

TAXONOMIC STUDIES IN THE *GAULTHERIA* GROUP OF GENERA OF THE TRIBE ANDROMEDEAE (ERICACEAE)

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The taxonomic status of each of the genera within the '*Gaultheria* group of genera' of the tribe Andromedeae (Ericaceae) has been investigated. These genera are *Gaultheria* L. (including *Pernettya* Gaud. and *Chiogenes* Salisb.), *Leucothoë* Don, *Zenobia* Don, *Diplycosia* Bl., *Pernettyopsis* King & Gamble and *Tepuia* Camp. The morphological characters have been discussed.

INTRODUCTION

The *Gaultheria* group of genera is an informal taxonomic grouping (within the tribe *Andromedeae*) of the genera *Gaultheria* Kalm ex L., *Leucothoë* Don, *Zenobia* Don, *Diplycosia* Bl., *Pernettyopsis* King & Gamble and *Tepuia* Camp (Stevens, 1969, 1971). *Pernettya* Gaud. and *Chiogenes* Salisbury have also been treated as generic segregates from *Gaultheria*.

The genus *Gaultheria* is one of the larger genera in the Ericaceae. Willis (1966) said that there were about 200 species circumpacific west to the Western Himalayas and South India with two species in Eastern North America and eight in Eastern Brazil. Sleumer (1967) estimated that there were about 150 species of which five are found in North America, c.32 in Eastern Asia (including Japan), c.10 in Australasia, c.85 in Central and South America and 24 in Malesia. I estimate 134 species including those species previously in *Pernettya*. It is a genus of tiny procumbent or trailing shrubs to small trees. There is enormous variation in many aspects of morphology including inflorescence, leaf size and shape, indumentum and fruit. *Pernettya* and *Chiogenes* are treated as synonyms of *Gaultheria* (Middleton & Wilcock, 1990a; Airy-Shaw, 1941).

Leucothoë has been revised by Melvin (1980). There are eight species, of which four occur in Eastern North America, one in Western North America, two in Japan and one in the Himalayas. Again variability is marked, resulting in the eight species being assigned to five separate genera on previous occasions (see Melvin, 1980). I have maintained *Agarista*, previously section *Agastia* of *Leucothoë*, as a separate genus from *Leucothoë* following the treatment by Stevens (1969, 1970) and Judd (1984).

Zenobia is a monospecific genus from Eastern North America most recently studied by Dorr (1980).

Tepuia has eight species from Venezuela (Steyermark, 1967), *Pernettyopsis* two from Peninsular Malaysia and North Borneo (Argent, 1982) and *Diplycosia* c.100 species

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from Malasia, Southern Thailand and Southern Vietnam (Sleumer, 1967; Argent, pers. comm.).

The major problem in the *Gaultheria* group is one of generic delimitation between the taxa (Stevens, 1971). The genera which are now placed in the *Gaultheria* group have only relatively recently come together (Stevens, 1969, 1971), being previously scattered in different families (Hooker, 1876) or tribes (Niedenzu, 1890; Drude, 1897). The classification of Hooker weighted fruit characters very strongly, so that *Chiogenes*, with a semi-inferior ovary, was placed in the family Vacciniaceae and the others in the Ericaceae. Niedenzu (1890) and Drude (1897) identified a tribe *Gaultherieae* within the subfamily Arbutioideae of the Ericaceae. This tribe included the fleshy fruited genera of the *Gaultheria* group sensu Stevens. The other genera were placed in the *Andromedeae*. The *Gaultherieae* also included *Wittsteinia* although its position in this tribe has been contested by all subsequent authors (see Burt, 1948; Watson *et al.*, 1967; Stevens, 1969, 1971; van Steenis, 1984). It is likely that *Wittsteinia* should not be included in the Ericaceae at all, but placed in the Alseuosmiaceae which is close to the Saxifragaceae (van Steenis, 1984).

Watson *et al.* (1967) included all the *Gaultheria* group within their Tribe 2 (corresponding to the *Andromedeae*) except for *Chiogenes* which they placed with the inferior ovary species in Tribe 3.

Stevens (1969, 1971) included *Chiogenes* and *Pernettya* within *Gaultheria* and made the *Gaultheria* group of genera an informal grouping within the tribe *Andromedeae* of the subfamily Vaccinioideae. The scale and thoroughness of Stevens' work has made his system the definitive authority on subclassification of the Ericaceae to date and as such should represent the starting point of any further taxonomic work within the Ericaceae.

The Problems of Generic Delimitation

Stevens (1969, 1971), although not recognizing the *Gaultherieae* and constructing the *Gaultheria* group within the *Andromedeae*, admitted that the group needed further work to clarify generic delimitation. He included *Pernettya* and *Chiogenes* within *Gaultheria* and questioned the generic status of *Leucothoë* and *Zenobia*.

The untenable generic status of *Pernettya* has recently been discussed (Middleton & Wilcock, 1990a) and a full account will be found in that paper. As *Chiogenes* has been treated most often as synonymous with *Gaultheria* in recent times the name *G. hispidula* is used when referring to this taxon. Of particular emphasis in this work is the generic evaluation and their relationship to the other genera. The relationships within the large genus *Gaultheria* will be published separately and the relationships within *Diplycosia* are still in need of further study. Morphological, chemical, chromosomal and anatomical data have been collected (Middleton, 1989) but only the morphological data will be discussed in detail here.

MATERIALS AND METHODS

Herbarium material was studied from the following herbaria: AAU, ABD, B, BA, BM, C, CAL, E, K, KLA, KUN, L, SJ, SU, SP, WELT, WIS.

A number of live specimens from the Cruickshank Botanic Garden, Aberdeen and the Royal Botanic Garden, Edinburgh were also studied.

Approximately 550 specimens were studied for morphological characters representing c.93% of the species of *Gaultheria* (including 100% of *Pernettya* and *Chiogenes* species), 100% of *Leucothoë*, *Zenobia* and *Pernettyopsis*, c.21% of *Diplycosia* and 38% of *Tepuia*, about 160 species in all. Sampling within species varied considerably depending on the availability of material and fewer duplicate samples per species of *Pernettyopsis*, *Diplycosia* and *Tepuia* were studied compared with the other genera. In addition, many species were studied for chemical, anatomical and chromosomal characters (Middleton, 1989; Middleton & Wilcock, 1990b; in prep.)

THE MORPHOLOGICAL CHARACTERS

Characters were surveyed for variability among the samples, potential taxonomic usefulness and historical usage.

In the Tables the following abbreviations are used: G = *Gaultheria*, Ch = *Chiogenes*, L = *Leucothoë*, Z = *Zenobia*, D = *Diplycosia*, Ps = *Pernettyopsis* and T = *Tepuia*.

The figures are expressed as percentages. Sometimes the combined percentage for a genus is more than 100 due to the fact that some species express two or more of the character states.

1. Habit:

Table 1. Plant habit characters in the *Gaultheria* group of genera.

	G	Ch	L	Z	D	Ps	T
epiphytic	<4	0	0	0	c.55	50	0
erect shrubs	c.88	0	100	100	c.55	100	100
prostrate	c.19	100	0	0	c.8	0	12

There is a wide variation in plant habit in the group (Table 1) with terrestrial and epiphytic plants; creeping, prostrate and erect plants; shrubs spreading by rhizomes and small trees. Many species of *Diplycosia* and *Pernettyopsis* are epiphytic (Sleumer, 1967) whereas the other genera in the *Gaultheria* group are generally terrestrial. All *Gaultheria* species are terrestrial although some have occasional epiphytic individuals (Sleumer, 1967; Wilbur & Luteyn, 1978). Corcoran (1981) used plant habit as one of the major diagnostic features in her delimitation of the Mexican species of *Gaultheria*.

All species of *Leucothoë* and *Zenobia* are erect with or without arching stems. Within *Gaultheria* there are both erect, prostrate and creeping species with some normally erect species such as *G. mucronata* (L.f.) Hook. & Arn. and *G. poeppigii* DC. having prostrate varieties.

This character must be used in classifications with caution because it is not always possible to determine it from herbarium specimens alone. The creeping habit of such species as *G. hispidula*, *G. suborbicularis* W.W. Smith and *G. nummularioides* D. Don is usually obvious on herbarium sheets but often the difference between prostrate and erect habit is not so clear unless herbarium notes are provided. Other details of habit, such as height and arching of stems are even more difficult to determine without

adequate herbarium notes. The height of an erect species is too variable both within and between closely related species to be of major taxonomic value.

2. Leaf Margin:

Table 2. Leaf margin characters in the *Gaultheria* group of genera.

	G	Ch	L	Z	D	Ps	T
entire	5	100	12	0	c.80	0	100
serr(ul)ate	96	100	88	100	c.20	100	0

The leaf margin may be serrate, serrulate or entire (Table 2) with the teeth in the former types of varying size and spacing. *Leucothoë griffithiana* Clarke is the only species of its genus with entire leaves. Several species of *Diplycosia* have entire margins. In *Tepuia* the margin is strongly inrolled thereby appearing entire, a feature shared by *Gaultheria tomentosa* and its close relatives; less strongly inrolled leaves also occur scattered elsewhere in this genus. Entire leaves are found in the smallest leaved species of *Gaultheria*: *G. hispidula*, *G. suborbicularis*, *G. antarctica* Hook. f. and *G. caespitosa* Poepp. & Engl.

The degree of serration of the leaves in the group is variable but no species examined had deeply toothed leaves. Some forms of *G. leucocarpa* Bl. have relatively large teeth but even *G. megaladonta* A.C. Smith, named after its large marginal teeth, has teeth less than 1mm long.

3. Leaf Nervation:

Table 3. Leaf nervation characters in the *Gaultheria* group of genera.

	G	Ch	L	Z	D	Ps	T
Melastomataceous	7	0	0	0	50	0	0
Pinnate	93	100	100	100	50	100	100

Although Airy-Shaw (1940) did not highlight the character much, melastomataceous leaf nervation is characteristic for most of his section *Brossaeopsis* in *Gaultheria* (Figure 1 – *G. dumicola*). In most other species the nervation is pinnate (Table 3) although all the major nerves often arise below the middle of the leaf. Melastomataceous nervation is more common in *Diplycosia*, but is absent in *Zenobia*, *Leucothoë* and *Tepuia*. In many species with very small leaves the nervation is obscure, only the midrib being clear.

4. Leaf venation:

In one species, *Gaultheria sleumeriana* Kinoshita-Gouvêa, there is a marginal vein round the entire leaf edge. Details of the secondary venation have not been studied except for the character of prominent reticulation. This character, where the veins are prominent above and below, is found in *G. reticulata* HBK (and species related to it) and some of those Asian species of *Gaultheria* with apical bracteoles and paniculate inflorescences such as *G. malayana* Airy-Shaw and *G. pullei* J. J. Smith. It is not variable within species and is therefore a useful diagnostic character.

5. Leaf Size:Table 4. Leaf lengths in the *Gaultheria* group of genera.

	G	Ch	L	Z	D	Ps	T
< 10mm long	37	100	13	0	14	0	25
> 10mm long	72	0	100	100	93	100	88

Leaf size can be very variable within a species which at times has caused them to be separated primarily on this character. However, broadly speaking there is an association between leaf size and other characters, such as inflorescence type, so that groups which characteristically have solitary flowers (such as *Chiogenes*, those species of *Gaultheria* previously placed in *Pernettya* and the other solitary-flowered species of *Gaultheria*) generally have a greater proportion of leaves less than 10mm long (Table 4). Several species characteristically have minute leaves (often less than 5mm long and 2mm wide), e.g. *G. tasmanica* (Hook. f.) Middleton, *G. parvula* Middleton, *G. caespitosa* and *G. antarctica* (Fig. 1). Other species have very large leaves (over 150mm long and 100mm wide), e.g. *G. codonantha* Airy-Shaw. The species of series *Dumicolae* Airy-Shaw often have very large leaves. No American species has the very large leaves found in some Old World species. The species of *Leucothoë* have a leaf size range similar to the raceme bearing species of *Gaultheria* and some *Diplycosia* species may have leaves approaching the size of those in *G. codonantha*.

6. Leaf Shape:

Airy-Shaw (1940) used leaf shape as one of the important characters in sectional delimitation. Numerous species described from Latin America have been distinguished on leaf shape, particularly the shape of the leaf base. Williams (1965) and Corcoran (1981) pointed out that many Central American species were described on differences which did not take account of the variation within a species. Corcoran's work showed that many species had extremely variable leaf shapes particularly in the shape of the leaf base. These findings greatly diminish the use of leaf shape characters.

One leaf shape character which is less subject to strong variation within a species is the presence of a mucronate leaf tip. This character is present in a few *Gaultheria* species.

7. Indumentum:

Indumentum types were studied for branches, leaves, pedicels, calyx, corolla and, if present, the rachis of the raceme. Corcoran (1981) warned that indumentum characters were extremely variable within some species. As for leaf shape, this has led to a bewildering number of specific names describing minor differences in indumentum. (Camp, 1939a) split the Mexican species of *Gaultheria* into two informal groups, the *Acuminatae* and the *Odoratae*, based on indumentum types. Airy-Shaw (1941) did not use this character for his classification of the Asian species.

Indumentum characters have been used in studies of the *Andromedeae* (Judd, 1979, 1981, 1982, 1984). Stevens stated that there were no overall differences in indumentum

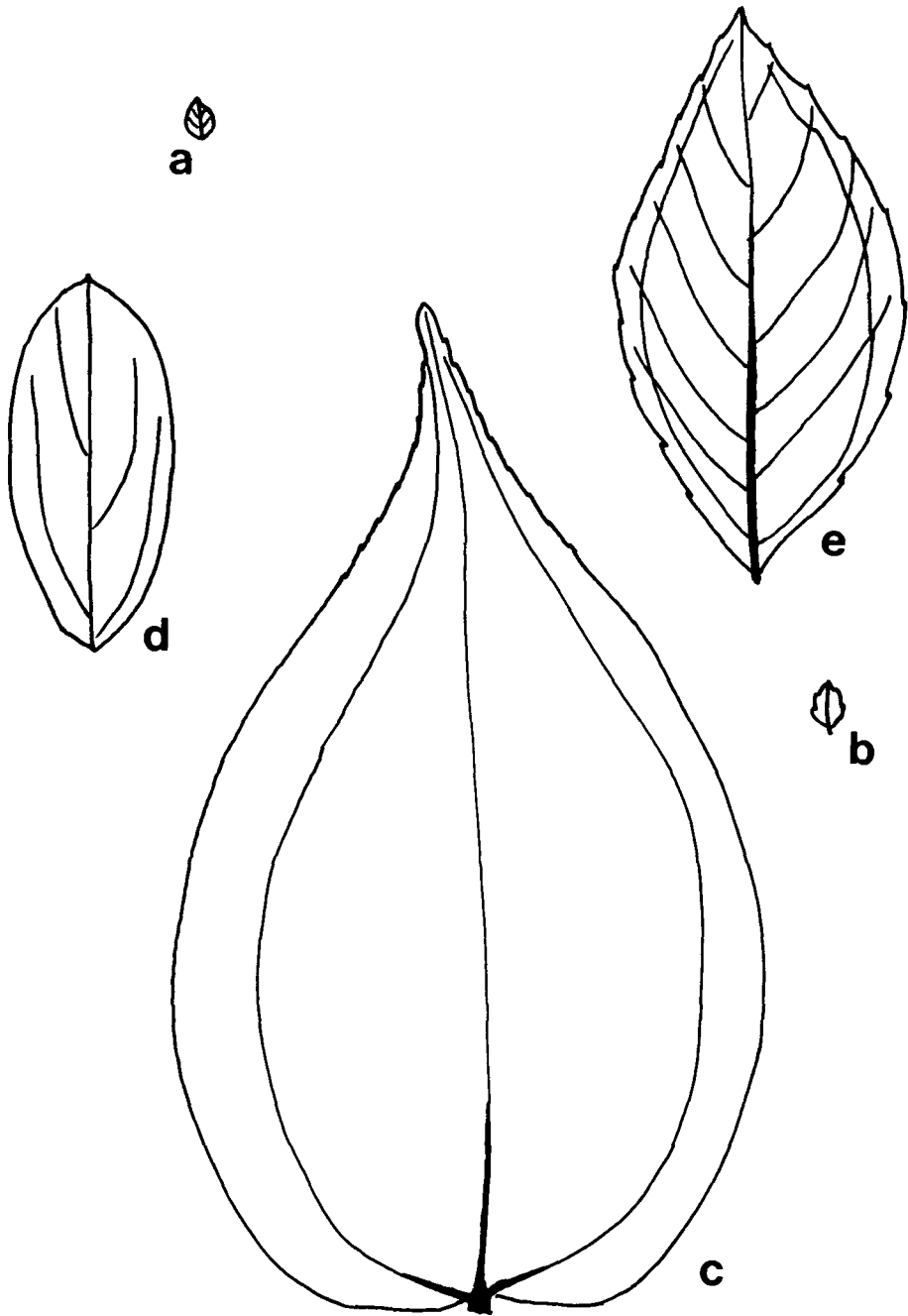


FIG. 1. Leaf shapes and sizes in the *Gaultheria* group of genera (actual size). a, *Gaultheria hispidula*; b, *G. antarctica*; c, *G. dumicola*; d, *Zenobia pulverulenta*; e, *Leucothoë racemosa*.

type between the *Gaultheria* group and the *Lyonia* group of the *Andromedeae* but that the *Gaultheria* group often had very robust hairs with a large multiseriate stalk.

There are many different types of hair within the *Gaultheria* group. Unicellular hairs are almost universal in occurrence, particularly on the adaxial surface of the leaf midrib. They are also often found on the stem, pedicel and rachis and as a ciliate margin to the calyx lobes. They are less common on the surface of the calyx and on the outside of the corolla although fairly frequently present on the inside of the corolla. The presence of unicellular hairs on the corolla is usually fairly uniform within species although this character is frequently very variable on the other organs particularly in that they are often caducous.

In some species there are unicellular hairs all over the lamina but this character is extremely variable within species. Baas (1985) found this character to be very variable in those species of *Gaultheria* previously placed in *Pernettya*, and that the length of the hair and whether the hair is curled or straight is variable within the species. Therefore, it is unlikely that data from unicellular hairs are of much taxonomic importance especially in taxonomic rankings above the species.

I have found uniseriate hairs in some species of *Diplycosia* and in *Tepuia*. In *Diplycosia* they are composed of short cells but in *Tepuia* the cells are very long and the hairs are dense and twisted. Uniseriate hairs have not been found in the other genera studied.

There is a large variety of multicellular hairs with multiseriate bases in the group. These range from short- to long-stalked, clavate to tapered, eglandular to glandular, with all grades in between these types. The hairs may be spreading-hirsute or strigose. Airy-Shaw (1952) used indumentum characters to key out Asian species. However, the Asian taxa are in need of revision and these characters may not prove to be so reliable. The absence of multiseriate hairs may be genotypic or because the hairs are caducous. If the latter then their previous existence is usually indicated by punctations, which are fairly common in the group (see Sleumer, 1967 on indumentum variation in *Diplycosia*).

Zenobia pulverulenta (Bartr.) Pollard has multiseriate hairs only on the leaf margin as do a number of *Gaultheria* species. No species were observed to completely lack multiseriate hairs except for the three species of *Tepuia* studied.

Glandular hairs are particularly common in the American species of *Gaultheria* and in *Leucothoë*, although in the latter case these are small and short-stalked. I have found this character to be extremely variable both in the length of the hair and in the size of the glandular head, such that there appears to be a complete intergradation between eglandular (e.g. *G. rigida* HBK) and large headed glandular hairs (e.g. *G. erecta* Vent.). Corcoran (1981) called particular attention to this character mentioning that indumentum type has historically been a very important character for delimiting taxa in *Gaultheria*. She concluded that many of the species described from Mexico were synonymous and that indumentum is a variable character. Her broader concept of species results in both eglandular and glandular plants occurring within the same species. Between species she suggested that the variability of this character should not lead one to discard it completely but that it should be used with care and in combination with other characters.

In general the American species of *Gaultheria* have more multiseriate hairs on the leaves, stems and particularly on the raceme, calyx and corolla than the Asian and Australasian species. There is also a group of species centred around *G. tomentosa* HBK which has a dense tomentum of twisted, narrow hairs on nearly all parts of the plant. Stevens (1969) compared the indumentum of *Tepuia* to a member of this group, *G. lanigera* Hook., but in *Tepuia* these hairs are exclusively uniseriate.

8. Inflorescence:

Table 5. Inflorescence types in the *Gaultheria* group of genera.

	G	Ch	L	Z	D	Ps	T
Solitary	c.37	100	0	0	36	0	0
Fascicle	0	0	0	100	64	100	0
Raceme	c.65	0	100	0	0	0	100

Inflorescence type has proved the most decisive character in the previous, limited, sectional treatments of the species of *Gaultheria*. There are three basic types: flowers solitary, in racemes, or in fascicles (Fig. 2).

Fascicles are found only in *Diplycosia*, *Pernettyopsis* and *Zenobia* (Table 5). Racemes are not found in these genera but some species of *Diplycosia* have solitary flowers. A number of species of *Gaultheria* sect. *Brossaeopsis* have what appear to be fascicles but on closer inspection are actually very short racemes where the flower pedicels are much longer than the rachis of the raceme.

Many species of *Gaultheria* have solitary flowers. Airy-Shaw (1940), Sleumer (1957) and Stevens (1969) have all argued that solitary flowers were formed from racemes in which all but one of the flowers have been suppressed.

All species of *Leucothoë*, *Tepuia* and many species of *Gaultheria* have racemes. These are of markedly different lengths and appearances, axillary and terminal. The raceme ranges from the almost fasciculate appearance of species such as *G. dumicola* W.W. Smith (Fig. 2) to over 10cm long in species such as *G. leucocarpa* (Fig. 2).

9. Bracts and Bracteoles:

The major problem in discussing bracts and bracteoles as a whole is one of homology. Solitary flowers may have evolved from the reduction of a raceme. In this case, buds in the axils of floral bracts are suppressed and only the terminal flower grows. Therefore, in many cases what is left is a multibracteolate pedicel presumably composed of the bracteoles, bracts and perules of its racemose progenitor. Because of the subjectivity involved, direct homologies between racemose and solitary-flowered species cannot easily be made with regard to determining which are bracts and which are bracteoles. Because of the fact that there are solitary flowered species with only two bracteoles it is, however, convenient to refer to a bibracteolate or multibracteolate pedicel in these species.

Diplycosia, *Pernettyopsis* and *Tepuia* always have apical bracteoles, *Leucothoë* has two bracteoles varying in position between species, and *Zenobia* has basal bracteoles (Table 6).

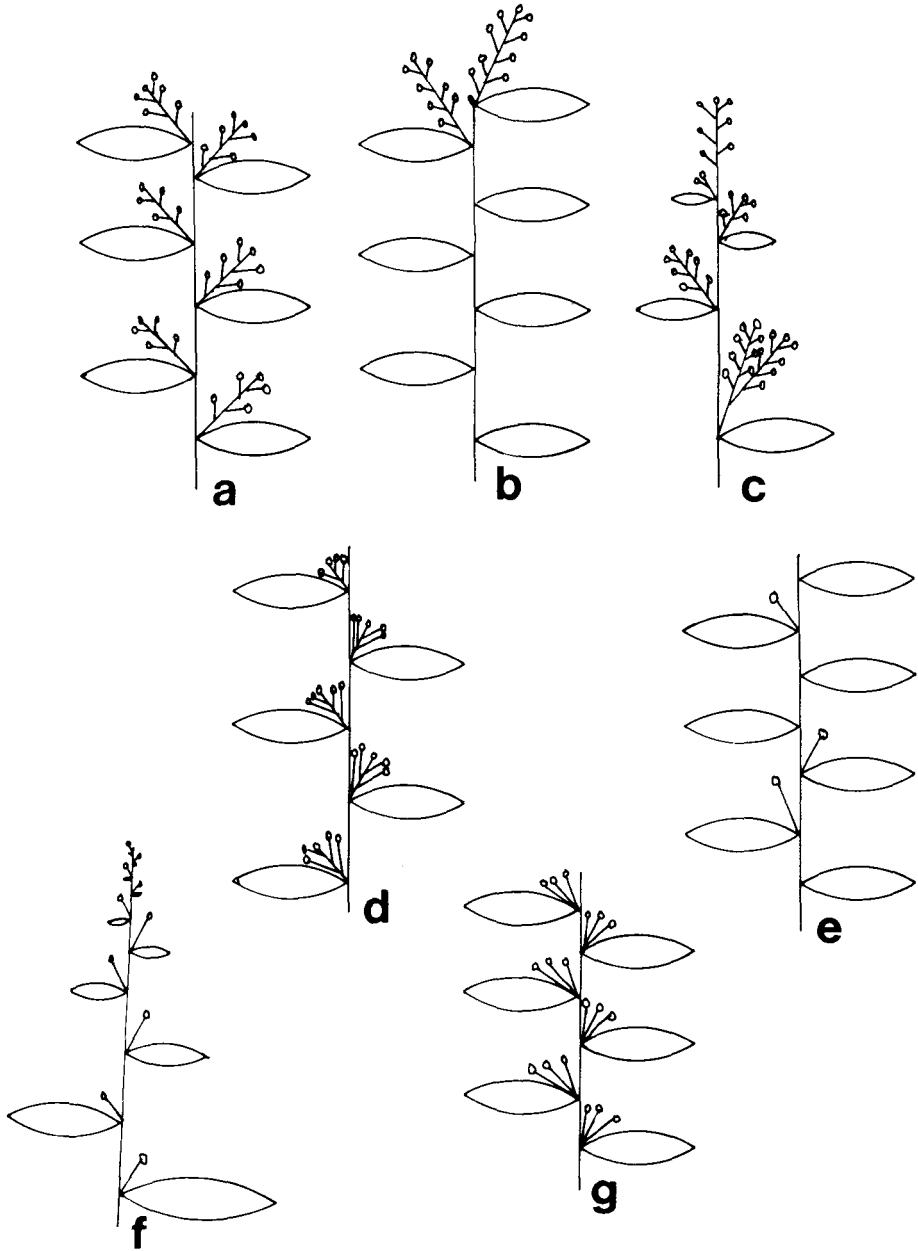


FIG. 2. Inflorescence types in the *Gaultheria* group of genera. a, axillary raceme (e.g. *G. leucocarpa*); b, axillary pseudoterminal raceme (e.g. *G. reticulata*); c, axillary and terminal racemes (e.g. *G. malayana*); d, contracted raceme (e.g. *G. dumicola*); e, solitary (e.g. *G. adenothrix*); f, solitary flower in a pseudoraceme (e.g. *G. itatiaiae*); g, fascicle (e.g. *Zenobia pulverulenta*).

Table 6. Bracteole type in the *Gaultheria* group of genera.

	G	Ch	L	Z	D	Ps	T
2 basal	23	0	25	100	0	0	0
2 on pedicel	36	0	50	0	0	0	0
2 apical	18	100	25	0	100	100	100
several	25	0	0	0	0	0	0

Within *Gaultheria* most solitary-flowered species, other than those centred around *G. trichophylla* Royle, *G. novaguineensis* J.J. Smith and *G. pernettyoides* Sleumer, are multibracteolate. A few solitary-flowered species have two basal bracteoles. This is true for most of the Brazilian solitary-flowered species and for *G. caespitosa*. The Australasian racemose species all have two basal bracteoles and the American racemose species have two bracteoles variable in position but never apical. The position of these bracteoles is often variable within species.

10. Flowers:

Gaultheria hispidula, *G. suborbicularis*, *G. caespitosa* and some individuals of *G. tetramera* W.W. Smith have tetramerous flowers whereas all other species in the group have pentamerous flowers.

Calyx length has been used to separate *Pernettyopsis* and *Diplycosia*. *Gaultheria domingensis* Urb., from the Caribbean, has very long calyx lobes as do some of the South American solitary-flowered species. In these the calyx lobes often equal the length of the corolla tube.

Table 7. Corolla shapes in the *Gaultheria* group of genera.

	G	Ch	L	Z	D	Ps	T
Urceolate	82	0	63	0	64	50	33
Campanulate	19	100	0	100	29	50	33
Tubular	0	0	37	0	14	0	33

Table 7 presents the range of corolla shapes in the different genera of the *Gaultheria* group. The corolla is frequently urceolate. In some species of *Gaultheria* the corolla is campanulate (e.g. *G. caespitosa*, *G. antarctica*, *G. griffithiana* Wight, *G. dumicola*). It is also campanulate in *Zenobia* and wide urceolate/campanulate in some species of *Gaultheria*. In some species of *Leucothoë* the corolla is tubular and in *Diplycosia* it is urceolate, campanulate or tubular. This character is not particularly variable within a species except that the mouth of urceolate species may vary in size.

The corolla length can be variable within species but it is also useful for delimiting species and provides a useful key character. Airy-Shaw (1940) suggested the extremely large corolla (c.15mm) of *G. codonantha* is a primitive condition. Long corollas also occur in a few species of *Leucothoë*, *Zenobia*, and in general the American racemose species of *Gaultheria* have longer corollas than their Asian and Australasian counterparts.

11. Stamens:

The stamens provide some of the most important taxonomic characters in the Ericaceae (Matthews & Knox, 1926; Stevens, 1969, 1970, 1971; Judd, 1979). They are extremely

diverse in the structure of the filament, the anther locules, appendages, and mode of dehiscence.

Stevens (1970) used stamen characters amongst others to separate *Agarista* and *Leucothoë* and suggested that the stamens linked *Agarista* more to the *Lyonia* group than to the *Gaultheria* group. In general he concluded that the *Lyonia* group have geniculate filaments and the *Gaultheria* group straight filaments, although there were a few species with straight filaments in the former group and a few species of *Diplycosia* with filaments approaching the geniculate type. Anther appendages were present in the *Lyonia* group are spurs whereas they are awns in the *Gaultheria* group.

Normally in the Ericaceae flowers are pentamerous with ten stamens. Stevens (1969) states that the stamens of most Ericaceae are dimorphic to some extent with the antesepalous stamens being larger. In the *Gaultheria* group the stamens appear more or less equal except in a few cases where dimorphism is noticeable. In most of these cases this is variable within the species and it is certainly of no taxonomic value. Except for the tetramerous species mentioned earlier where there are eight stamens, the only other species which does not always have ten stamens is *G. semi-infera* (Clarke) Airy-Shaw which often has five. This character is variable within the species and some individuals were seen with ten stamens. Apart from these there are cases of dioecism and gynodioecism in *Gaultheria* where stamens are completely missing, reduced in size, or functionally sterile (Middleton, 1989).

Table 8. Filament shape in the *Gaultheria* group of genera.

	G	Ch	L	Z	D	Ps	T
Not dilated	60	0	100	0	100	100	100
Dilated	40	100	0	100	0	0	0

There are a number of characters associated with the filament. In this study geniculate filaments have been observed in *Agarista* of the *Lyonia* group of genera and (though less well developed) in a number of species of *Diplycosia* (Fig. 3 – *D. salicifolia*). All the other species of the *Gaultheria* group which I have observed had more or less straight filaments.

The filaments of *Zenobia*, *Tepuia*, *Leucothoë*, *Pernettya* and most *Gaultheria* species are fairly broad at the base, whereas the filaments of *Diplycosia* and *Pernettyopsis* are generally narrower. In many *Gaultheria* species the filament is abruptly dilated at the base (Table 8). Although the occurrence of this feature does not exactly follow generic boundaries or the groups of Airy-Shaw, it is undoubtedly concentrated in specific groups, primarily among the solitary-flowered species (Fig. 3 – *G. poeppigii*).

The filaments of *Diplycosia*, *Pernettyopsis*, some species of *Leucothoë* and *G. caespitosa* are not papillose. All other species in the group have clearly papillose filaments to a greater or lesser extent. The filament is often also pubescent.

The length of the filament ranges from about 0.3–5.8mm and is extremely variable within some species, although on average the filament is longer in *Diplycosia* and the American racemose species of *Gaultheria*. It is also extremely long in isolated other species such as *G. procumbens* L., *G. codonantha* and *Leucothoë keiskii* Miq. Filament length is generally greater in larger species and shorter in smaller species, except for the

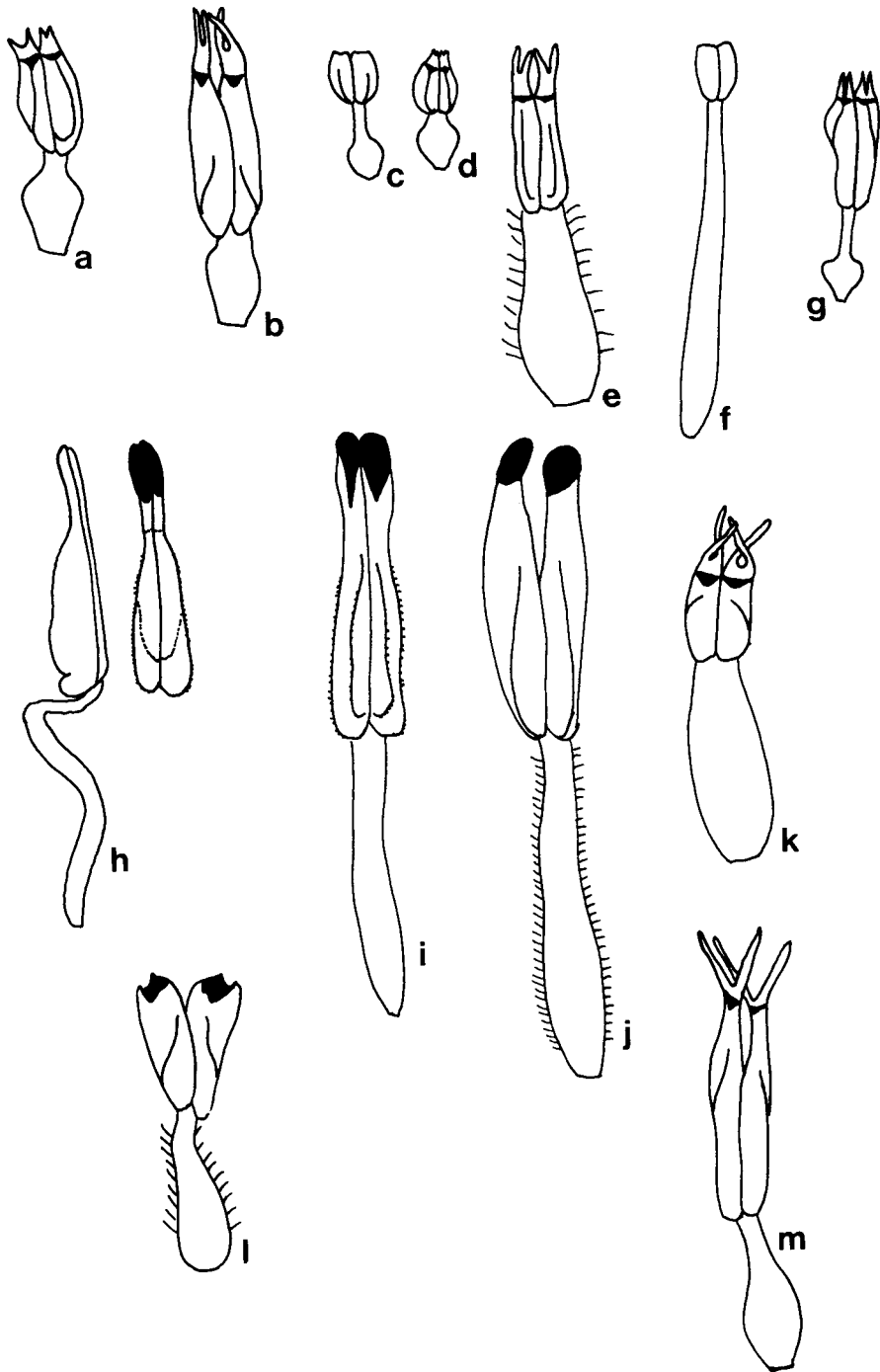


FIG. 3. Stamens of some species in the *Gaultheria* group of genera. a, *Gaultheria tenuifolia*; b, *G. leucocarpa*; c, *G. humifusa*; d, *G. hispidula*; e, *G. acuminata*; f, *G. caespitosa*; g, *G. poeppigii*; h, *Dipycosia salicifolia*; i, *D. memecyloides*; j, *Tepuia tatei*; k, *Leucothoe griffithiana*; l, *L. axillaris*; m, *Zenobia pulverulenta*.

extremely small species *G. caespitosa* (Fig. 3) which has relatively long filaments (3mm).

There are two locules per anther. The longest anthers found in the group were from *Diplycosia kinabaluensis* Stapf (4mm long), and *G. codonantha* and *L. keiskii* have anthers approaching this size. *Gaultheria hispidula* and *G. suborbicularis*, however, have anthers less than 0.5mm long.

Anther structure is the main character separating *Diplycosia*, *Pernettyopsis* and *Tepuia* from the other genera. These three genera have long tubules at the apex of the anther with a pore at the end for the release of pollen (Fig. 3). *Gaultheria*, *Leucothoë* and *Zenobia* mostly do not have a long anther tubule and dehisce by a terminal opening which rarely may split part way down the inward facing wall of the anther. Some of the Brazilian solitary-flowered species of *Gaultheria*, such as *G. sleumeriana* and *G. itatiaiae* Wawra. ex Drude, do have a tubule on the anther, although these species are clearly related to other species, such as *G. ulei* and *G. myrtilloides*, where the tubule is much shorter or absent. Also, the anthers of some of these species have tiny projections which is a character found in *Gaultheria* but absent from *Diplycosia*, *Pernettyopsis* and *Tepuia*. In all other respects the characters of this group of Brazilian species of *Gaultheria* are unremarkable for the genus.

Variability in anther size within species is quite marked although, as for the filament, the larger species tend to have larger anthers.

The back of the anthers in all plants without tubules has what is known as dissolution tissue (Stevens, 1969). Dorr (1980) was unable to find out what function this tissue had in *Zenobia pulverulenta*.

Table 9. Anther appendages in the *Gaultheria* group of genera.

	G	Ch	L	Z	D	Ps	T
No awns	10	0	38	0	100	100	100
Minute projections	29	100	50	0	0	0	0
Awned	66	0	50	100	0	0	0

Anther appendages are of many different types in the Ericaceae and have long been of major importance in the taxonomy of the family (Fig. 3). Stevens (1969) separated the *Lyonia* and *Gaultheria* groups of the *Andromedaeae* partly on stamen appendages. When present they are in the form of spurs, either at the base of the anther or on the filament, in the *Lyonia* group, and in the form of awns in the *Gaultheria* group. Awns do not occur throughout the *Gaultheria* group (Table 9). They are lacking in *Diplycosia*, *Pernettyopsis* and *Tepuia* and in many species of *Gaultheria* and *Leucothoë*. They vary enormously in size from being absent or represented by minute projections to being awns of various lengths. Sometimes it is not clear whether the minute projections in certain species are homologous with the awns of other species or whether they are a product of terminal dehiscence. Only developmental studies will answer this. When present, the awns are normally more or less equal in size and two per anther locule.

Sometimes closely related species differ in this character. *Gaultheria tasmanica* is exaristate but *G. parvula* has minute projections. Three species of *Leucothoë* are either

awnless or have minute projections and this appears to be variable within species. *Zenobia* has long awns.

The largest awns I have encountered were in *G. codonantha* (1.4mm), which is a large plant, although almost as long awns were found in *G. miqueliana* Takeda, a relatively small plant. Awn length is variable within species.

In some South American racemose species the outer awn of each pair is shorter than the inner awn and may be completely absent. In *G. regia* Sleumer and *G. rigida* some individuals have two awns and others one notched awn. This tendency towards one awn is quite marked in the *G. erecta* species complex. *Gaultheria sclerophylla* Cuatr. also has one notched awn and *G. trichophylla* has varieties with either one or two awns per locule.

Stevens (1969) reported an evolutionary progression in the fusion of the two awns to a single awn in *G. hypochlora* Airy-Shaw. *Leucothoë recurva* (Buckley) Gray has only one awn whilst the closely related *L. racemosa* Gray has two.

12. Ovary:

The ovary is globular, the style is columnar and usually slightly impressed on the ovary, and the stigma is truncate. There is very little variation of this basic pattern although the styles in *Leucothoë* tend to be somewhat longer than those in the other genera. The major exception to this generalization is the semi-inferior ovary of *G. hispidula* (*Chiogenes*) and *G. semi-infera*.

When present the hairs on the ovary are unicellular and usually fairly short. Pilose ovaries are absent from *Leucothoë* and *Zenobia* and appear to be uncommon in *Diplycosia*. Within *Gaultheria* pilose ovaries and styles are common and extremely variable within larger taxa and within some species.

13. Fruit:

The variation in fruit characters are the source of the taxonomic problems in the group. Hooker (1876) gave a strong *a priori* weighting to the fruit so that *Pernettya*, with a fleshy berry, was placed in a different tribe from *Gaultheria* with a dry capsule.

There are two main elements to the fruit of these genera: firstly whether the post fertilization ovary develops into a capsule or a berry and secondly whether or not the calyx becomes fleshy. Traditionally, *Gaultheria* and *Diplycosia* were characterized by having a dry capsule and a fleshy calyx, *Pernettya* and *Pernettyopsis* by having a fleshy berry and a dry calyx, and *Tepuia*, *Leucothoë* and *Zenobia* by having a dry capsule and a dry calyx. The inclusion of *Pernettya* within *Gaultheria* (Middleton & Wilcock, 1990a) has made the range of fruit types within *Gaultheria* more diverse. *Gaultheria hispidula* and *G. suborbicularis* (both placed by Hsu (1984) in *Chiogenes*) have a fleshy floral axis which includes the base of the calyx whilst the calyx lobes remain unchanged. Although unchanged calyx lobes with a fleshy calyx base is an unusual feature in *Gaultheria* it does occur in other undoubted *Gaultheria* species such as *G. discolor* Nutt. A number of *Gaultheria* species do not develop a fleshy calyx in the fruit; these include all the New Zealand racemose species as well as *G. nubigena* (Phil.) Burt & Sleumer, *G. wardii* Marq. & Shaw and *G. itatiaiae*.

Sleumer (1967) stated that the species of *Diplycosia* have capsules whereas *Pernettyopsis* is distinguishable from them by its berry. However, I have seen good berries half enclosed within a fleshy calyx in *D. elliptica* and I have been informed that berries are not uncommon in this genus (Argent, pers. comm.).

The flesh of these berries is thin and tends to split on drying thus giving the appearance of an irregularly dehiscent capsule in herbarium specimens. In *Gaultheria*, those species previously placed in the genus *Pernettya* have a berry. It has also been noted that *G. procumbens* has a somewhat fleshy 'capsule' in fruit (Stevens, 1969). I have seen a good berry, with a fleshy calyx, in herbarium specimens of *G. tenuifolia* (Phil.) Sleumer and *G. sinensis* Anth.; in the latter case a note was appended to the herbarium sheet because it so surprised the determiner (British Museum – Ludlow, Sherriff & Taylor 5293). In Ecuador, I observed that *G. rigida* and *G. glomerata* (Cav.) Sleumer had capsules which often dropped off the plant without ever drying out and dehiscent.

14. Seeds:

Stevens (1969, 1970, 1971) found seed characters to be very useful in his subfamilial and tribal treatment of the Ericaceae. Stevens (1970) and Judd (1979) pointed out that the *Lyonia* group of genera usually had thin-walled, elongated testa cells whereas those in the *Gaultheria* group were thicker walled and shorter. I have studied a few species of *Agarista* from the former group and these had very long thin seeds with long thin-walled testa cells. These characters were not found in *Gaultheria* where all species had seeds not normally more than twice as long as broad and the testa cells thick-walled and little elongated. However, the few species of *Diplycosia* for which seed characters were observed had seed and testa cell shapes more like those of *Agarista*.

Leucothoë is unique in the *Gaultheria* group in having a number of species with winged seeds, an obvious adaptation for wind dispersal. *Leucothoë recurva* (Buckley) Gray, *L. grayana* Max., *L. griffithiana* Clarke and *L. davisiae* (Torr.) Small all have winged seeds by virtue of having large cell outgrowths at the seed margin. *Leucothoë fontanesiana* (Steudel) Sleumer, *L. axillaris* (Lam.) D. Don and *L. keiskii* Miq. all have the appearance of slightly winged seeds because the testa is loose and flattened in one plane. The only species not to develop some sort of a winged seed is *L. racemosa*.

The testa cell walls are usually fairly thin in *Leucothoë* (8µm) whereas in *Gaultheria* the usual range is about 6–20µm although walls down to 2µm and up to 25µm have been seen. Seed size is very variable within species and between species which otherwise appear closely related. *Leucothoë* has the largest seeds.

DISCUSSION

The guidelines followed in this paper in determining the genus are as follows. The size of the genera should not be a criterion for delimitation even when this leads to one genus with over a hundred species and another, closely related genus, with only one species. The taxonomist must be as satisfied as is possible that the genus is a monophyletic group. Characters which are used to separate genera should not be found in an intermediate state as by definition these characters would then cease to be diagnostic. Coupled with

this is to avoid the use of single or very few characters to delimit genera and not to assume that a particular set of characters (e.g. fruit characters) are inherently more important. The size of groups compared to the number of intermediates between them is not an important factor in the delimitation of genera except when there is a need to err on the side of conservatism. Only if two genera are very much misrepresented by being maintained as two separate genera should they be united.

A large range of characters has been studied and found to be useful at the different taxonomic levels to varying degrees. The use of these characters at the infrageneric level in *Gaultheria* has been discussed in a separate paper (Middleton, in press). At the generic level a number of characters are particularly useful although good diagnostic characters for individual genera are rare. A wide range of stamen characters and inflorescence types are particularly interesting at the generic level. Leaf, indumentum, fruit and seed characters also provide useful characters to a more limited extent.

Chiogenes

The genus *Chiogenes* is now largely accepted as part of *Gaultheria*. The only challenges to this assumption have been from Löve & Löve (1973) and Hsu (1984) who have preferred to reinstate the genus *Chiogenes*. The last author also included *G. suborbicularis* within this genus. The single species traditionally placed in *Chiogenes* is *G. hispidula* from North America and Japan (sometimes var. *japonica* is treated as a separate species). *G. suborbicularis* is from China.

The genus was characterized by its semi-inferior ovary, tetramery and creeping habit. The ovary character is the reason for its frequent association with *Vaccinium* (see Hooker, 1876; Watson *et al.*, 1967). Airy-Shaw (1941) reinstated *Gaultheria hispidula* after more than a century of its treatment as *Chiogenes* and gave fairly detailed reasons why *Chiogenes* could not be maintained.

The evidence from this study supports the treatment of *Chiogenes* as synonymous with *Gaultheria*. It is true that *G. hispidula* does have a number of characters which are unusual in *Gaultheria* but each of these characters are found elsewhere in the genus. *Gaultheria suborbicularis* acts as a good intermediate between *G. hispidula* and series *Trichophyllae*. In flower type and stamen structure these species are similar to series *Trichophyllae*. Their stamen structure differs only in being somewhat larger in series *Trichophyllae*, in the rather shorter awns of *G. hispidula*, and in the absence of awns in *G. suborbicularis*. The indumentum of all these species is of shortish strigose multiseriate hairs (occasionally absent) with or without short unicellular hairs. The more or less eciliate calyx lobes of all these species is unusual in *Gaultheria*. Of the characters used to separate the two genera initially there is no discontinuity: *G. semi-infera*, a species unremarkable in *Gaultheria* in all other characters, has a semi-inferior ovary; *G. tetramera* often has, and *G. caespitosa* always has, tetramerous flowers; and many species of *Gaultheria* have a creeping habit.

Anatomically, *G. hispidula* is similar to many other species in *Gaultheria* (Middleton, 1989). This species, *G. suborbicularis* and the species of series *Trichophyllae* usually lack a hypodermis (one individual of *G. sinensis* had an extremely localized hypodermis), have no free fibres in the mesophyll, and have a weak or absent adaxial midrib

sclerenchyma. All species except *G. suborbicularis* have small thick-walled pith cells. Whereas *G. hispidula* and *G. suborbicularis* often have only paracytic stomata, the species of series *Trichophyllae* generally have large numbers of anomocytic stomata as well.

Towers *et al.* (1966) detected salicylic acid in *G. hispidula*, a substance common in *Gaultheria* but virtually absent in the rest of the family. Salicylic acid is unknown in *Vaccinium* which Löve & Löve (1973) have linked *Chiogenes* to but it has been found in a few species of *Cavendishia* of the same tribe (Luteyn *et al.*, 1980).

Löve & Löve (1973) reinstated *Chiogenes* as a separate genus because of its different base chromosome number of $x = 12$ ($2n = 24$), whilst *Gaultheria* sensu stricto has a base chromosome number of $x = 11$. They pointed out a number of morphological differences between the two genera and suggested that *Chiogenes* may have its affinities with *Vaccinium* rather than with *Gaultheria*. However, *Chiogenes* can be accommodated within the range of variation of *Gaultheria*. Counts of $x = 12$ have been recorded for *Gaultheria* and a count of $2n = 22$ for a plant of *G. hispidula* has been found (Middleton & Wilcock, 1990b).

The limits of Hsu's *Chiogenes* follows the delimitation of Airy-Shaw's series *Hispidulae*. I cannot agree with Hsu's conclusions on the generic status of *Chiogenes* because morphologically and anatomically these species are closely linked to series *Trichophyllae*.

To conclude, the genus *Chiogenes* is not maintainable and with *G. suborbicularis* should be treated as a group close to the *G. trichophylla* group of species.

Leucothoë

There can be no doubt that the division between *Leucothoë* and *Agarista* (Stevens, 1969, 1970, 1971) was necessary. However, species of *Agarista* are still frequently referred to as *Leucothoë* almost 20 years later (Mabberley, 1987) and new species of *Agarista* are sometimes described as species of *Leucothoë* (Kinoshita-Gouvêa, 1981). This practice is, however, changing with persistent use of the genus *Agarista* by authorities in the field (Judd, 1979, 1984).

There are eight species of *Leucothoë* from North America, Japan and the Himalayas. It is difficult to make generalizations about the genus because the eight species are very diverse and have at various times been treated as five separate genera. It was not until Stevens (1969, 1970, 1971) that *Leucothoë* was considered to belong in the same tribe as *Gaultheria* although Airy-Shaw (1941) and Wood (1961) had previously remarked on the similarities between them. Indeed *Gaultheria* and *Leucothoë* are very closely related. Stevens (1969) stated that 'The separation of *Leucothoë* and *Gaultheria* is not at all easy'.

I have examined three species of *Leucothoë* and they are all diploids based on $x = 11$, the same basic chromosome number as in *Gaultheria* (Middleton & Wilcock, 1990b). Harborne & Williams (1973) found dihydroquercetin in three species of *Leucothoë* and not at all in *Gaultheria*. I have detected dihydroquercetin in *Leucothoë fontanesiana* and also in species of *Gaultheria* (Middleton, 1989). However, salicylic acid has not been found in *Leucothoë*.

In morphology the two genera are close but there are differences. No species of *Leucothoë* has solitary flowers, particularly small leaves or prostrate habit, characters common in *Gaultheria*. All species of *Leucothoë* have short stalked glandular hairs which are not common in *Gaultheria* although it is difficult to delimit hair types with a high degree of consistency. This character is also somewhat variable within *L. grayana*. In inflorescence form *Leucothoë* is similar to many Asian *Gaultheria* species. The bracts and bracteoles are generally fairly small, the latter varying in position from apical to basal. The corollas are more tubular than the species of *Gaultheria*. The stamen structure is fairly similar to *Gaultheria* although a few species of *Leucothoë* do not have papillose filaments, an almost ubiquitous character in *Gaultheria*. Awns are present, very short or absent as occurs in *Gaultheria*.

The fruit characters are the ones which have distinguished *Leucothoë* in the past, all species having dry capsules and dry calyces which wither soon after flowering. Dry capsules and dry calyces are also found in a few species of *Gaultheria*, most notably the New Zealand racemose species although the calyx is persistent in these species. All the species of *Gaultheria* without fleshy calyces are easily linked to typical *Gaultheria* species through leaf, inflorescence and indumentum characters with the possible exception of the somewhat isolated *G. nubigena*. This is similar to the situation in *Pernettya* where fruit characters cannot be relied upon to provide a consistent separation between the two genera. Unlike the situation with *Pernettya* there are no instances of a partial fleshiness of the calyx in *Leucothoë* and no reports of intergeneric hybridization producing intermediate fruits. The capsules are larger than any produced in *Gaultheria*.

Seed characters in *Leucothoë* are very interesting. The seeds are generally larger than in *Gaultheria* and seven of the eight species have winged seeds, although these are produced in different ways. Four species, *L. recurva*, *L. grayana*, *L. griffithiana* and *L. davisiae* have large cell outgrowths at the margin of the partly flattened seed, whereas *L. fontanesiana*, *L. axillaris* and *L. keiskii* have a partly flattened seed with a loose testa giving the appearance of a wing around the edge. Only *L. racemosa* has an unwinged seed but in all other respects it is very close to *L. recurva*. The testa wall is generally much thinner in *Leucothoë* than in *Gaultheria*.

Three species of *Leucothoë* in sections *Eubotrys* and *Eubotryoides* are deciduous, a feature occurring in *Zenobia* but never in *Gaultheria*.

Anatomically, *Leucothoë* is fairly different from *Gaultheria*. *Leucothoë*, except for the two species of sect. *Eubotrys*, has a pith type not found in *Gaultheria* (Middleton, 1989). No species of *Leucothoë* has a continuous hypodermis, unusual in racemose *Gaultheria* species, and paracytic stomata are more predominant. No racemose *Gaultheria* species have the marginal sclerenchyma found in *L. axillaris* and *L. fontanesiana*.

Leucothoë and *Gaultheria* have produced no known intergeneric hybrids despite the fact that these two genera occur together in some parts of their distribution.

There are a number of characters which serve well to separate the two genera but most are not constant in *Leucothoë*. However, there are combinations of characters in particular species which are not found in *Gaultheria* and other characters which link the species of *Leucothoë* together. The fruit characters are certainly important although not

unique. The seed characters are different between the two genera as are the deciduous leaves of some species. The pith type and leaf anatomy are clearly different in the two genera.

If one were to unite *Gaultheria* and *Leucothoë* their characters are such that they would deserve subgeneric status, thus calling into question the need to unite them. With *Pernettya* the number of intermediates and the frequency of hybridization really makes it impossible to maintain this genus separate from *Gaultheria*. *Leucothoë* and *Gaultheria* have historically been treated as separate genera and to make them two subgenera would simply require new binomials without any significant change in our knowledge of these plants. Instead, I prefer to maintain their traditional use as separate genera.

Melvin (1980) placed the eight species in three sections: *Leucothoë*, *Eubotrys* and *Eubotryoides*. The first contained all five evergreen taxa and the last two the three deciduous taxa. In this he was following the line of thought of Wood (1961) in amalgamating the four evergreen sections of Sleumer (1959) into one. Melvin (1980) argued that by splitting the five species into four sections geographical considerations were being overemphasized to the detriment of morphological similarities. Wood (1961) noted that this has led to relationships between the species of Eastern Asia and North America being obscured.

These five species are certainly diverse morphologically and anatomically. *Leucothoë fontanesiana* and *L. axillaris* have a rather different leaf anatomy. They have a seed type like that of *L. keiskii* and an inflorescence like that of *L. griffithiana*. Melvin (1980) found *L. davisiae* to be quite isolated primarily because of its inflorescence type and habit. Wood (1961) suggested that *L. griffithiana* was closest to sect. *Leucothoë* (*L. fontanesiana* and *L. axillaris*).

I agree with the conclusions of Wood (1961) and Melvin (1980) that these taxa should be treated as one section, sect. *Leucothoë*. However, the old sections are quite distinct and could possibly be treated as series within sect. *Leucothoë*.

Sleumer (1959), Wood (1961) and Melvin (1980) all agreed as to the sectional treatment of the three deciduous species into sect. *Eubotrys* and sect. *Eubotryoides*. None of these workers agreed with the separate generic status which has been afforded these two sections in the past (see Melvin, 1980). This study agrees with these conclusions.

Zenobia

Zenobia has had a varied history having been placed in *Andromeda* and compared to *Lyonia*, *Leucothoë* and *Gaultheria* at various times. There is only one species, *Zenobia pulverulenta*, from North America.

Stevens (1969) dismissed the view that it may be congeneric with *Lyonia* but suggested that its relationships with *Leucothoë* and *Gaultheria* needed to be clarified.

I believe that its generic separation from *Leucothoë* and *Gaultheria* is realistic. The distinguishing characters from *Gaultheria* are a combination of a truly fasciculate inflorescence (which is not found in either *Leucothoë* or *Gaultheria* – although some species of sect. *Brossaeopsis* approach a fasciculate inflorescence), campanulate cor-

olla, deciduous or partially deciduous leaves, dry fruit, strong hypodermal lignification of the leaf margin, and anomocytic stomata.

Zenobia almost completely lacks an indumentum except for small multiseriate hairs on the leaf margin. This, the campanulate corolla, the fascicle, basal dilation of the filament, prominent leaf reticulation, strong hypodermal lignification of the leaf margin, strong adaxial sclerenchyma and anomocytic stomata distinguish it from *Leucothoë*

Airy-Shaw (1941), Wood (1961) and Stevens (1969) all point out the similarity between *Zenobia* and some species of *Gaultheria*. However, no species of *Gaultheria* has the combinations of characters found in *Zenobia*. Those *Gaultheria* species approaching *Zenobia* in inflorescence type differ in fruit, indumentum and leaf nervation. No *Gaultheria* species has deciduous leaves and none has such strong marginal hypodermal lignification. Completely anomocytic stomata are found in *Gaultheria* in only one species which in no other ways has affinities with *Zenobia*.

Although *Zenobia* is undoubtedly a distinct monotypic genus it is certainly close to *Gaultheria* and *Leucothoë*. An unconfirmed chromosome count of $2n = 66$ would give it a basic chromosome number of $x = 11$ as is most common in *Gaultheria* and *Leucothoë* (Middleton & Wilcock, 1990b).

Diplycosia* and *Pernettyopsis

Diplycosia and *Pernettyopsis* are more or less confined to the Malesian region although there is one species of *Diplycosia* in South Vietnam and three in peninsular Thailand, only one of which is endemic (Sleumer, 1967). In all there are two species of *Pernettyopsis* and c.100 species of *Diplycosia*.

There can be no doubt that these two genera are very distinct from *Gaultheria*. The clearest differences between the two groups are in inflorescence type, leaf type and stamen structure. The inflorescence of *Pernettyopsis* is a fascicle and that of *Diplycosia* a fascicle or solitary flower. True fascicles are unknown in *Gaultheria*. *Diplycosia* and *Pernettyopsis* usually do not have a papillose filament, the filament is narrow and often sinuous, the anther has a tubule and no awns, and the bracteoles are always apical. The leaves are usually entire and melastomataceous leaf nervation is common. Uniseriate hairs have been observed in some species which are unknown in *Gaultheria*. The leaf anatomy of *Diplycosia* and *Pernettyopsis* is characterized by having abundant leaf fibres and completely paracytic or with a strong predominance of paracytic stomata. The few species of *Gaultheria* from Brazil which have an anther tubule differ from *Diplycosia* in many other respects.

The species of *Diplycosia* for which a chromosome number is known are all found to be $2n = 36$. This is a qualitative difference from the other genera in the group which usually have a number based on $x = 11$ (Middleton & Wilcock, 1990b).

Only about 21% of the species of *Diplycosia* have been studied here so the sampling is not very extensive. However it is clear that these species of *Diplycosia* and *Gaultheria* are distinct.

The question of the generic status of *Pernettyopsis* has been raised (Argent, 1982, 1989). Stevens (1969) thought *Diplycosia* and *Pernettyopsis* were sufficiently distinct

to be kept separate but Argent (1982, 1989) suggested that this was not so certain. My sampling of *Diplycosia* has not been extensive enough to be certain on this point.

The characters which separate the two genera are in the nature of the fruit: *Pernettyopsis* has a berry and dry calyx lobes in fruit and *Diplycosia* theoretically has a dry capsule and fleshy calyx lobes in fruit (Sleumer, 1967). However, I have seen material of *D. elliptica* which clearly has a berry and Argent (pers. comm.) informs me that berries are not uncommon in *Diplycosia*. No species of *Diplycosia* has unchanged calyx lobes in fruit and furthermore the calyx lobes of *Pernettyopsis* are extremely long compared to anything in *Diplycosia*. These are quite possibly fairly trivial characters and may mean that with further sampling these two genera would need to be united.

Tepuia

Tepuia is a poorly known genus. Only relatively recently described (Camp, 1939b) it has only eight species, all from a fairly small area in the state of Bolivar, Venezuela (Steyermark, 1967). Stevens (1969, 1971) placed this genus in the *Gaultheria* group of genera based on literature descriptions as he was unable to examine any material. It is distinguished from all other genera in the *Gaultheria* group by a combination of apical bracteoles, racemose inflorescence, dry fruit, uniseriate hairs, anther tubules and extremely large glands at the base of the leaf. Only the large glands at the base of the leaf and the very long type of uniseriate hairs are unique in the *Gaultheria* group.

The indumentum has a similar appearance to some species of *Gaultheria* such as *G. lanigera*, but a closer examination shows that the hairs are in fact uniseriate and not multiseriate as is the case in *Gaultheria*.

Tepuia has rather more characters in common with *Diplycosia* although the geographical distributions give one reason to doubt that their relationship is particularly close. Both genera have a similar anther structure but otherwise many of the similarities are superficial. The filaments of *Tepuia* are wider and with a thick pubescence, the filament is papillose, there are no multiseriate hairs, the inflorescence is racemose and the fruit is always dry. In anatomy there are some similarities between the two genera but *Tepuia* has a very thick cuticle and there are fewer free leaf fibres. Stomatal type is unknown because of the difficulty of accurate observations due to the extremely dense indumentum.

While the affinities of *Tepuia* are rather obscure there can be little doubt as to its generic status.

SUMMARY

Within the *Gaultheria* group of genera as defined by Stevens (1971) *Pernettya* has already been merged with *Gaultheria* (Middleton & Wilcock, 1990a) and *Chiogenes* is being treated as synonymous with *Gaultheria* in line with the treatment by most recent authors. *Leucothoë* and *Zenobia* are closely related to *Gaultheria* but should remain separate. *Diplycosia*, *Pernettyopsis*, and *Tepuia* are more distinct from *Gaultheria* but the separation of *Pernettyopsis* from *Diplycosia* needs further clarification.

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