4234 (l, st); Sleumer & Vink 4207 (f).
C. pringlei S. Wats.; Meyer & Rogers 2654 (f, l, st); Arsène - Mexico, Dec. 1909 (se).
C. revoluta (R. & P.) Spruce; Bang 474.

EPACRIDACEAE

Richea scoparia Hook. f.; Cult. Ed.
Cyathodes colensoi Hook. f.; Cult. Ed.
Leucopogon albicans Brogn. & Gris.; Bonati 262 (f, l); McKee 1090 (l, st, se).
Lysinema conspicuum R. Br.; Fritzel 208.
Conostephium pendulum Benth.; A. Morrison - Subiaco, W. Australia 21/7/1897.
Prionotes cerinthoides R. Br.; Comber 2346.
Styphelia douglasii (A. Gray) Skotts.; Cult. Ed.
Lebetanthus myrsinites (Lam.) Endl.; Menzies - W. Coast of N. America (sic) 1787 & 1788.

ERICACEAE

RHODODENDROIDEAE

BEJARIEAE

Bejaria racemosa Vent.; Curtiss 4922.
B. aestuans Mutis; E. K. Balls 5676.
B. glauca H. & B.; Buchtien 5512.
B. parviflora Benth.; Hartweg 795.
B. mathewsii Field. & Gardn.; Hutchinson & Wright 5726.
B. laevis Benth.; McDougall - Ixtlan, Oaxaca, 21/5/69.
The following species have been studied in less detail:

R. arboreum Sm.: Cooper & Bulley 4981 - st.
R. campylogynum Franch.: Forrest 27569 - se
R. canadense Torrey: Baenitz 20/8/1909 - se.
R. chaetomallum Balf. f. & Forrest: Forrest 22883 - st, se.
R. crassifolium Stapf.: J. & M. S. Clemens 50968 - 1.
R. cuneatum W. W. Smith: Rock 17171 - se.
R. decorum Franch.: Yu 22910 - st & se.
R. degronianum Carr.: Hotta 12205 - st.
R. delavayi Franch.: Forrest 27717 - se.
R. durionifolium Becc.: J. & M. S. Clemens 40977 - se.
R. Hodgsonii Hook. f.: Ludlow, Sherriff & Hicks 16346 - st.
R. lacteum Franch.: Forrest 25776 - se.
R. cutsum L.: Davis 38076 - se.
R. mindansense Merr.: Elmer 11383 - 1.
R. occidentale A. Gray: Cusick 2911 - se.
R. primuliflorum Bureau & Franch.: Forrest 17093 - se.
R. scippenbachii Maxim.: Faurie 662 - se.
R. semibarbatum Maxim.: Togasi N.S.M. 344 - se, st.
R. stepfianum Hems.: J. & M. S. Clemens 40554 - st.
R. tashiroi Maxim.: Togasi 1460 - 1.

Therorhodion camtschaticum (Pall.) Small: Soule 510.
T. glandulosum Standley ex Small: I. W. Hutchinson - Anvil, Mt., July 1933.
Tsusiophullum tanakae Maxim.: Cult. Ed.

Ledum columbianum Piper: Cult. Ed.
L. decumbens Ait.: Karo 421.
L. glandulosum Nutt.: Macbride & Payson 3560.
L. groenlandicum Oeder: Cult. Ed.
L. macrophylla Tolm.: Motorina 3889a.

Menziesia pilosa Persoon: Cult. Ed.
M. globularis Salisb.: Curtiss 6568.
M. ferruginea Smith: Gillett & Mitchell 3739 (l, st, se); MacBride & Payson 3628 (f).
M. glabella A. Gray: Walker 456 (1, st); L. M. Umbach 525 (f).
M. lasiophylla Nakae: Cult. Ed.
M. purpurea Maxim.: Cult. Ed.
M. pentandra Maxim.: Mori 16173 (l, st, se); Shimizu (17393 (f)
M. multiflora Maxim.: Yokomizo 16174 (l, st, se); Togasi 31175 (f).
M. ciliicalx (Miq.) Maxim.: Kaga - Mt. Hatusen, August 1903, (l); Konta & Haruhashi 11 (f, s).

CLADOThAMNEAE

Cladothamnum pyroliflorus Bong.: Cult. Ed.
Tripetaleia (Cladothamnum) bracteata Maxim.: Cult. Ed.
T. paniculata Sieb. & Zucc. (=C.): J. Bisset 4392 (f, l, st);
M. Mochizuki Oct. 1916 (se).

Elliottia racemosa Muhl. ex Elliott: Harper 962 (f, l, st);
J. M. Crayton - Mahler, Ga., 11/10/1937 (se).

EPIGAAEAE

Epigaea repens L.: Cult. Ed. (f, l, st); Radford 33139 (se).
E. asiatica Maxim.: Cult. Ed. (f, l, st); Bisset 2129 (se).
E. gaultherioides (Boiss. & Bal.) Takht.: Cult. Ed. (f, l, st);
seed from Knox-Findlay (no voucher, but identification certain).

PHYLLODOCIAE

Kalmia angustifolia L.: Cult. Ed.
K. cuneata Michx.: Curtiss 6561.
K. ericoides Wright: Ekman 11024. K.
K. polifolia Wangenh.: Cult. Ed.

Kalmiopsis leachiana (Henderson) Rehder: Cult. Ed.

Rhodothamnus chamaecistus (L.) Reichenb.: Davis 17524 (f, l, st);
collector unknown, "Kalkfelsen am Linnz" (se).
R. sessilifolius P. H. Davis: Davis 29974.
Phyllodoce aleutica (Spreng.) Heller: Cult. Ed.
P. breweri (A. Gray) Heller: Cult. Ed.
P. coeruiea (L.) Sw. : Cult. Ed.
P. glanduliflora (Hook.) Coville: W. Spreadborough — Chilliwick Valley, B.C., 4/7/1906.
P. nipponica Makino: Cult. Ed.

x Phyllothamnus erectus (Lindl.) Scheider: Knox-Findlay, Keilour Castle.

Bryanthus gmelinii D. Don: Eyerdam — Petropavlovsk, Kamtschatka 14/7/1928.

Ledothamnus sessiliflorus N. E. Br.: Forest Dept., British Guiana 2880 K.
L. parviflorus Gleason: Steyermark 58215 K.
L. guayanensis Meissn.: Schomburgk — British Guiana (external morphology only) K.

Leiophyllum buxifolium (Berg.) Ell.: R. K. Godfrey 1170.

Loiseleuria procumbens (L.) Desv.: Cult. Ed. (f, l, s); H. Smith, Flora Norvegica 4595 (se).

Daboecia canadensis (L.) K. Koch: Cult. Ed.
D. azorica Tetin & Warburg: Cult. Ed.

Diplarche multiflora Hook. f. & Thompson: Ludlow, Sherriff & Hicks 17107.

**ARBUTOIDEAE**

Arbutus andrachne L.: Davis 47680 (s, l, se); Davis 42055 (f).
A. arizonica A. Gray: Godding 101 (f, s, l); Blumer 1233 (se).
A. glandulosa Mart. & Gal.: Cult. Ed. (l, s); Parry & Palmer 563 (f, se).
A. macrophylla Mart. & Gal.: Pringle 8011 (f, l, s); Pringle 6486 (se).
A. petiolaris H.B.K.: Pringle 1322 (l, s); Arsene — Morelia, 11/3/1909 (f).
A. prunifolia Kl.: Pedregal - Valley of Mexico, 16/4/1898.
A. texana Bulley: Palmer 9848 (s, l, se); Pringle 10255 (f).
A. varians Bentham: Pringle 2444.
A. xalapensis H.B.K., E. K. Balls 4398.
A. canariensis Duham., Burchard 67.
C. comnattii (Fern.) Small: Pringle 10182.
C. diversifolia (Parry) Greene: Cult. Ed. C894 (st, l, f);
H. Pollard - California, 27/6/1954 (se).
C. glabrata (Fern.) Small: Pringle 10183.
C. longifolia (Benth.) Kl.: Pringle 5725.
C. macronifera (DC.) Kl.: Pringle 5852.
C. rupestris (Rob. & Seaton) Small: Pringle 4318 (f).

Ornithostaphylia oppositifolia (Parry) Small: C. R. Bell 1376.

Xylococcus bicolor Nutt.: E.K. Balls 8146.

Arctostaphylos andersonii A. Gray: Hiller 7250 (st); Elmer 4610 (se); E.K. Balls 9790 (l, f).
A. canescens Eastw.: Rose 49017 (f, l, st); E.K. Balls 10376 (se).
A. ericicola D. Smith: J. D. Smith 2159 E.
A. drupacea Parry: LeRoy Abrams 3620.
A. glauca Lindley: Elmer 3967 (se, st, l); E.K. Balls 10395 (f).
A. hiapidula Howell: Balls 10425 (l, f); C. B. Wolf 9316 (l, st, se).
A. hookeri Don: E.K. Balls 8226 (f, l, st); J. T. Howell 28944 (se).
A. mariposa Dudley: C.B. Wolf 1104 (st, l, se).
A. manzanita Parry: E.K. Balls 10395 (se).
A. myrtifolia Parry: S.A. Cook 847 (se, l, st); Bracelin 145 (f).
A. nummularia A. Gray: H.E. Brown 806.
A. patula Greene: Hansen 1118 (l, st, se); E.K. Balls 10818 (f).
A. pungens H.B.K.: R.E. Collom, Arizona, 15/3/1937 (f, l, st);
Clokey 7618 (se).
A. sensitiva (Jeps.) McMinn: E.K. Balls 10597.

Arctotis alpina (L.) Nied.: Smith 4583 (l, st, se); Droward 62 (f).
A. rubra (Rehd. & Wils.) Fern.: Cody & Spicer 11902 (se, st, l);
Cody & McCasne 2147 (f).

ERICOIDEAE

Bruckenthalia spiculiflora (Salisb.) Rehb.: Guichard Tw/146/62.

Calluna vulgaris (L.) Hull: Cult. Ed.

Eremia totta Don: Schlechter 10687.
E. tubercularis Benth.: Schlechter 10728.

Erica arborea L.: Cult. Ed.
Pentapera boquetii Pegman (= Erica); Pegman 2158.
E. carneu L.: Cult. Ed.
E. ciliaris L.: Sinclair 4606.
E. cinerea L.: Hutchinson, Matthews & Riley 357.
E. curviflora L.: Cult. Ed.
E. oatesii Rolfe: Cult. Ed.
E. terminalis Salisb.: Cult. Ed.
E. taxifolia Doyd.: Cult. Ed. (l, s).
E. vagans L.: Cult. Ed.
E. walkeriana Andr.: Dümmer 1886.
E. woodii Bolus: Hilliard 4816.

Salaxis flexuosa Kl.: Schlechter 7643.
Philippia benguetensis (Welw. ex Engl.) Britten: Cult. Ed.

Scyphogynae inconspicua Brogni: Dümmer 956.

VACCINIIOIDEAE

ENKIANTHEAE

Enkianthus campanulatus (Miq.) Nichols: Cult. Ed.
E. cernus (Sieb. & Zucc.) Mak. var. rubens Maxim.: Cult. Ed. C843.
E. chinensis Franch.: E. H. Wilson 1012.
E. deflexus (Griff.) Schnieder: Cult. Ed.
E. pauciflorus Wilson, Forrest 17542 (se, l, st); Forrest 17845 (f).
E. quinqueflorus Lour.: Tsiang Ying 0051 (se, l, st); Bodinier 499 (f).
E. serrulatus (Wils.) Schnieder: Steward, Chiao & Chiou 443 (se, l, st);
Wang 22783 (f).
E. subsessilis (Miq.) Makino: Murata & Konta 479 (se, l, st);
Mochizuki - June, 1910 (f).
E. unmnamed: Cult. Ed.

CASSIOPEAE

Cassiope fastigiata (Wall. ) D. Don: Cult. Ed.
C. lycopodioides (Pall.) D. Don: Cult. Ed.
C. mertensiana (Bong) D. Don var. gracilis Piper: Cult. Ed.
C. pectinata Stapf: J. F. Rock 22687.
C. redowskii D. Don: Lehmann K.
C. tetragona (L.) D. Don: Cult. Ed.

Harrimaneula hypnoides (L.) Coville: Lt. Cdr. Stocken - 66.05 n
37.03E, Greenland, 16/7/1966.
Harrimaneula stelleriana (Pall.) Coville: Cult. Ed.
Andromeda polifolia L.; Cult. Ed.
A. glaucocephylla Link; D. W. Knight - Maine, 30/5/1905 (st, l, f);
W. J. Cody & R. Gutteridge 7514 (se).

Oxydendrum arboreum (L.) DC., Tracy 7053 (st, f); A. H. Curtiss
6937 (se, l).

Craibiodendron henryi W.W. Sm., Forrest 17492 (f); Forrest 4934
(st, l, se).
C. shanicum W.W. Sm.: Henry 9505 (st, l, f); Kerr 1282A (se).
C. stellatum (Pierre) W.W.Sm.: Anthony 9618 (f); Kerr 20060
(se, l, st).
C. yumanense W.W. Sm.: McLaran's collectors F 204 (f, l, st);
Forrest 12131 (se).

Unidentified: T. T. Yu 18028 & 17070.

Nuihonia selerantha Dop (= Craibiodendron): Peilane 6236 K.

Lyonia section Arsenococcus.
L. ligustrina (L.) D.C.; Cult. Ed.

L. section Maria.
L. mariana (L.) D. Don; Cult. Ed. C922.
L. lucida (Lam.) K. Koch: F. T. Aichmann - Sharon, Pa, 31/4/1887
(f, l, st); G. V. Nash - Fla, 16/8/1894 (se).

L. section Lyonia.
L. bushii Urban; Eckman 3417 K.
L. costata Urban; H. von Turokheim, 3119.
L. ferruginea Nutt.; S. M. Tracy, 7263 (l, f, st); Mt. Pisgah,
N. Carolina, 1905 (se).

L. fruticosa (Michx) Torrey ex Robinson; G. V. Nash - Lake Co., Fla.,
1894.

L. macrophylla (Britt.) Ekman; Morton & Aiana 3264 K.
L. squamulosa Mart. & Gal.; Meyers F. G. & Rogers D. J. 2723.
L. tinensis Urban; M. Fuertes 1917 (f, l, st); Ekman 10695 (se).

L. didymensis (Hand.-Mazz.) Hand.-Mazz.; Forrest 30647 (f); Tsai
56530 (st); Forrest 19860 (l); Tsai 54113 (se).

Kolisma foliolosa Fletcher (= Lyonia); Sorensen, Klarsen & Hansen 6327
(f, l, st); Kero 8637 (se).

L. macrolcalyx (Anthony) Airy Shaw; Forrest 25567 (f, l, st); Forrest
25829 (se).
L. ovalifolia (Wall,) Drude var. elliptica Rehd. & Wils.; Cult. Ed.
L. rubrovenia (Merrill) Chun; F. A. Maclure 9380 (f, l); C. Wang
35597 (st).

L. sphaeranthra (Hand.-Mazz.) Hand.-Mazz; Forrest 18131.
L. villosa (Hook. f) Hand.-Mazz.: Forrest 5842.
Pieris cubensis (Griseb.) Small: Ekman 16387 K.
P. floribunda (Pursh) Hook. f.: Cult. Ed.
P. formosa D. Don: Cult. Ed.
P. huiana Fang: H. T. Tasi 54413.
P. japonica (Thunbg.) D. Don: Cult. Ed.
P. phillyriifolia (Hook.) DC.: Harper 2052 (f, l, st); Harper 1472 (se).
P. taiwanensis Hayata: Cult. Ed.

Agauria salicifolia (Comm. ex Lam.) Hook. f. ex Oliver, var ?:
A. salicifolia var?: H. F. Mooney 8876.
A. salicifolia var acutissima Sleumer: Sieber - Mauritius.
A. salicifolia var buxifolia (Comm. ex Lam.) Sleumer: Balfour -
Bourbon, Madagascar, Oct. 1875 (se, l, st).
A. salicifolia var intercedens Sleumer: Götz 1299. (≠ A. goetzii)

Agarista: the following species all belong to this genus, but I have
followed the nomenclature of Sleumer (1959), and so the authorities
after the species refer to publication under Leucothoe.
L. bolivianensis Sleumer: Steinbach 3556.
L. chlorantha (Cham.) DC.: Burchell 5867 K.
L. ericoides (Taub.) Taub. ex Glaz.: Glaziou 19577 K.
L. eucalyptoides Cham. & Schl.: Gardner 4984.
L. oleifolia (Cham.) DC.: Gardner 4987.
L. organensis Gardn.: Glaziou 15170.
L. pistrixa (Cham.) DC: Stephan - Minas Gerais, S. Joas del Réy K.
L. pulchella (Cham.) DC: Hatschbach 10247 K.
L. reticulata (Walt.) Small: Curtiss 4657.
L. revoluta DC.: Glaziou 12926.
L. serrulata (Cham.) DC.: Dusen 7082 K.
L. subcordata (Dunal) Sleumer: Mathews 1635.

Arc runnerica nana (Maxim.) Makino: Cult. Ed.

Chamaedaphne calyculata (L.) Moench var angustifolia (Ait.)
Rehder & var. angustifolia (Ait.) Fernald: both Cult. Ed.


Leucothoe axillaris (Lam.) D. Don: Cult. Ed.
L. davisi (Torrey) Cult. Ed.
Pieris cavaleriei Léveillé & Vaniot (= L. griffithiana): Esquirol 412.
L. fontanesiana (Steudel) Sleumer: Cult. Ed.
L. grayana Maxim.: Cult. Ed.
L. griffithiana Clarke: J. F. Rock 22036.
L. keiskei Miq.: Yokohama Nursery Company, Sagami, Mt. Hakone,
August 1910.
L. racemosa (L.) A. Gray: Harper 1098 (se, l, st); E. C. Steele -
L. recurva (Buckley) A. Gray: Sharpe A. J. & Shanks R. E. 1440 (f);
A. Ruth 15 (st, l, se).
Gaultheria

G. abbreviata J. J. Smith: Beccari - Mt. Singilari, 2500m.; 1878 K.
G. adenothrix (Miq.) Maxim.: Cult. Ed. C900 (f, l, st); Okamoto TSM 762 (se).
G. anastamosana H.B.K.: Fr. - Apollinaire - Bogota, Colombia, 30/6/1869.
G. antarctica Hook. f.: J. Ball - Iter Australi Americani, June 1882.
G. appressa A.W. Hill: Lehmann & French - Mt. Mueller 1892 (f, l, st);
F.W. Barnard - Australia (se).
G. arachnoideas A. C. Smith: Jameson 499 (external morphology only) K.
G. atjehensis J. J. Smith: van Steenis 9580 K.
G. barisoides Rupby: Bang 707.
G. borneensis Stapf; J. & M. S. Clemens 29861 (f, l, s);
J. & M. S. Clemens 29954 (se).
G. brachybotrya DC.: E. K. Balls 7253 (f, l, s); Bang 1906 (se).
G. bracteata (Cav.) Don: Bang 667 (s, l, se); Buchtien 47 (f).
G. caespitosa Poeppl. & Endl.: Comber 505 (f, l, st); Comber 1075 (se).
G. cardiosepala Hand.-Mazz.: Furrer 895.
G. cicutaria Airy Shaw: Kingdon Ward 19231.
G. conferta Benth.: Buchtien 461.
G. discolor Nutt.: Ludlow, Sherriff & Elliot 12236.
G. domingensis Urban: Turokhaim 3152.
G. dumicola W. W. Smith: Forrest 26075 (st, l, se); Kingdon Ward 3486 (f).
G. eriophylla (Vell.) Mart.: Cult. Ed.
G. floridana Phil.: Werdemann 1171.
G. foliosa Benth.: Spruce 5128.
G. fragrantissima Wall.: Cult. Ed. C847 (f, l, st); Polunin, Sykes & Williams 463 (se).
G. glabra DC.: Bang 671 (f, l, st); Buchtien 713 (se).
G. glomerata (Cav.) Sleumer: Spruce 5156.
G. griffithiana Wight; Forrest 29840 (f, l, st); Tsai 56322 (se).
G. hispida R. Br.: Comber 2180 (se); Maclagan - Tasmania, Dec 1950 (f, l, st).
G. hispidula (L.) Muhlenb.: Cult. Ed. (f, l, st); Rolland-Germain 6256 (se).
G. Hirtiflora Benth.: Pringle 8896.
G. hookeri C. B. Clarke: Cult. Ed. (fl, l, st); Stainton 1676 (se).
G. humifusa (Graham) Rydb.: Cult. Ed. (f, l, st); A. & E. Nelson 6169 (se).
G. hypochila Airy Shaw: Farrer 1737 (fl, l, st); Farrer 1191 (se).
G. insipida Benth.: Jameson - Plants of the Andes (f, l, st); Spruce 5107 (se).
G. itatiaiae (Wawra ex Drude) Sleumer: Glaziou 4872 (external morphology only) K.
G. itoana Hayata: Tamura 21078.
G. lanigera Benth.: Jameson 1836 (external morphology only) K.
G. laxiflora Diels: Maire - 700m. nr. Zoung Ky (fl, l, st); Forrest 9296=9061 (se).
G. leschenaultii D.C.: Nilghirry Hills, April 1855 (no collector's name).
G. leucocarpa Blake: J. & M. S. Clemens 30427.
G. malayana Airy Shaw: J. Sinclair 9951.
G. mundula Sleumer var mundula: Cult. Ed.
G. myritilloides Cham. & Schlecht.: Glaziou 20375 (external morphology only) K.
G. nivea (Anth.) Forrest: Forrest 19269 (f, l, s); Forrest 13310 (se).
G. notabilis Anth.: Forrest 26722.
G. novaguineensis: A. Pulle - Mt. Wichman, 2/2/1913, K.
G. nubigana (Phil.) Burtt & Sleumer: Comber 450.
G. numularioides D. Don: Cult. Ed.
G. odorata H.B.K.: Pringle 8441 (f, l, s); Turokheim 1349 (se).
G. oppositifolia Hook. f.: S. J. Maclagan - Taupo-Napier Road, N.Z., 30/11/1964 (f, l, s); Leland et al. 124 (se).
G. ovata DC.: Pringle 8961.
G. ovatifolia A. Gray: Cult. Ed. (f, l, st); C. H. Shaw 1073 (se).
G. paniculata Burtt & Hill: J. D. Barron, Rainbow Mountain, Dec. 1928, (only external morphology) K.
G. permettyoides Sleumer: van Steenis 3648 K.
G. phillyreifolia (Pers.) Sleumer: Comber 738 (f, l, st); Wedermann 1071 (se).
G. pulle E. J. Smith: M. S. Clemens 12315 (f, l, st); M. S. Clemens 41139 (se).
G. Punctata Blake: J. & M. S. Clemens 30429 (l, st, se); O. Warburg 3293 (f, s).
G. pyrolifolia Hook. f. & Thomps.: Cult. Ed. C860 (l, st); Ludlow et al. 4920 (f).
G. ramayana A. C. Smith: Buchtien 4103 (f, l); Bang 223 (se, st).
G. rupestris R. Br.: Cambridge, N. Isle, Jan. 1879 (f, st);
Maclagan - 28/12/1964 (l).
G. temuifolia (Phil.) Cleumer: H. F. Comber 549 (f, l, st); Comber 1062 (se).
G. thymifolia Stapf: Kingon Ward 9693 (se, st, l); Farrer 1677 (f).
G. trichophylla Royle: J. D. A. Stainton 4541 (f, l, st); Stainton, Sykes and Williams 7914 (se).
G. saltensis Sleumer: Cult. Ed.
G. secunda Remy: Rusby 2025 (f, l, st); Bang 487 (se).
G. semi-infera Airy Shaw: Forrest 14216 (st, l, se); Forrest 29648 (f).
G. sinensis Anth.: Forrest 14216 (f, l, st); Ludlow, Sherriff & Taylor 5293 (se).
G. suborbicularis Airy Shaw: Forrest 20267 (se, st, l); Kingdon Ward 880 (f).
G. ulei Sleumer: Smith & Rietz 10157 (external morphology only) K.
Pernettyoid Caultherias.

P. ciliata (Cham. & Schl.) Small (includes P. buxifolia Mart. & Gal): Cult. Ed. C792.


P. lanceolata (Hook. f.) Burtt & Hill; R.C. Gunn - Tasmania.

P. leucocarpa DC.: Cult. Ed. C86A.

P. macrostigma Colenso: Lindsay - Dunedin, N.Z., Oct. 1861 (se, l, st); Lindsay - Saddlehill, Otago, 22/10/1861. (f).

P. multicnemata (L. f.) Gaud.: (includes P. rupeicolae Phil.), Cult. Ed. C877.

P. nana Colenso; Broken River, 610m., Jan. 1880.

P. prostrata (Cav.) Sleumer var. pentlandii (DC.) Sleumer; Cult. Ed.

P. pumila (L. f.) Hook; Cult. Ed. C878.

P. rigidia (Bert.) DC.; Elliot 145.

P. mexicana Camp; E. K. Balls, 4868.

P. tasmanica Hook. F.; Cult. Ed. (l, st); Comber 1923 (se); "Tasmania, 124" (f).

Pernettyopsis malayana King & Gamble: Woods 668.

Diplycosia abscondita Sleumer; J. & M. S. Clemens 33843.

D. aurea Sleumer; J. & M. S. Clemens 40682.

D. candelifolia Sleumer; J. & M. S. Clemens 32336.

D. chrysanthum Stapf; J. & M. S. Clemens 29956.

D. ciliolata Hook. f.; Sinclair 9074.

D. cinnamomifolia Stapf; J. & M. S. Clemens 33131.

D. clementium Sleumer; J. & M. S. Clemens 50849.

D. commutata Sleumer; J. & M. S. Clemens 26811.

D. crebula Sleumer; J. & M. S. Clemens 40573.

D. elliptica Ridley; Kerr 7585.

D. ensifolia Mex.; J. & M. S. Clemens 32478.

D. heterophylla Blume var. latifolia (Blume) Sleumer; King 8023.

Diplycosia kinsabulensis Stapf; J. & M. S. Clemens 50925.

D. luzonica (A. Gray) Merrill var. caleonanensis (Elm.) Sleumer Elmer 14252.

D. memecylides Stapf; J. & M. S. Clemens 33065.

D. microphylla Beccari; Cult. Ed. C5292.

D. morobeensis Sleumer; J. & M. S. Clemens 40974.

D. penduliflora Stapf; J. & M. S. Clemens 34458.

D. pinifolia Stapf; J. & M. S. Clemens 33044.

D. pseudorufescens Sleumer; J. & M. S. Clemens 29282.

D. punctulata Stapf; J. & M. S. Clemens 29961.

D. rufa Stapf; Sinclair et al. 9068.

D. rupeicolae Sleumer; Schodde 1788.

D. sanguinolenta Sleumer; J. & M. S. Clemens 33052.

D. spathophylla Sleumer; J. & M. S. Clemens 32546.

D. sumatrensis Merrill; Meijer 5848.

D. tinifera Elmer; Elmer 11676.

D. urceolata Stapf; J. & M. S. Clemens 33042.

D. viridiflora Sleumer; J. & M. S. Clemens 40706.
VACCINIEAE

Vaccinium section 1, Oxyccoccus.
V. macrocarpon Ait.: Cult. Ed. (st, 1); Dore, Senn & Gorham 45504 (f); Heller & Halbach - Central Pennsylvania, Sept 16-17 1892 (se).
V. microcarpon (Rupr.) Hook. f.: E. S. Marshall - Clova, Forfar, 18/6/1904.
V. oxyccoccus L.: Damsholt & Holmen 234.
V. vitis-idaea L.: Cult. Ed.
V. crassifolium Andr.: McHelms & Evans 1167.
V. confertum H. B. K.: Cult. Ed.
V. ovatum Pursh: E. K. Balls 8792.
V. crenatum (Don) Sleumer: Mathews 1172.
V. mathewaei Sleumer: Mathews 1471.
V. puberulum Kl.: Steyermark & Aristeguieta 63 K.
V. subcrenulatum Kl.: N. Y. Sandwith 1341 K.
V. emirense Hook. f.: Baron 2913 (l, st, se); Baron 1460 (f).
V. exul Bolus var africanum (Britten) Brenan: Whyte - Mount Mlanga.
V. fasciculatum Boj.: Baron 450.
V. secundiflorum Hook.: Madagascar (external morphology only) K.
V. stanleyi Schweinf.: Cambridge Congo Expedition, Mt. KahusI.
V. crenatum (Don) Sleumer: Mathews 1172.
V. mathewaei Sleumer: Mathews 1471.
V. puberulum Kl.: Steyermark & Aristeguieta 63 K.
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V. mathewaei Sleumer: Mathews 1471.
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V. subcrenulatum Kl.: N. Y. Sandwith 1341 K.
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V. fasciculatum Boj.: Baron 450.
V. secundiflorum Hook.: Madagascar (external morphology only) K.
V. stanleyi Schweinf.: Cambridge Congo Expedition, Mt. KahusI.
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V. fasciculatum Boj.: Baron 450.
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V. crenatum (Don) Sleumer: Mathews 1172.
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V. subcrenulatum Kl.: N. Y. Sandwith 1341 K.
V. emirense Hook. f.: Baron 2913 (l, st, se); Baron 1460 (f).
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V. fasciculatum Boj.: Baron 450.
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V. stanleyi Schweinf.: Cambridge Congo Expedition, Mt. KahusI.
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V. fasciculatum Boj.: Baron 450.
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V. stanleyi Schweinf.: Cambridge Congo Expedition, Mt. KahusI.
V. crenatum (Don) Sleumer: Mathews 1172.
V. mathewaei Sleumer: Mathews 1471.
V. puberulum Kl.: Steyermark & Aristeguieta 63 K.
V. subcrenulatum Kl.: N. Y. Sandwith 1341 K.
12. *Batodendron*.

- *V. cubense* Griseb.: Fuertes - 1348.
- *V. stenophyllum* Steudel: Mexia 1342.

12 b. *V. corymbodendron* Dunal: not studied in detail.

- *V. leucanthum* Cham. & Schlcht.: Arsène - Morelia, July 1909.
- *V. meridonale* Sw.: Clute 214.


- *V. caesium* Greene: Harbison 1161 (f, s); Bilmore Herbarium 13414 (l, se).
- *V. kunthianum* Kl.: Pringle 8899; Meyer & Rogers 1708 (se).
- *V. stamineum* L.: Wolf 1492 (f, l, s); Heller 611 (se).

14. *Oxyoecoidae*.

- *V. erythronarpoc (Pers.) Michx.: Biltmore Herbarium 5060 (f, l, s); Steele & Steele - 28/8/1903 (se).
- *V. lasiostemon* (Hayata) Maekawa: Tamura 21057.
- *V. japonicum* Nakai: Togashi TNS 1536.

15. *Myrtillus*.

- *V. caespitosum* Michx: Cult. Ed.
- *V. myrtillus* L.: Cult. Ed.
- *V. ovalifolium* Sm.: Shimizu 7639 (l, s; se); Takeda - Mr. Shivan, 3/7/1905 (f).
- *V. parvifolium* Sm.: Cult. Ed.


- *V. cerisum* Forst.: Sibbald - Tahiti.
- *V. calycinum* Sm.: O. & I. Degener 30695.
- *V. berberidifolium* (Gray) Skottsb.: Cranwell, Selling & Skottsb erg 2706 (only external morphology) K.
- *V. dentatum* Sm.: Keller 2393 (f, l, st); I. & O. Degener 30697 (se).
- *V. paleanum* Skottsb.: Cult. Ed. (l, st); O. & I. Degener 30698 (f).
- *V. rapa* Skottsb.: Collenette 762.
- *V. reticulatum* Sm.: Cult. Ed. (l, st); O. & I. Degener 30697 (f).

17. *Cyanophthalmos*.

- *V. modestum* W.W. Smith: Forrest 14218 (f, l, st); Forrest 14881 (se).

18. *Glistis*.

- *V. oldhami* Miq.: Togashi NSM 432.
- *V. sieboldii* Miq.: Her. Ludg. - Bat. 494 (only external morphology).

19. *Conchophyllum*.

- *V. conchophyllum* Rehd.: Fang 849.
- *V. delavayi* Franch.: Cult. Ed.
- *V. chaetothrix* Sleumer: Cult. Ed.
- *V. gaultheriifolium* (Griff.) Hook. f. ex C. B. Clarke: Yü 21063 (se, s; l).

- *V. glauco-album* Hook. f.: Cult. Ed.


- *V. monetaria* Sleumer: Kingdom Ward 6857 (external morphology only) K.

- *V. moupinense* Franch.: Cult. Ed.

- *V. pumilum* Kurz: S. Kurz 541 (external morphology only) K.

- *V. nummularia* Hook. f. & Thompson: Cult. Ed.
V. retusum (Griff.) Hook. f.: Cult. Ed. (l, st); Watt 5962 (f).
V. sickimense Clarke: Cult. Ed.
V. dendrocharis Hand.-Mazz.: J.F. Rock 22914 (external morphology only) K.
V. merrillianum Hayata: not studied in detail.

V. boninense Nakas: Beechey 156 (external morphology only) K.
V. bracteatum Thbg: Cult. Ed.
V. carlesii Dunn: Gressit 1819.
V. eberhardtii Dop: Smitinand, 1167 (external morphology only) K.
V. fragile Franch.: Maclaren's collectors 34.
V. griffithianum Wight: Cox & Hutchinson 543.
V. iteophyllum Hance: Ching 2607.
V. macgillivrayi Seem.: Milne "Peejee" (= New Hebrides).
V. neilgherrense Wight: Wight 2129.
V. nhatrangense Dop: Poilane 6223 (external morphology only) K.
V. oreogena W. W. Smith: Kingdon Ward 1732 (l, st).
V. pubicalyx Franch.: Forrest 7541.
V. sprengelii (D. Don) Sleumer: Kerr 2053 (l, f); Garrett 759 (se, st).
V. subfalcatum Merrill: Tsang 22166 & 22281 (external morphology only) K.

BM.
V. symplacifolium (D. Don) Alston: Wight 2128.
V. trichocladum Merrill & Metcalf: Tsang 21122 (external morphology only) K.
V. wrightii A. Gray: Shimizu 12614.

V. acrobracteatum K. Schum.: Darbyshire 474.
V. bancanum Miq.: J. & M. S. Clemens 29952.
V. barandanum Vid.: Merrill 8334 (Philippine Island Plants).
V. claeyxylon J. J. Smith: J. & M. S. Clemens 32475 = 32828.
V. cordifolium Stapf: J. & M. S. Clemens 33151.
V. coriaceum Hook. f.: Clemens 50615 = 50828 (f); Clemens 27825a (se, l, s).
V. cuneifolium Miq.: Warburg 15078.
V. horizontale Sleumer: Womersley 15271.
V. pachydermum Stapf: Flora of North Borneo 102 (native collector).
V. palawanense Merrill: A. D. Elmer 11470.
V. stapfianum Sleumer: J. & M. S. Clemens 27116.
V. stricacule Sleumer: Hoogland & Schodde 7402.
V. temuipes Merrill: Philippine Island Plants 9819.
V. varingifolium Miq.: Cult. Ed.

Unnamed:— M. S. Clemens 1172; Miller, New Guinea Flora 14698; Black 238, Cult. Ed.; Woods 660; Woods 289.

24. Rigolepis.
V. acuminatissimum Miq.: Wray 1418.
V. bigibbum J. J. Smith: Anderson 14739 (external morphology only) K.
V. borneense W. W. Smith: Flora of Sarawak 66 (native collector).
V. leptanthum Miq.: Sinclair 10627.
V. uniflorum J. J. Smith: Sibat ak Luang S 21783 K.
V. urogllossum Sleumer: J. & M. S. Clemens 29854 = 29857 (f, l); J. & M. S. Clemens 40889 = 40802 (st); J. & M.S. Clemens 29851 (f).
23. Neojunghuhnia.
V. kostermansii Sleumer: Sleumer & Vink 4249 K.
V. spaniotrichum Sleumer: Vink & Schram BW 8824 K.

24. Oarianthe.
V. amblyandrum F. v M.: Cult. Ed.
V. microphyllum Reinw.: Philippine Island Plants 11394 (se, l, s);
Copeland 1417 (f).
V. whitmeei F. v M.: Whitme - Samoa 1866 & 1867.
Unnamed: - Woods 200; Woods 659; Woods 1361.

25. Epigynium.
V. ardisioides Hook. f.: Lace 4647.
V. bulleyanum (Diels) Sleumer: Forrest 1069.
V. chinense Brandis: Forrest 29476.
V. kingdon-wardii Sleumer: Kingdon Ward 6322 (external morphology only) K.
V. nuttallii (Clarke) Sleumer: Ludlow & al. 12251.
V. vaccinicum (Rooburgh) Sleumer: Lace 2223.
V. venosum Wight: Griffith 3461 (external morphology only) K.
Also included: - Keenan et al. 3253. Agapetes acuminata (Wall.)
D. Don; Griffith K. A. leptanthera Airy Shaw, Kingdon Ward 5541.

V. dunalianum Wight: Cult. Ed.
V. dialypetalum J. J. Smith; Sinclair & Kiah 3883.
V. dunnianum Sleumer: Tsai, Flora of Yunnan 55129.
V. lanigerum Sleumer: Kingdon Ward 2999 (external morphology only) BM.
V. petelotii Merrill; Tsai, Flora of Yunnan 60228.
V. pseudorobustum Sleumer: Sin & Whang 623.
V. urceolatum Hemsl.; E. H. Wilson 1072.
V. yaoshanicum Sleumer: Sin & Whang 453.

27. Disterigmopsis.
V. didymanthum Dunal; Mathews - Prov. Chachapoyas.

V. dependens (Don) Sleumer: Dunal 78 K.
V. sphyroceroides Sleumer; Mathews 1466.

29. Nemochaeton.
V. latifolium (Griseb.) Hook. f.: Beard 1284 K.

30. Oreadee.
V. peasanum Donn. Smith; C. H. Lankester K 246 K.

Agapetes affinis (Griff.) Airy Shaw; Hooker & Thompson - Khasia.
A. angulata (Griff.) Hook. f.; Keenan et al. 3939 (1, st); Keenan et al. 3798 (f); Keenan et al. 3921 (se).
A. angustifolia Knagg; Kingdon Ward 5566 (f); Keenan et al. 3171 (1, st).
A. auriculata (Griff.) Hook. f.: Ludlow & Sherriff 7236.
A. brachypoda Airy Shaw var. gracilis Airy Shaw; Kingdon Ward 3066.
A. braeata Hook. f.; Lobb - Moelmim K.
A. forrestii W. E. Evans; Forrest 27755.
A. griffithii Clarke; Nullah, 1524m (1, st) K.
A. hillii Brandis: Hilsley 112 (external morphology only) K.
A. hosseana Diels: Winit 1342 (se, l); Hosseus - Siam 19/1/1905 (f, l, st).
A. hyalocheilos Airy Shaw: Keenan et al. 3915 (se); Keenan et al. 3205 (f, l, st).
A. incurvata (Griffith) Sleumer: Laccé 2303 (f, l, st); Stainton 707 (se).
A. interdicta (Hand.-Mazz.) Sleumer: Forrest 25678 (se); Farrer 1517 (f, l, st).
A. kanjilaii Das: Kanjilali 4090 (external morphology only) K.
A. lacei Craib var. tomentella Airy Shaw: Forrest 26990 (f, l, st); Forrest 21597 (se).
A. linearifolia Clarke: Kingdon Ward 8021 K.
A. lobii Clarke: Forrest 26591 (se); Keenan et al. 3468 (f, l, st).
A. nana Hook. f.; Griffith 3473 (external morphology only) K.
A. neriifolia (King & Prain) Airy Shams: Kingdon Ward 20403 (se),
A. nutans Dunn: Burkill 36347 (external morphology only) K.
A. nuttallii Clarke: Nuttall - Bhutan (external morphology only) K.
A. macrophylla Clarke: Kingdon Ward 8032 K.
A. macrostemon Clarke: Robertson 131 K.
A. manii Hemel.: Cult. Ed.
A. marginata Dunn: Burkill 36340 (external morphology only) K.
A. megacarpa W. W. Smith: French consul, Yunnan.
A. miranda Airy Shaw: Ludlow et al. 3718.
A. mitrarioides Hook. f.; Herb. East India Company 3466 (external morphology only) K.
A. miniata (Griffith) Hook. f.; Griffith 3475 (external morphology only) K.
A. oblonga Craib, Yu 20539.
A. obovata (Wight) Hook. f.; Cult. Ed.
A. oddontocera (Wight) Hook. f.; Khasia Hills, Native collectors (se);
Keenan 3424 (f, l, st).
A. parishii C. B. Clarke: Laccé 5046 (se); Laccé - spur to Mulegit,
Burma, Jan. 1912 (f, l, st).
A. pensilis Airy Shaw: Yu 20038.
A. pilifera Hook. f.; Hooker & Thompson - Khasia.
A. praeclara Marquand; Ludlow et al. 12262.
A. pseudogriffithii Airy Shaw: Kingdon Ward 5551.
A. pubilora Airy Shaw: Yu 21058.
A. pyrolifolia Airy Shaw: Kingdon Ward 54771.
A. refracta Airy Shaw: Cox & Hutchinson 487, (l, st).
A. salicifolia Clarke: Herb. late East India Company 3477.
A. saligna Hook. f.; Cave - 30/5/1913 (se), Ludlow & Sherriff 2926
(f, l, st).
A. saxicola Craib: Kerr 36696 (f); Sørenson 2378 (l, st).
A. serpens (Wight) Sleumer: Cult. Ed. 2750.
A. setigera D. Don; Griffith - Khasia, 1844.
A. sikkimensis Airy Shaw: Clarke 10177 (external morphology only) K.
A. similis Airy Shaw: Cox & Hutchinson 550 (se, l, st).
A. smithiana Sleumer var. major Airy Shaw: Cult. Kew from Cox
& Hutchinson 413 K.
A. spissa Airy Shaw: Kingdom Ward 8479, sheet 2 K.
A. variegata (Roxb.) D. Don ex G. Don var. macrantha (Hook.) Airy
Shaw: Cult. Ed.
A. vermayana Merrill: Kingdom Ward 3697.
A. toppinii Airy Shaw: Keenan et al. 3409.
Also included: Vaccinium triflorum Rehder, Esquierol, probably no. 2095; Vaccinium pseudotonkinense Sleumer, Fang - 8/6/1937, Yunnan; unidentified, Wang, Chang & Liu 82637.

Dimorphanthera
section Dimorphanthera.
D. amblyornidia (Bee.) F. v M.: Forbes 784.
D. amoena Sleumer: Woods 53.
D. apoana (Merrill) Schltr.: Philippine Island Plants 11258.
D. cornuta J. J. Smith: Hoogland & Schodde 7587.
D. dryophila Sleumer: Woods.
D. denticulifera Sleumer: Woods 60.
D. kempteriana Schl.: van Royen NGF 15039.
D. lancifolia Sleumer: Darbyshire 441 (external morphology only).
D. womersleyi Sleumer: Womersley 15310.
section Pachyantha (see Appendix 1).
Vaccinium amplifolium F. v M.: Cult. Ed.
V. fissiflorum Sleumer: Hoogland & Pullen 5881 (external morphology only) K.
V. ingens Sleumer: Womersley & Sleumer NGF 13942 K.
V. keyseri Schltr. ex Diels: Hoogland & Schodde 7223.
V. macbainii F. v M.: Guilanetti - Mt. Scratchley, 1896 K.

Paphia (see appendix 1).
Agapetes alberti-eduardii Sleumer: Brass 4380 K.
A. carrui Sleumer: Carr 13708 (external morphology only) BM.
A. costata C. H. Wright: Brass 4320 K.
Paphia meiliana F. v M.: Brass 20445 K.
A. neo-caledonica Guill.: McKee 8209 K.
A. sclerophylla Sleumer: Woods 3067.
A. scortechini (King & Gamble) Sleumer: Melville & Landon 4822 K.
F. vitiensis Seem.: Gibb 703 (external morphology only) K.
A. vitis-idaea Sleumer: Pullen 5004 K.
P. stenanthe Schltr.: Cruttwell 523.

Costera cyclophylla (Airy Shaw) Airy Shaw: Richards 1716 K.
C. lanaeensis (Merrill) J. J. Sm.: Philippine Island Plants 10103.
C. loheri (Merrill) Copeland: Loher 5187.
C. ovalifolia J. J. Smith: Sinclair et al. 10427 (se, 1);
J. & M. S. Clemens 32401 (f, 1, st).
G. braebyaca (Michx) Gray: Cult. Ed. (1, st); Jameson et al.
G. brachycera (Michx) Gray: Cult. Ed. (1, st); Jameson et al.
G. braziliensis Meissn. var. ovalifolia Meissn.: Bambo 42740.
G. c.f. decipiens Cham.: Bambo 45385.
G. dumosa (Andr.) Torrey & Gray: Eames 587.
G. gardneri Meissn.: Gardner 4977.
G. hispida Meissn.: Glaziou 6075.
G. pinifolia Cham & Schlecht.: Sellow - Brasilia.
G. pseudovaccinium Cham. & Schlecht.: Martius 1827.
G. resinosa (Ait) Torrey & Gray: Mackenzie 287 (se, l, st);
Mackenzie 594 (f).
G. rigida Casaretto: Gardner 474.
G. salicifolia Cham. & Schlecht.: Gardner 4975.
G. virgata Mart. ex Meissn.: Gardner 4982.

Anthopteropsis insignis A. C. Smith: Allen 2946 K.

Cavendishia acuminata (Hook.) Hemsl.: Cult. Ed.
C. callista (Don) A.C. Smith; Tuckheim II 327.
C. cordifolia (H.B.K.) Hoerold; E. K. Balls 5685.
C. hartwegiana (Kl.) Hoerold; Spruce 5095.
C. strobilifera (H.B.K.) Hoerold; E. K. Balls 5782.

Ceratostema calycinum (Smith) Sleumer; Spruce 5094.
C. reginaldii (Sleumer) A.C. Smith; W. H. Camp E 4342 K.
C. macranthum A. C. Smith; E. Andre - Loja, Ecuador, Oct. 1876
(external morphology only) K.

Demosthenesia buxifolia (Field. & Gardn.) A. C. Smith; Mathews 1176.
D. graebneriana (Hoer.) Sleumer; Mathews 1175 (f, l, st); Buchtien 31 (se).
D. mandoni (Britton) Sleumer; Bang 1939.
D. pearcei (Britton) A. C. Smith; Steinbach 8986.

Disasterigma acuminata (H.B.K.) Nied.; Spruce 5403.
D. codonanthum Blake; Spruce 5138.
D. empetrifolium (H.B.K.) Drude; Jameson 454.
D. pentandrum Blake; Prieto P270 K.
D. pernettyoides (Griseb.) Nied.; E. K. Balls 6703.
D. ovatum (Rueby) Blake; Bang 876.
D. c.f. weberbaueri Hoer.; Appollinaire 10.

Eleutherostemon bolivianum (Benth.) Herzog; Bang 852.
E. floribundum A. C. Smith; Camp El572.
E. racemosum Herzog; Steinbach 9628.

Findlaya apophysata Hook. f.; Fendler 489 (l, st); Sandwith 1252 (f) K.
F. hispida A. C. Smith; Schomburgh 35 (l, f) K.

Gonocalyx pulcher Planch. & Lindl.; Purdie 1845 K.

Hornemannia racemosa Vahl.: A. C. Smith 10242 K.

Killipiella stereophylla A. C. Smith; Andre 3399 K.
Macleania hirtiflora (Benth.) A. C. Smith; Purdie – Ste. Miguel & Sta. Marta, Colombia.
M. insignis Mart. & Gal.: Cult. Ed.
M. longiflora Lindley: Jameson – Andes, Quito, 550m.
M. macarantha Benth.; Jameson – west side of Andes.
M. reducta A. C. Smith; Spruce 5842.
M. salapa (Benth.) Benth. & Hook. f.: André 4340.

Notopora schomburgkii Hook f.: N. Y. Sandwith 1300 K.

Orthaea boliviensis Fedtsch. & Basil.: Buchtien 5518.
O. ferreyrae A. C. Smith; Sandeman – Huacapistana, Peru, June 1938.
(external morphology only) K.
O. weberbaueri Hoerold: Pearce – Sandillani, April 1866 K.

Pellegrinia hirsuta (Ruiz & Pavon ex Don) Sleumer; Sandeman 5091 K.

Plutarchia guascensis (Cuatr.) A. C. Smith; E. K. Balls 5756.

Psammisia ferruginea A. C. Smith; Andre 3341 K.
P. graebneriana Hoerold; E. K. Balls 7510.
P. guyanensis Kl.: Spruce 5036.
P. pacificaflora Benth.; Bang 1516.
P. penduliflora (Dun.) Kl.: Killip & Smith 20481 (l, st, se);
Grubb et al. 645 (f).

Rusbya taxifolia Britton; Bang 624.

Satyria ovata A. C. Smith; Friedrichstahl 3 K.
S. panurensis (Benth.) Hook, f.; Forest Dept., British Guiana,
Field Number F 1087 K.
S. warszewiczii Kl.: Veitch 232 K.

Semiramisia speciosa (Benth.) Kl.: Hartweg 785.

Siphonandra elliptica (Ruiz & Pavon) Kl.: Mathews 884.

Sphyrospermum cordifolium Benth.; Cult. Ed.
S. majus Griseb.: Turckheim II 430.
S. spruceanum Sleumer: Spruce 6167.
S. c.f. weberbauerii (Hoer.) A. C. Smith; Jameson 72.

Themistoclesia inflata A. C. Smith; Camp E3363 K.
T. mucronata (Benth.) Sleumer: Hartweg 1210 K.
T. octandra (Sulm.) A. C. Smith; Lechler 2614 K.
T. recurva A. C. Smith; Purdie – New Grenada (Kew 106) K.
"T. epiphytica" A. C. Smith; Schultes & Villareal 7781 K. This specimen is misnamed.

Thibaudia angustifolia Hook.: Mathews – Peru, province of Chachapoyas.
T. diphylia Dun.; Killip & Smith 24244 K.
T. macrocalyx Perry; Buchtien 30.
T. martiniana A. C. Smith; Jameson – Andes, Quito.
Chimaphila umbellata (L.) Pursh: Booth - Boston (f, l, s); Walton - Gaspé, Aug. 1949 (se).

Moneses uniflora (L.) A. Gray: Davis 17153 (f, l, s); Walton - Manitoba 14-20 Sept. 1949.

Orthilia secunda (L.) Rafin.: Gillett & Findlay 5372 (f, l, s); Marie-Victorin & Germain 1923 (se).

Pyrola asarifolia Michx: Cody & Gutteridge 7761 (f, l, s); Umbach 664 (se).

Pterospora andromedea Nutt.: Macbride 539 (f, l, st); Blumer - Arizona, 10/4/1909 (se).

Sarcodes sanguinca Torr.: E. K. Balls 10827.

Wittsteinia vacciniacea F. v M.: T. M. Howard - Mt. Donna Buang, 21/11/1967 (f, l, s); Williamson - Mt. Erica, Baw Baws, Victoria, Dec. 1904 (se) MEL.
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Rehder A. 1921. Azalea or Loiseleuria. J. Arnold Arbor. 2: 156-159.

1924. New species, varieties and combinations from the herbarium and collections of the Arnold Arboretum. J. Arnold Arbor. 5: 549-559.


1966. in Flora Malesiana, Ser. 1, Vol. 6, part 5.


PLATE 1.

1. Kalmia latifolia, x1.75 - flower on the left with stamens undisturbed, on right with some stamens triggered and at rest in the centre of the flower;

2. Rhododendron semibarbatum, x1.75 - flower with odd petal abaxial, the normal condition in the Ericaceae, but abnormal in this species. Note that the largest stamens and the stigma are at opposite sides of the flower;

3. Elliottia racemosa, x1.75 - terminal/paniculate inflorescence with cymose partial inflorescences.
PLATE 5.
1-3 *Sphrospermum cordifolium* 1./x45 - swollen vein ending in leaf, general view; 2. x170 - the same, close up; 3. x45 - thickened seleridal cells at the edge of the lamina; 4. *Haecleania insignis*, x170 - swollen vein ending in leaf; 5. *Leucothoe racemosa*, x90 - fibres at the edge of the lamina.
PLATE 4.

1 & 2 Rhododendron lapponicum, x75 - two photographs of a thick section taken at different focal depths, showing the curtains of mesophyll;

3. Vaccinium retusum, x80 - homogenous pith, with all cells unthickened and of a similar size; 4. "Pernettya" mucronata, x75 - heterogenous pith, with small, thick walled cells mingled with groups of larger, thinner walled cells;

5. Cithra arborea, x40 - pith, almost Calluna-type (see next plate), but with isolated smaller cells in amongst the large, thin-walled cells.
1-5 Leucothoe racemosa 1. x60 — pith cells clearly heterogenous in size, but all unthickened; 2. x50 — older stem, all cells still unthickened but larger in size; 3. x120 — older stem, showing the thick-walled cells adjacent to the xylem tissue and the thin-walled central cells (Calluna-type pith).
INDEX TO THE GENERA DESCRIBED.

This index includes those names commonly used as those of genera, but which are incorrect or which have not been maintained at this level in the present study (indicated by an asterisk).

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