

## Infrageneric classification of the genus *Gaultheria* L. (Ericaceae)

DAVID J. MIDDLETON\*

Department of Plant and Soil Science, Cruickshank Building, Aberdeen University,  
St. Machar Drive, Aberdeen, AB9 2UD

Received December 1989, revised and accepted for publication January 1991

MIDDLETON, D. J., 1991. **Infrageneric classification of the genus *Gaultheria* L. (Ericaceae).** The genus *Gaultheria* has been classified into ten sections (one with two subsections) and 22 series of which five are new combinations and 21 are new taxa. Seven of these sections are composed primarily of solitary flowered species and the other three sections of racemose species. About half of the species of the genus are included in section *Brossaea*. A summary of the classification is here presented.

1. Section *Gaultheria*
2. Section *Chiogenopsis* Middleton
  - series *Trichophyllae* Airy-Shaw
  - series *Hispidulae* Airy-Shaw
  - series *Novaguineenses* Middleton
  - series *Pernettyoideae* Middleton
3. Section *Amblyandra* Airy-Shaw
4. Section *Chamaephyta* Middleton
  - series *Antarcticae* Middleton
  - series *Nubicolae* Middleton
5. Section *Gymnocaulos* Middleton
6. Section *Monoanthermona* Middleton
  - series *Antipodae* Middleton
  - series *Nummularioideae* Airy-Shaw
  - series *Myrtilloideae* Middleton
7. Section *Pernettya* (Gaud.) Middleton
8. Section *Pseudogaultheria* (Sleum.) Middleton
9. Section *Brossaeopsis* Airy-Shaw
  - series *Dumicola* Airy-Shaw
  - series *Atjehenses* Airy-Shaw
  - series *Codonanthes* Middleton
10. Section *Brossaea* (L.) Middleton
  - Subsection *Dasyphyta* Middleton
    - series *Domingenses*
    - series *Tomentosae* Middleton
  - series *Reticulatae* Middleton
    - series *Insipidae* Middleton
    - series *Parvifoliae* Middleton
  - Subsection *Botryphoros* Middleton
    - series *Leucothoides* (Airy-Shaw) Middleton
    - series *Gymnobotrys* (Airy-Shaw) Middleton
    - series *Hispidae* Middleton
    - series *Rupestres* Middleton
    - series *Nubigenae* Middleton

\*Present address: School of Botany<sup>1</sup>, Trinity College, University of Dublin, Ireland.

ADDITIONAL KEY WORDS:—*Pernettya* – Systematics – Taxonomy

## CONTENTS

Introduction . . . . .	230
Material and methods . . . . .	231
Infrageneric classification . . . . .	231
Key to sections of <i>Gaultheria</i> . . . . .	233
References . . . . .	257

## INTRODUCTION

*Gaultheria* is a large genus, within the tribe Andromedeae, distributed through the Americas, eastern Asia and Australasia. Stevens (1971) suggested there were a group of genera centred around *Gaultheria* which he referred to as the “*Gaultheria* group”. The generic limits within this group have been investigated by Middleton (1989) with the main conclusion that *Pernettya* is not maintainable as a genus separate from *Gaultheria* (Middleton & Wilcock, 1990a).

Up to the present there has been no overall subgeneric treatment of the genus *Gaultheria*. According to Stevens (1969) the genus will be difficult to classify satisfactorily at the infrageneric level although others have said that the problem may be solved by an extensive worldwide study of the genus (Sleumer, 1952, 1957; Corcoran, 1981).

Linnaeus (1753) recognized two genera, *Gaultheria* and *Brossaea*, that were separable on fruit characters alone. De Candolle (1839) made *Brossaea* a section of *Epigaea* with only one species from the West Indies. Hooker (1876) later noted that there was no generic distinction between *Brossaea* and a large number of species which had been included in *Gaultheria*. He therefore combined both genera with the name *Gaultheria* taking priority.

Although others had commented on groupings in the genus the first real attempt to provide a subgeneric treatment of *Gaultheria* was made by Copeland (1931). Later, Airy-Shaw (1940) divided the genus into five sections with some sections further divided into series but, unfortunately, his work only included the Old World species and a few North American species. Hsu (1981) proposed a somewhat different scheme using the Chinese species only.

These major works on subgeneric classification have dealt with Asian and North American species but only superficial comparisons have been made with Latin American and Australasian species.

One scheme which does address Latin American subgeneric classification, however, is by Camp (1939) who proposed two informal groups for the Mexican species: the *Acuminatae* and the *Odoratae*.

*Pernettya* has been treated separately by previous workers (Sleumer, 1935, 1985) although Stevens (1971) included it within the genus *Gaultheria*. Middleton & Wilcock (1990a) have argued this case further and provided binomials within *Gaultheria* for the 14 species.

We are left with a fairly confused picture of infrageneric classification in *Gaultheria*. Baas (1985) suggested that phylogenetic relationships within the *Gaultheria-Pernettya* complex were truly reticulate which would “...defy any attempt at a phylogenetic, hierarchical classification”. Although hybridization between potential sections or series is known to occur, I still believe that sectional delimitation is both desirable and possible.

## MATERIAL AND METHODS

Approximately 500 specimens, representing 125 species, were studied for a range of vegetative and reproductive morphological characters. These were mostly from herbarium specimens but include a number of living specimens from the Royal Botanic Garden, Edinburgh and the Cruickshank Botanic Garden, Aberdeen. Field studies were also carried out in Ecuador.

Chromosome studies were made on 27 specimens of *Gaultheria* (Middleton & Wilcock, 1990b). Over 250 specimens representing *c.*113 species were studied for a range of pith and leaf anatomical data and over 210 specimens representing *c.*37 species were studied for leaf flavonoids and simple phenols. These studies will be published separately.

## INFRAGENERIC CLASSIFICATION

It seems likely that all the solitary flowered species were derived from the racemose species by a reduction in the number of flowers in the raceme to one (see Airy-Shaw, 1940). The important question to be asked is how often has this occurred and are these derivatives particularly different from their progenitors to be given sectional treatment? In most cases they are indeed substantially different from the racemose groups although there are a few exceptions. I here propose seven sections to encompass the solitary flowered species. A number of species do not fit easily into this scheme, particularly *G. parvifolia*, *G. phillyreifolia*, *G. oreogena* and *G. adenothrix*. *Gaultheria parvifolia* has solitary flowers but in other respects is very similar to the American racemose species. *Gaultheria oreogena*, *G. phillyreifolia*, and very occasionally *G. adenothrix*, sometimes have few-flowered racemes whereas in other respects they are very like the solitary flowered groups. More will be mentioned on these species later.

The racemose species of *Gaultheria* are much more homogeneous than the solitary flowered species and I have proposed only three sections to encompass the majority of the species of the genus. One of these sections contains only *G. insana* (Molina) Middleton (formerly *P. insana* (Molina) Sleumer) and another contains over half of the species of *Gaultheria* and is further split into two subsections and a number of series.

The species included in each taxon are those currently recognized from a variety of sources. The completion of Flora Neotropica and a needed revision of the Asian species will undoubtedly reduce some to synonymy.

***Gaultheria* L., *Sp. Pl.*, 1: 395 (1753).**

*Gualteria* Duhamel, *Traite Arbr. Fruit*, 1: 285 (1755).

*Gaulteria* Adanson, *Fam.*, 2: 165 (1763).

*Gualtieria* J. Hill, *Veg. Syst.*, 9: 24 (1765).

*Gualtieria* J. Hill, *Hort. Kew.*: 146 (1768).

*Gaulthiera* Corthenius, *Disp.*: 21 (1790).

*Gaultheria* J. F. Gmelin, *Syst.*, 2: 697 (1791).

***Brossaea* L., *Sp. Pl.*, 1: 1190 (1753).**

*Epigaea* L. section *Brossaea* DC., *Prodr.*, 7: 591 (1838).

*Chiogenes* Salisb., *Trans. Hort. Soc. London*, 2: 94 (1817).

*Glyciphylla* Raf., *Am. Month. Mag.*, 4: 192 (1819).

- Phalerocarpus* G. Don, *Gen. Syst.*, 3: 841 (1834).  
*Lasierpa* Torr., *Geol. Rep. New York*: 152 (1839).  
*Shallonium* Raf., *Amer. Month. Mag.*, 2(4): 266 (1818).  
*Pernettya* Gaud., *Ann. Sci. Nat. (Paris)*, 5: 102 (1825).  
 (*Pernettia orth. rej.*)  
*Hippomanica* Molina, *Sag. Stor. Nat. Chili*, 126: 351 (1782).

Evergreen shrubs; hermaphrodite, dioecious or gynodioecious; creeping, procumbent, arching erect or upright erect to as much as 3.5 m high, rarely epiphytic. Branch indumentum more or less absent or of unicellular and/or multicellular hairs; spreading or appressed, glandular or eglandular; subsessile or stalked if glandular; often caducous. Leaves spirally arranged (in one species opposite) although often appearing two ranked; coriaceous; serrate, serrulate or entire; nervation pinnate or melastomataceous; 2–185 mm long, 1–110 mm wide; base cordate to cuneate, apex rounded to caudate; glabrous or with unicellular and/or multicellular glandular or eglandular hairs especially below. Inflorescence of either solitary flowers (sometimes appearing as a terminal pseudoraceme) or racemes situated in the axils of the leaves (sometimes appearing fasciculate) or terminal racemes often forming a panicle with axillary racemes. Raceme, if present, with or without perules at the base, these perules varying in size and shape. Inflorescence glabrous or with unicellular and/or multicellular glandular or eglandular hairs, spreading or appressed. If flower is solitary, then many bracteoles or only 2 bracteoles either basal or apical. If flower is racemose then 2 bracteoles on the pedicel and a subtending bract present. Bract varying in size, shape and indumentum; up to 14 mm long. Bracteoles varying in shape; opposite or alternate; basal, on the middle of the pedicel or apical immediately beneath the calyx. Corolla urceolate, cylindric or campanulate; 2–15 mm long; glabrous or with unicellular and/or multicellular glandular or eglandular hairs outside and glabrous or with unicellular hairs inside. Stamens usually 10, occasionally 8 or 5, slightly dimorphic. Filament papillose or rarely smooth; glabrous or with unicellular hairs; filiform, broader at the base or noticeably dilated at the base; straight. Two anther locules opening by a terminal pore which may split a short way down the front of the locules; only very few species with a terminal tubule; awned, with minute projections or awnless; awns 2 (occasionally 1) per anther locule when present. Ovary 5-lobed (occasionally 4); superior or semi-inferior; pilose or glabrous. Style columnar, truncate. Fruit a thick or thin walled berry or a globose capsule dehiscing loculicidally or irregularly; with or without a fleshy calyx surrounding the capsule or base of the berry; occasionally only the floral axis becoming fleshy. Seeds small to 1.3 mm long; unwinged; testa of more or less isodiametric to slightly elongated cells with thick walls to 24  $\mu\text{m}$ .

Approximately 134 species in Eastern Asia (including Japan), South India and Sri Lanka, South East Asia, Malesia, southern Australia, Tasmania, New Zealand and South, Central and North America.

**TYPE:** *Gaultheria procumbens* L.

The type species of *Gaultheria* was first collected by Peter Kalm in Canada and the genus was described from this material in *Nova Plantarum Genera* by Linnaeus (1751). However, none of the herbarium material is still in existence, the only

specimen of *Gaultheria procumbens* in the Linnaean herbarium clearly being a later addition. The original description of the genus (Linnaeus, 1751) carries with it an illustration (figure 6 in the work) of *G. procumbens* and this must now be designated as the lectotype of the genus *Gaultheria*.

*Key to the sections of Gaultheria*

- 1 At least some flowers in a few or many flowered true raceme or panicle
  - 2 Leaf tip mucronate; temperate South America . . . . . **6. section *Monoanthe mona***
  - 2 Leaf tip blunt
    - 3 Many flowers on the plant solitary in the axils of the leaves up to 4 flowers in the raceme
      - 4 Corolla urceolate
        - 5 Corolla more or less glabrous outside; South America. . . . . **6. section *Monoanthe mona***
        - 5 Corolla densely hirsute; Mexico . . . . . **10. section *Brossaea***
      - 4 Corolla campanulate; Japan . . . . . **3. section *Amblyandra***
    - 3 Solitary flowers absent, or at least some racemes with more than 4 flowers
      - 6 Corolla cylindric; anther ending in a marked tubule; awns absent . . . . . **6. section *Monoanthe mona***
      - 6 Corolla urceolate or campanulate; anther without a marked tubule; usually with awns or tiny projections
        - 7 Fruit a berry with the calyx not completely swollen and surrounding it; temperate South America . . . . . **8. section *Pseudogaultheria***
        - 7 Fruit a capsule, or a very thin walled berry and then completely surrounded by a fleshy accrescent calyx
          - 8 Nervation melastomataceous; bracteoles basal. . . . . **9. section *Brossaeopsis***
          - 8 Nervation pinnate; bracteoles variable in position . . . . . **10. section *Brossaea***
- 1 Flowers solitary in the axils of the leaves or appearing as a terminal leafy raceme (pseudoraceme)
  - 9 Corolla externally densely hirsute; several bracteoles, large and broad . . . . . **10. section *Brossaea***
  - 9 Corolla usually glabrous or only minutely puberulent, occasionally very sparsely hirsute; two or several bracteoles not longer than the calyx lobes
    - 10 Bracteoles 2, inserted immediately beneath the calyx
      - 11 Leaves more than 1 cm wide; inside of corolla and staminal filaments pilose. . . . . **1. section *Gaultheria***
      - 11 Leaves usually less than 1 cm wide; inside of corolla and filaments glabrous . . . . . **2. section *Chiogenopsis***
    - 10 Bracteoles several, or if only two then basally situated
      - 12 Fruit a berry, with the calyx unchanged or swollen but not completely enclosing the berry . . . . . **7. section *Pernettya***

- 12 Fruit a capsule, with or without a swollen calyx
- 13 Leaves always less than 10 mm long, not or only obscurely serrulate; plants caespitose
- 14 Flowers tetramerous (very rarely pentamerous); filament very slender, more than 2.5 times as long as anther; Tierra del Fuego . . . . . **5. section *Gymnocaulos***
- 14 Flowers pentamerous; filament broad or dilated at base, less than 2.5 times as long as anther . . . . . **4. section *Chamaephyta***
- 13 Leaves variable in size usually with at least some longer than 10 mm; if caespitose, or with all leaves less than 10 mm, then with a clearly serrulate leaf margin
- 15 Corolla wide campanulate, anthers exaristate . . . . . **3. section *Amblyandra***
- 15 Corolla urceolate, cylindrical or cylindrical-campanulate; anthers with or without awns . . . . . **6. section *Monoanthemona***

### 1. Section *Gaultheria*

SYNONYM: Section *Eugaultheria* Airy-Shaw series *Procumbentes* Airy-Shaw (1940).

Plant prostrate, branch tips growing upward. Few pilose hairs on leaves and stems, multicellular hairs only on leaf margin. Leaf nervation pinnate. Leaves 20–60 mm long, 10–30 mm broad; apex obtuse to rounded, base cuneate. Flowers pentamerous, solitary in the axils of the leaves. Pedicel pilose. No bract, 2 bracteoles opposite immediately beneath the calyx. Calyx lobes ciliate. Corolla urceolate, pilose inside. Filament *c.* 4 mm long; densely pilose; papillose. Anthers *c.* 1.5 mm long with 2 long reflexed awns per locule. Ovary superior, glabrous. Fruit a capsule but persistently slightly fleshy and not fully dehiscent; calyx lobes becoming fleshy and surrounding the capsule. North America.

TYPE: *Gaultheria procumbens* L.

This is the type section of the genus and contains the single isolated species *G. procumbens*. Airy-Shaw (1940) placed this species in the series *Procumbentes* of the section *Eugaultheria* (*Gaultheria* in modern nomenclature) which also contained the series *Trichophyllae* and *Hispidulae*. I have separated these latter two series into another section, *Chiogenopsis*. *Gaultheria procumbens* differs from series *Trichophyllae* and *Hispidulae* in general appearance, larger leaves, urceolate flowers (although see *G. cardiosepala* Hand.-Mazz.), pilose filaments, pilose inside of the corolla, ciliate calyx margin and by having all flower parts much larger. In anatomy, it differs by having a local hypodermis, whereas it is absent altogether in the other two series, and in the strong development of marginal sclerenchyma fibres, a character scarce in the genus as a whole. Airy-Shaw (1940) suggested his section *Eugaultheria* may be diphyletic. He noted that *G. procumbens* appeared to be most closely related to *G. miqueliana* Takeda and that the rest of the section appeared to have its origins in species such as *G. cuneata* Bean and *G. prostrata* W. W. Smith. In both cases the resemblances are superficial. In fact it is difficult to trace clearly the origins of *G. procumbens* from any of the racemose groups in the genus.

It is more interesting cytologically because the single species exhibits a number of different ploidy levels, and possibly different base chromosome numbers (Middleton & Wilcock, 1990b).

## 2. Section *Chiogenopsis* Middleton, **sect. nov.**

SYNONYM: Section *Eugaultheria* Airy-Shaw (1940), *pro parte*. Pedicelli apicaliter bibracteolati, bracteolae oppositae. Flores solitarii. Corolla intra et filamenta glabra. Folia penninervia usque 10 (–15)mm lata.

TYPE: *Gaultheria hispidula* (L.) Muhlenb.

Plants creeping, prostrate or erect. Stems and leaves glabrous or pilose and/or with short strigose hairs on stems and underside of leaves. Leaf nervation pinnate. Flowers solitary, in a pseudoraceme or not in successive leaf axils. Bracts absent; bracteoles 2 opposite, immediately beneath the calyx. Corolla urceolate or campanulate, glabrous outside and inside. Filament basally dilated, papillose, glabrous. Fruit a capsule either with a fleshy accrescent calyx or with the floral axis fleshy and the calyx lobes unchanged.

This section includes the series *Trichophyllae* and *Hispidulae* of Airy-Shaw's section *Eugaultheria*. The reasons for removing them from that section are discussed above. The name of the section is derived from the genus *Chiogenes* Salisb., now recognized as *G. hispidula* (L.) Muhlenb. of series *Hispidulae*. Two new series are also included in this section.

- 1 Flowers tetramerous, plants very small, creeping . . . **series Hispidulae**
- 1 Flowers pentamerous
  - 2 Plants erect; flowers in terminal pseudoracemes **series Novaguineenses**
  - 2 Plants prostrate; flowers not in terminal pseudoracemes
    - 3 Ovary glabrous; East Himalayas and South-West China . . . . .  
**series Trichophyllae**
    - 3 Ovary pilose; Sumatra . . . . . **series Pernettyoideae**

**Series *Trichophyllae*** Airy-Shaw, *Kew Bulletin*, 1940: 308 (1940).

SYNONYM: Section *Eugaultheria* series *Trichophyllae* Airy-Shaw (1940).

Plant prostrate. Leaves 2–20 mm long, 1–9 mm broad. Flowers pentamerous not in a pseudoraceme. Corolla usually campanulate, rarely urceolate. Anthers with awns. Ovary superior, glabrous. Fruit a capsule with a fleshy accrescent calyx. E. Himalayas and S.W. China.

TYPE: *Gaultheria trichophylla* Royle.

SPECIES INCLUDED: *G. cardiosepala* Hand.-Mazz., *G. dolichopoda* Airy-Shaw, *G. hypochlora* Airy-Shaw, *G. nana* Wu & Hsu, *G. nivea* (Anth.) Airy-Shaw, *G. sinensis* Anth., *G. thymifolia* Stapf, *G. trichophylla* Royle.

This series contains a group of closely allied species from the eastern Himalayas and south-west China. Airy-Shaw (1940) noted that the knowledge of this group of plants is far from satisfactory. He gave a key for seven species, and since then Hsu (1981) has described a new species attributable to this group. From my observations of the species in this group it is clear that the species are in need of revision. There appear to be more species than the number of published

names, particularly amongst those plants which previous workers have ascribed to *G. trichophylla* Royle. *Gaultheria nana* C. Y. Wu & T. Z. Hsu, recently described, is only dubiously distinct from *G. sinensis* Anthony. *Gaultheria sinensis* and *G. hypocholora* Airy-Shaw are not always easily separated on morphological characters.

Anatomically, this series is characterized by a weak or absent hypodermis, weak or absent adaxial sclerenchyma, no free fibres and usually having pith of small, thick-walled cells.

The chromosome number is known for only one species, *G. thymifolia*,  $2n = 44$  (Middleton & Wilcock, 1990b).

**Series *Hispidulae*** Airy-Shaw, *Kew Bulletin*, 1940: 308 (1940).

SYNONYM: Section *Eugaultheria* series *Hispidulae* Airy-Shaw (1940).

Plant creeping. Leaves 2–10 mm long, 1–7 mm wide. Flowers tetramerous not in a pseudoraceme. Corolla campanulate. Anthers exaristate or with minute projections. Ovary superior or semi-inferior. Fruit a capsule with a fleshy floral axis and unchanged calyx lobes. N. America, Japan, Himalayas.

TYPE: *Gaultheria hispidula* (L.) Muhlenb.

SPECIES INCLUDED: *G. hispidula* (L.) Muhlenb., *G. suborbicularis* W. W. Smith.

This series contains the old genus *Chiogenes* Salisb., which is now treated as *G. hispidula*, and *G. suborbicularis* W. W. Smith, the species which links this series to series *Trichophyllae*. The similarities with series *Trichophyllae* are quite marked, particularly in flower shape, stamen structure, indumentum and many aspects of anatomy. The differences from series *Trichophyllae* are particularly in habit, leaf size and shape and the number of floral parts.

*Gaultheria hispidula* contains methyl salicylate, a chemical which has been discovered in series *Trichophyllae* in *G. trichophylla* (Towers, Aide Tse & Maas, 1966).

Airy-Shaw suggested that this series represented at once the most reduced and the most advanced type within the genus.

The chromosome number of *G. suborbicularis* is unknown. Chromosome numbers of  $2n = 24$  and  $2n = 22$  have been reported from *G. hispidula* (Löve & Löve, 1973; Middleton & Wilcock, 1990b).

**Series *Novaguineenses*** Middleton, **ser. nov.**

Frutex erectus. Folia 10–21 mm longa, 5–9(–15) mm lata. Flores pentameri in pseudoracemis dispositi. Corolla urceolata. Antherae biaristatae. Ovarium superum.

TYPE: *Gaultheria novaguineensis* J. J. Smith.

Plant erect. Leaves 10–21 mm long, 5–9(–15) mm broad. Flowers pentamerous in a pseudoraceme. Corolla urceolate. Anthers with two awns per anther locule. Ovary superior. Fruit a capsule with a swollen accrescent calyx. New Guinea.

Airy-Shaw (1940) included *G. novaguineensis* in his section *Leucothoides* despite the fact that this section was characterized by having perulate racemes. *Gaultheria novaguineensis* clearly has solitary flowers in a terminal pseudoraceme. In this



character and in bracteole position, leaf shape and size and some aspects of leaf anatomy it is similar to series *Trichophyllae*. It differs in its erect habit, urceolate flowers (although *G. cardiosepala* also has urceolate flowers), position of the flowers and filament shape and size. It is found only in New Guinea, a considerable distance away from the range of series *Trichophyllae* (although cf. series *Dumicolae* of section *Brossaeopsis*).

No details of its chemistry are known except that it smells of wintergreen oil. No chromosome numbers have been reported from this series.

**Series *Pernettyoideae* Middleton, ser. nov.**

Suffrutex prostratus. Folia 8–13 mm longa, 2.0–3.5 mm lata. Flores pentameri, non in pseudoracemis dispositi. Corollae ignotae. Filamenta ignota. Ovarium superum, pilosum.

TYPE: *Gaultheria pernettyoides* Sleum.

Plant prostrate. Leaves 8–13 mm long, 2.0–3.5 mm broad. Flowers pentamerous, not in a pseudoraceme. Floral characters unknown. Ovary superior, pilose. Fruit a capsule with a fleshy accrescent calyx. Sumatra.

This species is superficially quite similar to *G. novaguineensis* and also occurs in Malasia. The most obvious difference is that *G. pernettyoides* is reported to be prostrate (Sleumer, 1967). However, the plant has only been collected twice and there is no information available in the literature on flower characteristics. The leaf anatomy is unusual in this section by having numerous free fibres in the mesophyll. Stevens (1969) indicated that the leaf anatomy, bracteole position and aspects of its general appearance coupled with the fact that no floral information was available, may mean that this species was in fact a species of *Diplycosia*. However, this is not certain and the position of *G. pernettyoides* remains uncertain until flowers are discovered. In the meantime its general characteristics are compatible with those of section *Chiogenopsis* and different enough from the other series, especially in leaf anatomy to warrant serial treatment. Further information may well affect this taxonomic treatment.

**3. Section *Amblyandra* Airy-Shaw, *Kew Bulletin*, 1940: 308 (1940).**

Plant prostrate. Stems and leaves glabrous or with fine spreading eglandular or glandular hairs. Leaf nervation pinnate. Leaves 4–35 mm long, 4–25 mm broad; base weakly cordate to obtuse, apex acuminate to rounded. Flowers pentamerous, solitary or rarely a few flowered raceme. Several bracteoles along pedicel but not immediately beneath the calyx. Corolla campanulate, glabrous. Filament dilated at the base, papillose, glabrous. Anthers exaristate. Ovary superior, glabrous. Fruit a capsule with a fleshy accrescent calyx. North America, Japan.

TYPE: *Gaultheria humifusa* (Grah.) Rydb.

SPECIES INCLUDED: *G. adenostrix* (Miq.) Maxim., *G. humifusa* (Graham) Rydb., *G. ovatifolia* Gray.

This section remains unchanged from that proposed by Airy-Shaw (1940). Airy-Shaw believed that this was a small isolated group of species showing a simplified type of anther structure and solitary flowers. However, he did not tackle the numerous solitary flowered species which occur elsewhere in the range

of *Gaultheria*, particularly South America, and so did not have problems circumscribing this group. Indeed, the only other solitary flowered species without apical bracteoles in the area he covered are *G. nummularioides* D. Don and *G. mundula* F.v.M. The former he recognized as a series of section *Brossaeopsis* and suggested it may represent a link between these two sections and the latter he simply included in his section *Leucothoides* drawing no attention to its solitary flowers at all (*G. mundula* actually keys out under section *Amblyandra* in the key he provided). I have studied all these solitary flowered species and still agree that *Amblyandra* is distinct and isolated. The reasons for this are that the species of this section have campanulate flowers, exaristate and basally dilated stamens and large leaves for solitary flowered species. Anatomically they have a very distinctive marginal sclerenchyma band (a 'Randbast') and *G. humifusa* also has adaxial stomata. These characters as a whole, or in part in some cases, serve to distinguish these species from sections *Pernettya*, *Gymnocaulos* and *Monoanthe mona*.

The distinction from section *Chamaephyta* is not so easily argued. In size of vegetative parts the two sections differ quite strikingly, section *Chamaephyta* having extremely reduced habit and leaf size, so that on first appearance they appear quite different. However, in leaf anatomy and in corolla shape the two sections overlap. Both sections have the 'Randbast' and *G. antarctica* Hook. fil. shares the campanulate corolla. *Gaultheria nubicola* Middleton has exaristate anthers although it has an urceolate corolla (Sleumer, 1985). Both species of section *Chamaephyta* have adaxial stomata as in *G. humifusa*. However, the size differences, the indumentum characters, the habit and to an extent the disjunct distribution lead me to conclude that the two sections should be kept separate.

All three species of section *Amblyandra* have catechol (Towers, Aide Tse & Maas, 1966). This chemical has not been detected anywhere else in the genus although the species of section *Chamaephyta* have not been surveyed. Salicylic acid has not been detected in this section.

The chromosome number is known only for one species,  $2n = 22$  for *G. adenothrix* (Middleton & Wilcock, 1990b).

#### **4. Section *Chamaephyta* Middleton, sect. nov.**

Suffrutex caespitosus. Folia glabra, 3–8 mm longa, 1.5–4.0 mm lata, integra. Flores pentameri, solitarii. Pedicelli pluribracteolati (raro basaliter bibracteolati). Ovarium superum.

TYPE: *Gaultheria antarctica* Hook. fil.

Plants caespitose. Leaves glabrous; 3–8 mm long, 1.5–4.0 mm broad; entire or only obscurely serrulate; base obtuse, apex obtuse to acute. Flowers pentamerous, solitary, not in a pseudoraceme. Bracteoles several (rarely 2 basal). Ovary superior. Temperate South America, New Zealand.

This section consists of just two species in two series and is distinguished from section *Gymnocaulos* in the number of floral parts, stamen structure and leaf anatomy although all the species from these two sections have adaxial stomata. *Chamaephyta* can be distinguished from section *Monoanthe mona* on habit, leaf size, stamen structure and particularly leaf anatomy.

In leaf anatomy both species are particularly characterized by a combination of adaxial leaf stomata and marginal sclerenchyma, found elsewhere in *Gaultheria* only in *G. humifusa* of section *Amblyandra*.

1 Corolla campanulate, anthers with tiny projections; Tierra del Fuego .

**series *Antarcticae***

1 Corolla urceolate, anthers exaristate; New Zealand **series *Nubicolae***

**Series *Antarcticae* Middleton, ser. nov.**

Ramuli hirsuti. Corolla campanulata, glabra. Filamenta basaliter dilatata. Antherae cum breviter aristatae. Ovarium superum, pilosum.

TYPE: *Gaultheria antarctica* Hook. fil.

Stems hirsute. Corolla campanulate, glabrous. Filament basally dilated. Anthers with minute projections. Ovary superior, pilose. Fruit a capsule with a fleshy calyx. Temperate South America.

This series contains only the species *G. antarctica* which is found in Tierra del Fuego. In general appearance it looks somewhat like *G. caespitosa* Poepp. & Endl. It is reported to hybridize with *G. pumila* (L. fil.) Middleton. It is distinguished from series *Nubicolae* in indumentum, corolla shape and stamen structure.

**Series *Nubicolae* Middleton, ser. nov.**

Ramuli glabri vel pilosi. Corolla urceolata, intra parce pilosa. Filamenta linearia. Antherae exaristatae. Fructus ignotus.

TYPE: *Gaultheria nubicola* Middleton.

Stems glabrous or pilose. Corolla urceolate, inside sparsely pilose. Filament linear. Anthers exaristate. Fruit characters unknown. New Zealand.

This contains the single species *G. nubicola* Middleton which was formerly *Pernettya alpina* D. Franklin. I have separated this species from the other species of section *Pernettya* because it has more similarities, particularly in leaf anatomy, with *G. antarctica*. Very little material is available for study and I have seen no flowering specimens. No fruiting material has been seen by me or by Dr Sleumer (Personal communications) and no mention of fruits is recorded in the literature. Discovery of its fruits may cause the taxonomic treatment of *G. nubicola* to be reviewed.

*Gaultheria nubicola* differs enough from *G. antarctica* to deserve serial status. From the literature, it is reported to have urceolate flowers, a different filament type and exaristate anthers.

**5. Section *Gymnocaulos* Middleton, sect. nov.**

Suffrutex caespitosus. Folia 2–4 mm longa, *c.* 1.5 mm lata,  $\pm$  integra. Flores tetrameri, solitarii. Pedicelli basaliter bibracteolati. Corolla campanulata. Filamenta filiforma, multo longiora quam antherae. Antherae exaristatae. Ovarium superum.

TYPE: *Gaultheria caespitosa* Poepp. & Endl.

Plants caespitose. Leaves 2–4 mm long, *c.* 1.5 mm broad; base cuneate, apex acute; short hairs on margin; more or less entire. Flowers tetramerous (rarely pentamerous), solitary. Bracteoles 2 basal. Corolla campanulate, glabrous. Filament filiform, much longer than the anthers; only sparsely and obscurely papillose. Anthers exaristate. Ovary superior, glabrous. Fruit a capsule with a fleshy accrescent calyx. Temperate South America.

This section has only one species, *G. caespitosa*. Its general appearance is

somewhat like section *Chamaephyta* but it differs in the number of floral parts, stamen structure, lack of papillae on the filament, number of bracteoles and in leaf anatomy. Its affinities are more likely to be with section *Monoanthe mona* although again it differs quite considerably. *Gaultheria caespitosa* has much smaller habit and leaves than any species in section *Monoanthe mona*. It is also different in its tetramery, campanulate flowers, extremely long filament, lack of filament papillae, complete lack of a hypodermis, lack of adaxial sclerenchyma and in the possession of adaxial stomata.

### 6. Section *Monoanthe mona* Middleton, **sect. nov.**

Suffrutices prostrati vel erecti. Folia plus quam 10 mm longa, serrulata. Flores pentameri, solitarii (raro in racemis). Pedicelli pluribracteolati vel basaliter bibracteolati semper a calyce distantes. Corolla urceolata vel cylindrica-campanulata.

TYPE: *Gaultheria antipoda* Forst. fil.

Plants prostrate or erect. Leaves mostly more than 10 mm and up to 50 mm long, distinctly serrulate. Flowers pentamerous, solitary with 2 basal, or several, bracteoles which are never apical. Corolla urceolate or cylindric-campanulate. Filament variable in shape, dilated at the base or not. Anthers mostly awned or with minute projections; sometimes with a terminal tubule and then exaristate or muticous. Ovary superior. Fruit a capsule, usually with a fleshy accrescent calyx, occasionally remaining unchanged. South America, New Zealand, Tasmania, Malesia, Himalayas.

This is a large section which contains most of the solitary flowered species without apical bracteoles. *Monoanthe mona* is extremely variable in the attributes of its constituent species and extremely widespread in its geographical distribution. Series *Antipodae* alone occurs in Malesia, Australasia and South America.

There are two species in this section which sometimes have racemes. *Gaultheria phillyreifolia* (Pers.) Sleum. and *G. oreogena* A. C. Smith. In both cases solitary flowers are more numerous. I have seen no racemose material of *G. oreogena* but it is reported (Luteyn, personal communication) that individuals occur where there are up to three flowered racemes occurring on the same plant as solitary flowers. In all other respects it is a typical member of this section related to the *G. buxifolia* Willd. group. *Gaultheria phillyreifolia*, on the other hand, occasionally produces plants with all flowers in few flowered racemes. Again this species more often has solitary flowers and in many respects is similar to *G. tenuifolia* which invariably has solitary flowers. It is certainly very unlike the South American species of section *Brossaea*.

- 1 Corolla cylindric or cylindric-campanulate; bracteoles frequently only 2, basal; some species with a terminal tubule on the anther; awns minute projections or absent; S.E. Brazil. **series Myrtilloideae**
- 1 Corolla urceolate; bracteoles usually several; no terminal tubule on the anther and frequently awns present
  - 2 Plant creeping, stem with broad, flat strigose hairs; anthers clearly awned, ovary glabrous; Himalayas to Malesia . . . . .  
**series Nummularioideae**

- 2 Plant erect or prostrate; stems glabrous, strigose (without broad, flat hairs) or hirsute; anthers with or without awns; ovary glabrous or pilose; Malesia, Australasia and western South America .

**series *Antipodae***

**Series *Antipodae* Middleton, ser. nov.**

Suffrutices prostrati vel erecti. Indumentum variabile. Pedicelli plerumque pluribracteolati. Corolla urceolata. Antherae sine tubulis, cum vel sine aristis. Fructus cum calycis lobis carnosus.

TYPE: *Gaultheria antipoda* Forst. fil.

Plants prostrate or erect. Indumentum variable but not of broad flat strigose hairs. Leaves 3–45 mm long, 3–30 mm broad, occasionally mucronate at the tip. Flowers usually solitary with several bracteoles (sometimes 2 basal). Flowers occasionally in a few flowered true raceme and then with 2 basal bracteoles. Corolla urceolate; glabrous or pilose inside. Anthers without a tubule; mostly awned, sometimes with minute projections, rarely exaristate. Ovary glabrous or pilose. Fruit a capsule with a fleshy accrescent calyx. Western South America, New Zealand, Tasmania, New Guinea.

SPECIES INCLUDED: *G. amoena* A. C. Smith, *G. anastomosans* H.B.K., *G. antipoda* Forst. fil., *G. buxifolia* Willd., *G. depressa* Hook. fil., *G. foliolosa* Benth., *G. mundula* F. v. M., *G. oreogena* A. C. Smith, *G. phillyreifolia* (Pers.) Sleum., *G. stereophylla* A. C. Smith, *G. tenuifolia* (Phil) Sleum., *G. vaccinioides* Griseb.

This is the largest series in the section and includes *G. mundula* from New Guinea, *G. antipoda* Forst. fil. and *G. depressa* Hook. fil. from Australasia and all the solitary flowered species from western South America except *G. caespitosa*, *G. antarctica* and section *Pernettya*. It is tempting to conclude that the Australasian and Malesian species should be attributable to another series but it is impossible to do so without using geographical data to the exclusion of morphological and anatomical evidence. The series is very variable in indumentum type, stamen structure and leaf size and shape but there are no strong disjunctions. The similarity between *G. mundula* of New Guinea and *G. antipoda*/*G. depressa* of Australasia has been noted previously (Sleumer, 1966). There is also a striking similarity in overall appearance between *G. mundula* and species from South America such as *G. anastomosans* H.B.K. Indeed the most distinctive species in this series are *G. phillyreifolia* and *G. tenuifolia* (Phil.) Sleum. both from temperate South America. Both species have a mucronate leaf tip, markedly serrate leaves, strongly dilated filaments and short awns. In many respects the variation encountered in this series, particularly in leaf shape, is paralleled in section *Pernettya*. All the species have urceolate corollas, very occasionally with five rows of setose hairs. *Gaultheria mundula*, *G. antipoda* and a number of South American species also sometimes form pseudoracemes.

There have been many species, attributable to this series, described from tropical South America. However, Luteyn (personal communication), will reduce the number of species from this area to around seven in his revision for Flora Neotropica.

Anatomically the series is very variable in pith type, presence of a hypodermis,

adaxial sclerenchyma, presence of fibres in the mesophyll and stomatal type. This variation is often seen within a single species.

Chemically this series is not well known. *Gaultheria antipoda* and *G. depressa* both have dihydroquercetin but this has not been detected in *G. mundula*, *G. foliolosa* Benth. or *G. tenuifolia*. Salicylic acid has been detected in *G. tenuifolia*. Apart from a trace amount in *G. nummularioides* var. *elliptica* Rehd. & Wils., it is unknown anywhere else in the section.

Chromosome numbers are known only for *G. antipoda*,  $2n = 22$  (see Middleton & Wilcock, 1990b).

**Series *Myrtilloideae* Middleton, ser. nov.**

Suffrutices prostrati vel erecti. Rami glabri vel dense hirsuti. Flores solitarii interdum in pseudoracemis dispositi. Pedicelli plerumque basaliter bibracteolati. Corolla cylindrica, extra glabra, intra pilosa. Antherae cum tubulis exaristatae vel breviter aristatae.

TYPE: *Gaultheria myrtilloides* Cham. & Schlecht.

Plants prostrate or erect. Stems and other plant parts glabrous or dense long hirsute. Flowers solitary, sometimes in a pseudoraceme. Bracteoles usually 2 basal (sometimes up to 5). Corolla cylindrical; glabrous outside, pilose inside. Anther with a tubule, this long or quite short; usually exaristate, sometimes with minute projections. Ovary pilose or glabrous. Fruit a capsule with or without a fleshy accrescent calyx. South-east Brazil.

SPECIES INCLUDED: *G. braedeana* Sleum., *G. itatiaiae* Wawra ex Drude, *G. myrtilloides* Cham. & Schl., *G. sleumeriana* Kinosh.-Gouvêa, *G. ulei* Sleum.

This is the most distinct series in this section. It comprises five species from S.E. Brazil. All five species are very distinct from one another but are linked by a number of unusual characters. They all have cylindrical (cylindric-campanulate or cylindric-urceolate) corollas and longer than usual anther tubules for *Gaultheria*. Indeed the tubules of *G. itatiaiae* Wawra. ex Drude and *G. sleumeriana* Kinoshita-Gouvêa are more like those of *Diplycosia* Bl. than of *Gaultheria*. Unlike *Diplycosia*, these tubules sometimes have minute projections. There is also a tendency in the group to form terminal pseudoracemes which is so extreme in *G. sleumeriana* that it takes careful study to realize that the 'raceme' is in fact produced only by the leaves subtending the axillary flowers becoming progressively smaller and bract like. *Gaultheria itatiaiae* and *G. ulei* Sleum. have similar but somewhat less advanced inflorescence types. Four of the species have only two basal bracteoles unlike most of the solitary flowered species. *Gaultheria braedeana* Sleum. from the inadequate material I have seen appears to have several near the base. I have been unable to study any flowers of this species but Sleumer (1952) has argued that it is a species related to *G. ulei*. If this is so it may form a link with series *Antipodae*. Sleumer (1952) suggested these species (i.e. the Brazilian solitary flowered species) could be placed in Airy-Shaw's section *Amblyandra* but commented on the fact that they readily hybridized with Brazilian racemose species which he said could be included in section *Leucothoides*.

The fruits of *G. itatiaiae* are completely dry with an unchanged calyx. This is

the only species of the section not to have a fleshy calyx in the fruit although the fruits of *G. sleumeriana* are unknown.

Chemical and cytological information is not available for these species. Anatomically the four species which have been studied all lack a complete hypodermis and the adaxial sclerenchyma is consistently well developed.

**Series *Nummularioideae*** Airy-Shaw, *Kew Bulletin*, 1940: 308 (1940)

SYNONYM: Section *Brossaeopsis* series *Nummularioideae* Airy-Shaw (1940).

Formerly a series of section *Brossaeopsis*. Plant creeping. Stems with broad flat strigose hairs. Flowers solitary, not in a pseudoraceme. Bracteoles several. Corolla wide urceolate; glabrous outside, pilose inside. Filament papillose, pilose. Awns long. Ovary glabrous. Fruit a dry capsule with a fleshy accrescent calyx. Malesia, Himalayas.

TYPE: *G. nummularioides* D. Don.

This is a monospecific series which is difficult to separate from series *Antipodae*. Airy-Shaw (1940) placed this series in section *Brossaeopsis*, describing it as an apparently successful type derived from the unsuccessful series *Dumicolae* that may provide a link between this section and section *Amblyandra*. I do not agree with this interpretation. Airy-Shaw's study did not include the wealth of solitary flowered species found in South America. It is certainly difficult not to be impressed by the similarity between these species across such a wide geographical area but it is distinctive. It has a characteristic indumentum type and a very wide urceolate, almost campanulate, corolla. It has dihydroquercetin like *G. antipoda* and *G. depressa* and salicylic acid has been detected in trace amounts in var. *elliptica*. Perhaps the most striking feature of this species is its stomata. It is unique in *Gaultheria* in consistently having only anomocytic stomata. The only other species in which I am aware of this in the *Gaultheria* group is in *Zenobia pulverulenta* (Bartr.) Pollard.

The chromosome number has been found to be  $2n = 44$  (Middleton & Wilcock, 1990b).

## **7. Section *Pernettya*** (Gaud.) Middleton, **stat. nov.**

SYNONYM: *Pernettya* Gaudichaud in Mirbel, *Ann. Sci. Nat. (Paris)*, 5: 102 (1825).

SYNONYM: section *Archipernettya* Sleumer (1935).

Plant dioecious, gynodioecious or hermaphrodite; prostrate or erect. Stems and leaves glabrous, weakly pilose and/or hirsute or strigose. Leaves 2–25 mm long, 0.5–12 mm wide; pinnate or with only the midrib clearly visible; base truncate to cuneate, apex rounded to acuminate, sometimes mucronate; serrulate or (sub)entire. Flowers solitary sometimes in a pseudoraceme. Bracteoles usually several remote from the calyx. Corolla urceolate, sometimes wide urceolate approaching campanulate. Filament linear or dilated at the base; glabrous or pilose; papillose. Anthers awned, with minute projections or exaristate. Ovary superior, glabrous. Fruit a berry, sometimes quite thin walled; calyx usually unchanged in fruit, sometimes slightly or highly swollen and

surrounding the base of the berry. Western South America, Central America, New Zealand, Tasmania.

TYPE: *Gaultheria pumila* (L. fil.) Middleton.

SPECIES INCLUDED: *G. howellii* (Sleumer.) Middleton, *G. lanceolata* Hook. fil., *G. macrostigma* (Colenso) Middleton, *G. marginata* (N. E. Brown) Middleton, *G. mucronata* (L. fil.) Hook. & Arn., *G. myrsinoides* H.B.K., *G. parvula* Middleton, *G. poeppigii* DC., *G. purpurascens* H.B.K., *G. racemulosa* (DC.) Middleton, *G. pumila* (L. fil.) Middleton, *G. tasmanica* (Hook. fil.) Middleton.

The status of the genus *Pernettya* has already been discussed by Middleton & Wilcock (1990a) with the conclusion that *Pernettya* cannot be maintained as a separate genus.

Within the old genus, I agree with the limits of the sections proposed by Sleumer (1935, 1985), except that I have removed *G. nubicola* to section *Chamaephyta*. The two sections, *Pernettya* and *Pseudogaultheria*, are quite distinct in a number of characters including inflorescence, size, indumentum and anatomy. Within section *Pernettya* Sleumer (1935) recognized three series: *Pumilae*, *Purpureae* and *Mucronatae*. In his updated revision of 1985 he preferred to make these informal groups. I agree with this later position because these groups may not be natural. His 1935 series *Pumilae* contained two species, *P. pumila* L. fil. and *P. leucocarpa* DC. In his 1985 work *P. leucocarpa* had been made a variety of *P. pumila*. *Pernettya pumila* is here treated as *G. pumila* (L. fil.) Middleton and is the most distinct of section *Pernettya*. However, it does have many characters overlapping with other species and is unique only in its total lack of adaxial sclerenchyma. Series *Purpureae* and *Mucronatae* are certainly unnatural groups. There are many similarities between *G. poeppigii* and *G. mucronata* which are representatives of each series respectively. They have a similar morphology (except the mucronate leaf tip), anatomy, chromosome number and chemistry and I believe they are closely related. There is much more of a gap between all the South American species of *Purpureae-Mucronatae* on the one hand and the species from Tasmania and New Zealand, which were all placed in series *Purpureae*, on the other. However, even this difference is not particularly great and is largely only in habit.

I therefore conclude that this section cannot be divided into natural series.

Hydroquinone has been detected in *G. mucronata* and *G. poeppigii* alone of the species in the *Gaultheria* group. Dihydroquercetin has also been detected in these two species as well as in other species of *Gaultheria* and *Leucothoe*.

The chromosome number is known for a number of species all of which are based on  $x = 11$ . Diploids, tetraploids and hexaploids are known (Middleton & Wilcock, 1990b).

### 8. Section *Pseudogaultheria* (Sleumer) Middleton, **comb. nov.**

SYNONYM: *Pernettya* Gaud. section *Pseudogaultheria* Sleumer (1935).

Plant dioecious, erect. Stems pilose and strigose. Leaves glabrous or setulose beneath; nervature pinnate; 25–100 mm long, 12–40 mm wide; base truncate to cuneate, apex acute to acuminate, slightly mucronate; margin weakly serrulate. Flowers pentamerous in axillary racemes. Bract short, 2–4 mm long. Bracteoles



2, opposite, basal. Corolla urceolate; glabrous outside, pilose inside. Filament dilated at the base, papillose, glabrous. Anthers with minute projections. Ovary superior, glabrous. Fruit a berry with calyx becoming slightly fleshy. Temperate South America.

TYPE: *Gaultheria insana* (Molina) Middleton.

*Gaultheria insana*, the only species in this section, was first described as *Hippomanica insana* Molina in 1810 and transferred to *Pernettya insana* (Molina) Gunckel in 1972 (Sleumer, 1985). However, it is still more commonly known as *P. furiens* which is a later synonym.

Sleumer placed this species in his monospecific section *Pseudogaultheria* of the genus *Pernettya* (Sleumer, 1935, 1985). It differs from section *Pernettya* in the same way that section *Brossaea* differs from section *Monoanthea*, primarily in the nature of the inflorescence and the size of the leaves. As mentioned above it also differs in indumentum and aspects of its anatomy.

Stevens (1969) likened *G. insana* (which he referred to as *P. furiens*) to the South American racemose species. There are, however, an enormous number of differences between these two groups and the similarities are quite superficial.

*Gaultheria insana* has strongly heterogeneous pith, strong adaxial sclerenchyma, a complete hypodermis, abundant free fibres in the mesophyll and paracytic stomata.

Two different chromosome numbers have been discovered for *G. insana*. Callan (1941) found a chromosome number of  $2n = 66$  and I have twice counted this species at  $2n = 44$  (Middleton & Wilcock, 1990b).

### 9. Section *Brossaeopsis* Airy-Shaw, *Kew Bulletin*, 1940: 307 (1940).

Stems glabrous, punctate or hirsute. Leaves glabrous, punctate or hirsute beneath; nervature melastomataceous; 13–185 mm long, 7–110; mm wide; base cordate to cuneate, apex obtuse to acuminate; serrulate. Inflorescence a perulate raceme which may be so short as to appear fasciculate. Bracts 2 basal. Fruit a capsule with a fleshy accrescent calyx. Himalayas, Malesia.

TYPE: *Gaultheria dumicola* W. W. Smith.

This section remains much the same as that proposed by Airy-Shaw with the exception of series *Nummularioideae* which has been removed to section *Monoanthea*. *Gaultheria nummularioides* was the oldest name of the species he placed in *Brossaeopsis* but he did not designate a type for the section. Therefore it avoids confusion to retain the name *Brossaeopsis* for the remainder of the section, designating *G. dumicola* as the type, rather than to transfer the name *Brossaeopsis* with *G. nummularioides* to the solitary flowered species.

Airy-Shaw (1940) suggested that this section represented an ancient and unsuccessful type. This conclusion was reached primarily because of the widespread but fragmentary distribution of the section and the relative scarcity of its component species.

Airy-Shaw (1940) also believed that section *Brossaeopsis* was closely related to the South American racemose species, hence the name. I disagree with this and believe that the South American species are much more closely related to the Asian and Australasian racemose species other than *Brossaeopsis*.

No chemical data or chromosome numbers are known for any species in this section. In anatomy the species so far studied are all very similar. They all have a similar type of pith, an entire hypodermis, well-developed adaxial sclerenchyma and no free fibres. *Gaultheria codonantha* Airy-Shaw is somewhat different in having completely paracytic stomata.

Airy-Shaw divided the section into three series. One, *Nummularioideae*, has been removed from this section. The other two series, *Dumicolae* and *Atjehenses*, are recognized here with the only difference being that *G. codonantha* is removed from the series *Dumicolae* to form a new series *Codonanthae*.

- 1 Corolla urceolate; inside of corolla and filaments pilose  
**series *Atjehenses***
- 1 Corolla campanulate; inside of corolla and filaments glabrous
  - 2 Raceme very short appearing fasciculate; corolla c.5 mm long  
**series *Dumicolae***
  - 2 Raceme longer than pedicel lengths; corolla more than 10 mm long  
**series *Codonanthae***

**Series *Codonanthae* Middleton, ser. nov.**

Frutex erectus. Folia 67–185 mm longa, 40–110 mm lata. Flores in racemis axillaribus dispositi aspectum fasciculorum non habent. Corolla campanulata, 9–14 mm longa, glabra. Filamenta papillosa, glabra, plus quam 3 mm longa.

TYPE: *Gaultheria codonantha* Airy-Shaw.

Plant erect. Leaves 67–185 mm long, 40–110 mm broad. Flowers in axillary racemes to 45 mm long. Corolla campanulate 9–14 mm long, glabrous. Filament papillose, glabrous, over 2.5 mm long. Anther with awns over 1 mm long. Ovary glabrous. Fruit a capsule with a fleshy accrescent calyx. Himalayas.

Airy-Shaw (1940) included the sole species in this series, *G. codonantha*, in series *Dumicolae*. He described it as probably the nearest known species to the prototype of the genus since, apart from the short raceme rachis, it has very little specialization in any other characters.

It is, however, very different from the other species of series *Dumicolae*. The rachis is considerably longer and all the floral parts are very much larger, the largest flowers in the genus. It is also the only species in section *Brossaeopsis* to have completely paracytic stomata.

**Series *Dumicolae* Airy-Shaw, *Kew Bulletin*, 1940: 307 (1940).**

Plant erect. Leaves 18–150 mm long, 9–90 mm wide. Flowers in very short axillary racemes appearing like fascicles. Corolla campanulate c.5 mm long; glabrous. Filament weakly basally dilated; papillose; glabrous. Anther awned. Ovary glabrous or pilose. Himalayas, Malesia.

TYPE: *Gaultheria dumicola* W. W. Smith.

SPECIES INCLUDED: *G. abbreviata* J. J. Smith, *G. dumicola* W. W. Smith, *G. kemiriensis* Sleum., *G. losirensis* Sleum., *G. notabilis* Anth., *G. seshagiriana* Subbarao & Kumari.

This series is as defined by Airy-Shaw with the exclusion of *G. codonantha* and the inclusion of *G. seshagiriana* Subbarao & Kumari, *G. losirensis* Sleum. and *G. kemiriensis* Sleum.

Airy-Shaw (1940) noted the occurrence of *G. notabilis* Anth. from this series in Sumatra whereas the other species of the series were Himalayan. Since then there has been one new species from the Himalayas and two from Sumatra. Despite this large disjunction the similarities within the group are quite striking.

All the species have extremely short racemes which appear fasciculate. It then becomes difficult to tell the perules, bracts and basal bracteoles apart. All the species also have relatively large leaves, over 150 mm occasionally in *G. dumicola*, small campanulate corollas and reduced floral parts in general. In all the specimens I have seen the filaments and inside of the corolla have been glabrous, which agrees with the description given by Airy-Shaw. However, Stevens (1969) queried this and said that filament hairs were found in *G. dumicola* and *G. notabilis*.

**Series *Atjehenses*** Airy-Shaw, *Kew Bulletin*, 1940: 307 (1940).

Plant prostrate. Leaves 13–25 mm long, 7–15 mm broad. Flowers in short axillary racemes not appearing fasciculate. Corolla urceolate 5–6 mm long; outside glabrous, inside pilose. Filament papillose; pilose. Anthers awned. Ovary glabrous or pilose. Malesia.

TYPE: *Gaultheria atjehensis* J. J. Smith.

SPECIES INCLUDED: *G. atjehensis* J. J. Smith, *G. solitaria* Sleum.

Airy-Shaw (1940) described this as a monospecific series which formed a link between series *Dumicolae* and *Nummularioideae*. This seems most unlikely. Since then another species, *G. solitaria* Sleumer, has been described which belongs in this series. It differs from series *Dumicolae* in that the leaves are relatively short for members of this section, the corolla is urceolate and the inside of the corolla and filaments are pilose. In general appearance they are most like *G. notabilis* from series *Dumicolae*.

Airy-Shaw (1940) suggested that *G. atjehensis* of this series recalled the American racemose species, especially the West Indian species *G. cordifolia* (Sw.) Raeusch (not *G. cordifolia* H.B.K.) and *G. domingensis* (now both referred to as *G. domingensis*). This similarity is only superficial and the species which are most similar to section *Brossaeopsis* are *G. insipida* and *G. strigosa* from the Andes. Even here the similarities are not great.

## 10. Section *Brossaea* (L.) Middleton, **stat. nov.**

SYNONYM: *Brossaea* Linnaeus (1753).

Plant prostrate, arching erect or upright erect. Stems glabrous, punctate, pilose and/or hirsute, tomentose or strigose, the hairs being long or short eglandular or glandular. Leaves pinnate; indumentum variable as on stems; size and shape variable. Flowers pentamerous; racemose, rarely solitary; perulate or eperulate. Bract and two bracteoles varying in size and shape. Bracteoles opposite or alternate; basal, on pedicel or apical immediately beneath the calyx. Corolla urceolate, rarely campanulate; glabrous, pilose and/or hirsute outside; glabrous or pilose inside. Filament usually broad, sometimes dilated at the base; papillose; glabrous or pilose. Anthers without tubules; exaristate, with minute projections or awned. Ovary superior (rarely semi-inferior); pilose or glabrous.

Fruit a capsule, sometimes not completely drying out; calyx fleshy and accrescent, or unchanged.

TYPE: *Gaultheria domingensis* Urb.

This section derives its name from the genus *Brossaea* L., a name which was used for the racemose West Indian species now included in *G. domingensis* Urb. (Hersey & Vander Kloet, 1976). *Brossaea* is now treated as a synonym of *Gaultheria*. Considerable nomenclatural problems have accompanied the inclusion of *Brossaea coccinea* within *Gaultheria* with the name *G. swartzii* being established by Howard (1975). This species has now been treated as a synonym of *G. domingensis* (Hersey & Vander Kloet, 1976) which is taken as the type of the section.

This is by far the largest section in the genus encompassing over half of the species and including all the American, Australasian and Asian racemose species barring *G. insana* and the species of section *Brossaeopsis*. At first appearance the section is extremely variable, but there are very few marked discontinuities between the species which would allow for sectional delimitation. It could be argued that each of the subsections I have created should be treated as sections but I believe this would be overstating their differences.

- 1 Flowers solitary . . . . . **series *Parvifoliae***
- 1 Flowers in racemes
  - 2 Bracteoles lanceolate, never present immediately beneath the calyx; bracts 4–14 mm long, these and the perules present at the base of the raceme spatulate; no truly terminal racemes; plants of South America
    - 3 Reticulum prominent on both sides of the leaf **series *Reticulatae***
    - 3 Reticulum not prominent on both sides of the leaf
      - 4 Leaves densely tomentose beneath . . . . . **series *Tomentosae***
      - 4 Leaves not densely tomentose beneath
        - 5 Racemes shorter than the leaves, bracteoles basal, stems strigose . . . . . **series *Insipidae***
        - 5 Racemes usually longer than the leaves; if stems strigose then the bracteoles are not basal . . . . . **series *Domingenses***
  - 2 Bracteoles not lanceolate, variable in position, bracts usually less than 6 mm long, very occasionally to 8 mm and then not spatulate; truly terminal racemes often present
    - 6 Calyx not fleshy in fruit, bracteoles basal, raceme rachis much longer than the pedicels
      - 7 Leaf margin not ciliate; plants erect; New Zealand . . . . . **series *Rupestres***
      - 7 Leaf margin with long ciliate hairs; plants procumbent; temperate South America . . . . . **series *Nubigenae***
- 6 Calyx usually fleshy in fruit, if not then raceme rachis very short and leaves densely hirsute beneath
  - 8 Bracteoles basal
    - 9 Inflorescence a panicle; Australia and Tasmania . . . . . **series *Hispidae***
    - 9 Inflorescence of short axillary racemes; South America . . . . . **series *Insipidae***

- 8 Bracteoles not basal, or if the pedicel is so short that the bracteoles appear basal then the inflorescence is not a panicle
- 10 Bracteoles much smaller than calyx lobes, opposite, immediately beneath the calyx; raceme more or less eperulate, slender and usually geniculate. Corolla often campanulate. . . . . **series *Gymnobotrys***
- 10 Bracteoles variable in size and position. Raceme usually perulate although often the perulae are small and obscure; if the bracteoles are apical and no perules are present then the raceme is not slender, geniculate; corolla very rarely campanulate . . . . . **series *Leucothoides***

**Subsection *Dasyphyta* Middleton, *subsect. nov.***

Frutices prostrati vel erecti. Indumentum variabile. Inflorescentiae plerumque racemosae, rarissime solitariae. Racemi perulati, paene numquam terminales. Bracteae 4–14 mm longae, plerumque spathulatae. Bracteolae 2 alternantes vel suboppositae, dispositae in imo pedicello vel usque ad medium, rarissime paulo altiores, sed semper a calyce distantes. Corolla urceolata, glabra.

TYPE: *Gaultheria domingensis* Urb.

Plant prostrate or erect. Indumentum variable. Flowers usually racemose, rarely solitary. Racemes perulate; almost never terminal although often pseudoterminal. Bracts 4–14 mm long, usually spathulate, rarely smaller and not spathulate. Bracteoles usually lanceolate, basal or about middle of the pedicel, never apical. Corolla urceolate; glabrous, pilose and/or hirsute outside; pilose (rarely glabrous) inside. Filament variable in length; usually not dilated at base; pilose (rarely glabrous). Anthers with minute projections or awned; 1 or 2 awns per anther locule. Ovary glabrous or pilose. Fruit a capsule, sometimes not completely drying out; calyx fleshy and accrescent. North, Central and South America.

This subsection includes *G. parvifolia* and all those racemose species of *Gaultheria* from the Americas except *G. nubigena* (Phil.) Burt & Sleum. and *G. insana* (and *G. phillyreifolia* and *G. oreogena* which sometimes have racemes).

The subsection is characterized by the large size of its perules, bracts and bracteoles and the tendency to have more extensive multicellular and unicellular hair coverings. The indumentum characters of this subsection are particularly interesting and extremely variable. Camp (1939) divided the Mexican species into the *Acuminatae* and *Odoratae* based on indumentum characters but Corcoran (1981) found an enormous variation in indumentum type and distribution within species. Strigose hairs are relatively rare in this subsection being found only in *G. gracilis* Small and series *Insipidae* whilst in the other subsection, *Botryphoros*, they are more common. Only a very few species have little or no multicellular hairs covering at least some part of the plant.

Perules are never missing or even inconspicuous in this group. There is very little overlap in maximum perule or bract lengths between this subsection and *Botryphoros*. A few species of series *Leucothoides* in subsection *Botryphoros* have bract lengths which overlap with the smaller ones of subsection *Dasyphyta* but they mostly differ in perule, bract and bracteole shape. Most species of this subsection

also have narrow lanceolate bracteoles which are never immediately beneath the calyx. The bracteoles of *Botryphoros* are never lanceolate and there is a strong tendency towards apical bracteoles culminating in series *Gymnobotrys* with very small apical bracteoles.

*Gaultheria parvifolia* is included in this subsection rather than in one of the solitary flowered sections because it clearly has more characters in common with these species than with those of any other group.

The Neotropical component of *Gaultheria* is currently being revised by J. L. Luteyn of the New York Botanical Garden. This includes most of the species of this subsection. It is in this group in particular that there appear to be more published names than recognizable taxa. (Corcoran, 1981) has reduced many of the names to synonymy for the Mexican species and a similar process will undoubtedly occur in the South American species. Unfortunately Corcoran's nomenclature has never been validly published.

### **Series *Domingenses* Middleton, ser. nov.**

Atque subsect. *Dasyphyta* sed ramis non tomentosus et rarissime strigosus. Foliis non prominenter reticulatis. Perulis et bracteis spatulatis, bracteolis lanceolatis.

TYPE: *Gaultheria Domingensis* Urb.

As for subsection *Dasyphyta* but stems and leaves never tomentose and only rarely strigose. Leaves not raised reticulate on both surfaces. Perules and bracts spatulate, bracteoles lanceolate. North, Central and South America.

SPECIES INCLUDED: *G. acuminata* Schlecht. & Cham., *G. bracteata* (Cav.) Don, *G. cordata* Mart. & Gal., *G. cordifolia* H.B.K., *G. cordifrons* Sleum., *G. domingensis* Urb., *G. erecta* Vent., *G. glaucifolia* Hemsl., *G. glomerata* (Cav.) Sleum., *G. gracilis* Small, *G. hapalotricha* A. C. Smith, *G. hartwegiana* Klotz ex Loes., *G. meridensis* A. C. Smith, *G. montana* Brandeg., *G. odorata* Willd., *G. ornata* A. C. Smith, *G. regia* Sleum., *G. rigida* H.B.K., *G. santanderensis* A. C. Smith, *G. serrata* (Vell.) Sleum., *G. shallon* Pursh, *G. trichocalycina* DC.

This series includes all the racemose species of Central America, *G. shallon* Pursh from North America, the species from the West Indies and many South American species. It is a large and polymorphic group characterized by having a smooth (not prominent) adaxial leaf reticulum and fairly robust spreading hairs (strigose in *G. gracilis*). The racemes are usually longer than the subtending leaves. The indumentum can be extremely variable within the species (Corcoran, 1981) and any attempt to split this series into two based on the presence or absence of glandular hairs is not feasible. Within a species the hairs can range from eglandular to ones with a microglandular head to very large glandular heads. This variation in indumentum type as well as the wide variation in leaf shape partly explains why there have been more published names than recognizable taxa.

Some species of this series have only one awn on each anther locule whilst others show a progression from the normal two awn state to one with intermediates having a notched awn. This variation, currently spread amongst a group of species may all be incorporated in *G. erecta* Vent. when the group is revised.

Anatomy is very variable within this group and sometimes within species.

Most species have an entire hypodermis but a few species have a local or subentire hypodermis. They also vary in pith type and adaxial sclerenchyma. Some species have numerous fibres in the mesophyll.

The chromosome number is known for four species in this group. For three of them  $2n = 22$  and in the other, *G. shallon*,  $2n = 88$  (Middleton & Wilcock, 1990b).

Dihydroquercetin was found in one species in this group, *G. cordifolia* H.B.K., the only racemose species to contain this chemical. The only species of this subsection in which methyl salicylate has been detected is *G. acuminata* Schlecht. & Cham. (Corcoran, 1981). This contrasts strongly with the Asian species of this section where methyl salicylate is almost ubiquitous.

**Series *Reticulatae* Middleton, ser. nov.**

Foliis utrinque distincte prominenter reticulatis. Perulis et bracteis spatulatis, bracteolis lanceolatis.

TYPE: *Gaultheria reticulata* H.B.K.

Differs from series *Domingenses* in the scarce or absent indumentum and the raised reticulum on both sides of the leaf. Western South America.

SPECIES INCLUDED: *G. alnifolia* (Dun) A. C. Smith, *G. megalodonta* A. C. Smith, *G. reticulata* H.B.K., *G. sclerophylla* Cuatr.

This series is characterized by having a prominent reticulum on both sides of the leaf. The leaves are generally glabrous, or with only a very few multicellular hairs. The racemes are pseudoterminal and are fairly stiff and erect. *Gaultheria reticulata* H.B.K. of this series has been found to form frequent hybrids with *G. myrsinoides* H.B.K. (Middleton, 1991).

They all have particularly well developed adaxial sclerenchyma and some have many free fibres in the mesophyll. There is quite a difference in hypodermis between the species though, as some have an entire hypodermis and others have a very localized one.

The chromosome number for *G. reticulata* is  $2n = 44$  (Middleton & Wilcock, 1990b).

**Series *Tomentosae* Middleton, ser. nov.**

Folis subtus tomentosis-lanatis. Perulis et bracteis spatulatis, bracteolis lanceolatis.

TYPE: *Gaultheria tomentosa* H.B.K.

Differs from series *Domingenses* in the dense tomentum covering nearly all plant parts especially when young. Perules and bracts spatulate, bracteoles lanceolate. South America.

SPECIES INCLUDED: *G. eriophylla* (Pers.) Sleum., *G. lanigera* Hook., *G. tomentosa* H.B.K.

The most obvious feature of this series is the dense covering of thin twisted brown hairs on most plant parts including the raceme, calyx and corolla. All species have inrolled leaf margins to a greater or lesser extent. *G. eriophylla* (Pers.)

Sleum. is the only species of *Gaultheria* which occurs in both the Andes and S.E. Brazil.

Although they have these characters in common, in terms of habit, leaf size and leaf shape the three species are quite different. Again this series is close to series *Domingenses*.

No chromosome numbers are known.

**Series *Insipidae* Middleton, ser. nov.**

Foliis bullatis. Ramis strigosis. Racemis brevibus (foliis longioribus quam racemis). Perulis, bracteis et bracteolis plus deltoideis quam spathulatis.

TYPE: *Gaultheria insipida* Benth.

Leaves bullate. Stems strigose. Racemes shorter than leaves. Perules, bracts and bracteoles more deltoid than spathulate. Western South America.

SPECIES INCLUDED: *G. insipida* Benth., *G. strigosa* Benth.

This series and series *Parvifoliae* are the most atypical of subsection *Brossaea*.

Series *Insipidae* is characterized by strigose hairs on the stem, short racemes, bullate leaves, perules and bracts which are smaller and not as spathulate as other species in this subsection and bracteoles which are deltoid and basal. The appearance of the raceme is more like that of *G. atjehensis* than of the other South American species. However, in flower, fruit, leaf and anatomical characters it is very like the other South American species so is best included in this subsection.

**Series *Parvifoliae* Middleton, ser. nov.**

Frutex erecta. Rami juniores glandulosi et eglandulosi hirsuti. Flores solitarii (raro in racemis brevibus). Pedicelli pluribracteolati. Bracteolae spathulatae. Corolla extra hirsuta, intra pilosa.

TYPE: *Gaultheria parvifolia* Small.

Plant erect. Branches glandulose and eglandulose hirsute especially when young. Flowers solitary (rarely in short racemes). Pedicels multibracteolate. Bracteoles spathulate. Corolla hirsute outside, pilose inside. Mexico.

*Gaultheria parvifolia* is the only solitary flowered species of section *Brossaea*. I have decided not to include it in any of the solitary flowered sections based on the fact that its resemblances are clearly with series *Domingenses*. It has the large spathulate perules and bracts of the series *Domingenses*, the perules and bracts actually appearing as a number of bracteoles situated on the lower half of the pedicel, because the flower is usually solitary. It also has a dense indumentum of multicellular hairs on the corolla. The stem and leaves, particularly when young, have an indumentum reminiscent of many species of series *Domingenses* and the leaves are somewhat larger than most solitary flowered species. Also some plants do have a small number of few flowered racemes.

These characters link *G. parvifolia* with series *Domingenses*. However, there are a number of differences. This is the only species of subsection *Dasyphyta* to have solitary flowers. Corcoran (1981) suggested that confusion over delimitation between, and recognition of, *G. conzattii* Camp var. *mijorum* Camp, *G. schultesii* Camp and *G. parvifolia* could be due to hybridization between *G. parvifolia* and *G. trichocalycina* DC. This is why *G. parvifolia* has in the past been described as



having racemes whilst *G. schultesii* has been described as having solitary flowers (Camp in Schultes, 1941). Corcoran (1981) argued that *G. schultesii* could be accommodated within the range of variation of *G. parvifolia* and that the number of raceme-bearing plants in this species is actually quite small. I have seen no racemes in this species.

*Gaultheria parvifolia* is also shorter leaved than the other species of *Gaultheria sensu stricto* in the same area. *Gaultheria myrsinoides* has smaller leaves but is clearly only distantly related. Camp in Schultes (1941) believed that the solitary flowers of *G. schultesii* (= *G. parvifolia*) related this species more to *Pernettya* than to *Gaultheria* and that this species and other unnamed South American species are genetically stabilized entities resulting from hybridization between *Gaultheria* and *Pernettya*. As each of these solitary flowered species has very few other characters in common with *Pernettya* this would appear most unlikely.

Corcoran (1981) concluded that this species was the most distinct and isolated of the Mexican species of *Gaultheria* (she did not include *G. myrsinoides* in *Gaultheria*), there being no species of section *Monoanthemona* in Central America.

### **Subsection *Botryphoros* Middleton, *subject. nov.***

Frutices prostrati vel erecti. Indumentum variabile, saepe glabri. Inflorescentiae racemosae; racemi perulati vel eperulati, perulae non spathulatae; racemi axillares et saepe terminales, interdum facientes paniculas. Pedicelli basaliter, in medio vel apicaliter bibracteolati, bracteolae alternae vel oppositae. Corolla urceolata vel campanulata.

TYPE: *Gaultheria hispida* R. Br.

Plant prostrate or erect. Indumentum variable, often glabrous. Flowers racemose; racemes perulate or eperulate; perules not spathulate; axillary and often terminal, then usually forming panicles. Bracts usually less than 6 mm long. Bracteoles basal, on pedicel or apical; opposite or alternate. Corolla urceolate or campanulate, not hirsute outside, glabrous or pilose inside. Filament dilated or not; pilose or glabrous. Anthers with minute projections or awned. Ovary glabrous or pilose. Fruit a capsule, with or without a fleshy accrescent calyx. Himalayas, south east Asia, Malesia, Australasia, temperate South America.

This subsection contains all the Asian and Australasian racemose species outside section *Brossaeopsis* and also contains *G. nubigena* from temperate South America.

In this subsection the bracteoles are far more variable in position between the series and even within some series. The bracteoles, bracts and perules are generally much smaller than subsection *Dasyphyta* and the perules are sometimes completely missing. The indumentum is often missing or only very sparse. When multicellular hairs are present they are often strigose. There is a strong tendency in all the series of this subsection to form terminal panicles which virtually never occurs in subsection *Dasyphyta*.

The Asian component of this subsection is in need of thorough recollection and revision.

In anatomy they are quite variable. Parts of some series or whole series have strongly heterogeneous pith. Most species have an entire hypodermis but some of the prostrate species of series *Leucothoides*, series *Gymnobotrys* and those species of

*Leucothoides* which approach *Gymnobotrys* in a number of other characters also have a local hypodermis. In all other characters they are very variable.

**Series *Leucothoides*** (Airy-Shaw) Middleton, **stat. nov.**

SYNONYM: Section *Leucothoides* Airy-Shaw (1940).

Plants prostrate or erect. Stems glabrous, punctate or pilose and/or dense or sparsely hirsute or strigose; glandular or eglandular. Leaf indumentum similarly variable. Leaves usually obovate, rarely ovate. Flowers pentamerous, rarely tetramerous; racemose axillary and often terminal and forming panicles; perulate or eperulate. Bracteoles rarely basal, more often alternate on the pedicel or apical immediately beneath the calyx. Corolla urceolate, rarely campanulate. Filament weakly dilated; glabrous or pilose. Anthers with minute projections or awned. Ovary superior or semi-inferior; pilose. Fruit a capsule with a fleshy accrescent calyx, rarely unchanged. Himalayas, south-east Asia, Malesia.

TYPE: *Gaultheria fragrantissima* Wall.

SPECIES INCLUDED: *G. acroleia* Sleum., *G. barbulata* Sleum., *G. berberidifolia* Sleum., *G. borneensis* Stapf, *G. celebica* J. J. Smith, *G. cuneata* Bean, *G. dialypetala* Sleum., *G. discolor* Nutt., *G. forrestii* Diels, *G. fragrantissima* Wall., *G. griffithiana* Wight, *G. hookeri* Clarke, *G. itoana* Hayata, *G. leschenaultii* DC., *G. malayana* Airy-Shaw, *G. miqueliana* Takeda, *G. praticola* C. Y. Wu, *G. prostrata* W. W. Smith, *G. pullei* J. J. Smith, *G. punctata* Bl., *G. pyroloides* Miq., *G. tetramera* W. W. Smith, *G. semi-infera* (Clarke) Airy-Shaw, *G. sleumeri* Smitin. & Pham-houng, *G. stapfiana* Airy-Shaw, *G. trichoclada* Yang, *G. wardii* Marq. & Shaw.

This series corresponds to Airy-Shaw's section *Leucothoides* although many new species have been discovered since 1940. He distinguished this section from section *Gymnobotrys* on the basis of bracteole position, leaf shape and on the presence or absence of perules. However, none of these characters are completely discontinuous between the two sections. The racemes of section *Gymnobotrys* are usually eperulate but in a few specimens small, few and insignificant perules do occur. In section *Leucothoides* there are many specimens of species, such as *G. malayana* Airy-Shaw, *G. pullei* J. J. Smith and *G. punctata* Bl., all ascribed to this section by Airy-Shaw, which also do not have perules. In addition these species as well as others such as *G. celebica* J. J. Smith and *G. berberidifolia* Sleum. have small apical bracteoles. *Gaultheria fragrantissima* Wall., the type of *Leucothoides*, also has small apical bracteoles and not the "subopposite or alternate bracteoles at about the middle of the pedicel" generally characteristic of this group. *Leucothoides* and Airy-Shaw's section *Gymnobotrys* are clearly closely related and should not be separated sectionally from each other. Hsu (1981) included both sections in his group II except for *G. wardii* Marq. & Shaw which he placed in group I with the species of section *Brossaeopsis*. Despite this obviously close relationship there are a number of features which characterize a few species centred around *G. leucocarpa* Bl. The eperulate raceme, apical bracteoles, ovate leaves condition is usual. Also the racemes are generally geniculate and much more slender than those of *Leucothoides* and some of the plants have campanulate corollas. Although these differences do not warrant sectional treatment, it is probably best to maintain them separately as series.

Within series *Leucothoides* there is a great deal of variation. There are the typical species of this series based in the Himalayas and S.W. China such as *G. fragrantissima*, *G. forrestii* Diels, *G. stapfiana* Airy-Shaw and *G. hookeri* Clarke. *Gaultheria leschenaultii* DC. is an outlier from southern India and Sri Lanka. Differing in fairly unusual ways, but otherwise typical of this group, are *G. griffithiana* Wight with a campanulate corolla, *G. tetramera* W. W. Smith with tetramerous flowers, *G. wardii* with an extremely condensed raceme rachis and a completely dry fruit and *G. semi-infera* (Clarke) Airy-Shaw with a semi-inferior ovary. *Gaultheria discolor* Nutt. appears to be somewhat in between this group and another group which have large eperulate, sometimes branching panicles, consistently small apical bracteoles and occur in Malesia. This includes *Gaultheria punctata*, *G. malayana*, *G. pullei*, *G. celebica* and *G. berberidifolia*. Another group with *G. acroleia* Sleum. and *G. barbulata* Sleum. has the appearance of this group but has longer bracteoles situated at the middle of the pedicel. One other group is a collection of species which Airy-Shaw recognized where the raceme is more or less sympodial to the branches and the plant is usually prostrate. This includes *G. pyrolloides* Miq., *G. miqueliana*, *G. cuneata*, *G. itoana* Hayata, *G. borneensis* Stapf and *G. prostrata* and is most closely related to the *G. fragrantissima* group. Copeland (1931) included these latter species in his "allies of *G. nummularioides*", a conclusion with which I cannot agree. Even though each of these groups within series *Leucothoides* is recognizable they are by no means very distinct taxa and cannot be formally classified. What remains is a heterogeneous, but natural series.

*Gaultheria mundula* and *G. novaguineensis*, included in this group by Airy-Shaw cannot be maintained here, as explained previously.

All the species studied chemically from this group have been found to contain methyl salicylate. Quite a number of species have been studied cytologically and numbers of  $2n = 22, 26, 44$  and  $n = 11, 22, 24$  have been found (Middleton & Wilcock, 1990b).

### **Series *Gymnobotrys* (Airy-Shaw) Middleton, stat. nov.**

SYNONYM: Section *Gymnobotrys* Airy-Shaw (1940).

Differs from *Leucothoides* in that the plants are always erect, never strigose. Leaves usually ovate. Flowers always pentamerous, racemes usually eperulate, geniculate, slender. Bracteoles always apical opposite. Corolla campanulate or urceolate. Filament glabrous. Anthers always awned. Ovary superior. Fruiting calyx always fleshy accrescent. Himalayas, south-east Asia, Malesia, Taiwan.

TYPE: *Gaultheria leucocarpa* Bl.

SPECIES INCLUDED: *G. arfakana* Sleum., *G. gracilescens* Sleum., *G. intermedia* J. J. Smith, *G. leucocarpa* Bl., *G. longiracemosa* Y. C. Yang, *G. hirta* Ridl., *G. viridiflora* Sleum., *G. yunnanensis* Rehder.

This group was recognized as a group of closely related species by Copeland (1931), who referred to them as "the allies of *G. leucocarpa*". He included in this group *G. pullei* (including *G. calyculata* Wernh.) and *G. celebica* both of which were included in *Leucothoides* by Airy-Shaw (1940). It does indicate that some delimitation is difficult in this area.

Many of those species recognized by Copeland (1931) are now treated as synonyms of *G. leucocarpa*. This includes often-quoted species like *G. crenulata* Kurz and *G. cumingiana* Vidal. The reason for the large number of segregates from this species in the past is because of its widespread distribution. It is found in the Himalayas, down through Burma to Malaysia and through the Indonesian islands and across to Taiwan. Over this enormous area it is morphologically very variable. Sleumer (1957, 1967) and Hsu (1981) have provided fairly detailed subspecific classification of *G. leucocarpa*. *Gaultheria yunnanensis* is quite similar, also having campanulate flowers and similar overall appearance, the two species probably being conspecific. The other species of this series, *G. intermedia* J. J. Smith, *G. longiracemosa* Y. C. Yang (which I have not seen), *G. hirta* Ridl., *G. gracilescens* Sleum., *G. arfakana* Sleum and *G. viridiflora* Sleum. all have urceolate corollas but all share the geniculate slender racemes of *G. leucocarpa* and densely pilose ovaries. Except in *G. hirta* the indumentum is either sparse or absent. Many species in this group are undercollected.

The species of this series all lack a complete hypodermis. All the species which have been studied have salicylic acid. A chromosome number is known only for *G. leucocarpa* at  $2n = 44$  (see Middleton & Wilcock, 1990b).

**Series *Hispidae* Middleton, ser. nov.**

Frutices erecti. Rami strigosi. Inflorescentiae paniculatae. Racemi perulati. Bracteolae breves, *c.* 2.5 mm longa. Pedicelli basaliter bibracteolati, bracteolae oppositae. Corolla urceolata, intra pilosa. Filamenta glabra. Antherae aristatae. Ovarium glabrum. Fructus cum calycis lobis carnosus.

TYPE: *Gaultheria hispida* R. Br.

SPECIES INCLUDED: *G. appressa* A. W. Hill, *G. hispida* R. Br.

Plant erect. Stems strigose. Inflorescence a panicle formed from axillary and terminal perulate racemes. Bracts small, *c.* 2.5 mm. Bracteoles opposite, basal. Corolla urceolate; glabrous outside, pilose inside. Filament glabrous, slightly dilated at the base. Anthers awned. Ovary glabrous. Fruit a capsule and calyx fleshy in fruit. Southern Australia, Tasmania.

This series comprises two closely related species, *G. hispida* R. Br. and *G. appressa* A. W. Hill. Both species have small, deltoid, opposite, basal bracteoles, large panicles and strigose stems.

This series is found in Southern Australia and Tasmania and seems to be intermediate between the series *Leucothoides* and *Rupestres*. It has the fleshy fruiting calyx of series *Leucothoides* but the general appearance and indumentum of *Rupestres*. In anatomical characters it has strongly heterogeneous pith and a high number of paracytic stomata. *Gaultheria hispida* is the oldest described species in subsection *Botryphoros*.

The chromosome number for *G. hispida* is  $2n = 22$  (Callan, 1941).

**Series *Rupestres* Middleton, ser. nov.**

Frutices erecti. Rami pilosi, strigosi vel hirsuti. Folia alterna vel opposita. Inflorescentiae saepe paniculatae. Racemi perulati. Pedicelli basaliter bibracteolati, bracteolae oppositae. Filamenta basaliter dilatata. Antherae aristatae. Ovarium glabrum vel sparsim pilosum. Fructus sine calycis lobis carnosus.

TYPE: *Gaultheria rupestris* (L. fil.) D. Don.

Plants erect. Stems pilose, strigose or hirsute. Leaves alternate or opposite. Flowers in perulate racemes; axillary, terminal or both, often forming a panicle. Bract small. Bracteoles opposite basal. Filament dilated at the base, glabrous. Anthers awned. Ovary glabrous or sparsely pilose. Fruit a capsule with unchanged calyx. New Zealand.

SPECIES INCLUDED: *G. colensoi* Hook. fil., *G. crassa* Allan, *G. oppositifolia* Hook. fil., *G. paniculata* Burt & Hill, *G. rupestris* (L. fil.) Don.

This is a well circumscribed group because all the species have completely dry fruits, basal bracteoles, panicles, erect habit and are confined to New Zealand. Most have glabrous ovaries, relatively short awns, thick leaves, entire hypodermis and heterogeneous pith. They appear to be linked to series *Leucothoides* through series *Hispidae*. A number of the species hybridize quite freely with members of sections *Monoanthezona* and *Pernettya* as well as each other. There are five species, *G. oppositifolia* Hook. fil., *G. paniculata* Burt & Hill, *G. crassa* Allan, *G. colensoi* Hook. fil. and *G. rupestris* (L. fil.) D. Don. The first two are closely related and the latter three have been treated as conspecific until fairly recently (Burt & Hill, 1935; Allan, 1961). In addition *G. rupestris* var. *subcorymbosa* (Col.) Burt & Hill is sometimes treated as a separate species. The unusual feature in this series is *G. oppositifolia* with opposite leaves, the only species in the genus with this character.

This series and series *Hispidae* mostly have heterogeneous pith, strong adaxial sclerenchyma and always have a complete hypodermis.

### **Series *Nubigenae* Middleton, *ser. nov.***

Suffrutex procumbens. Rami glabri. Folia setosa ciliata. Inflorescentiae paniculatae. Racemi perulati. Bracteae breves. Pedicelli basaliter bibracteolati, bracteolae oppositae. Corolla urceolata, glabra. Filamenta glabra. Antherae brevissime aristatae. Ovarium glabrum. Fructus sine calycis lobis carnosus.

TYPE: *Gaultheria nubigena* (Phil.) Burt & Sleum.

Plant procumbent. Stems glabrous. Leaves setose ciliate. Flowers in axillary and terminal racemes forming panicles; perulate. Bract small. Bracteoles 2 opposite basal. Corolla urceolate, glabrous. Filament glabrous. Anthers with minute projections. Ovary glabrous. Fruit a capsule with unchanged calyx. Temperate South America.

The sole species in this series, *G. nubigena* was originally described as a species of *Pernettya*. However, its affinities appear to be more with series *Rupestres* making it the only species of section *Brossaea* in America not in subsection *Dasyphyta*. It has the dry fruit, small basal bracteoles and terminal panicles like series *Rupestres* but a procumbent habit, a different indumentum, minute projections rather than awns on the anthers and a different pith type to that series.

In the leaves it has strongly developed adaxial sclerenchyma and a complete hypodermis.

### ACKNOWLEDGEMENTS

I would like to thank Dr C. C. Wilcock for his help with this work and the staff of the various herbaria and institutions which lent me material and offered

advice. I would also like to thank Dr T. Pearce for assistance with my Latin diagnoses.

## REFERENCES

- AIRY-SHAW, H. K., 1940. Studies in the Ericales IV. Classification of the Asiatic species of *Gaultheria*. *Kew Bulletin*, 1940: 304–330.
- ALLAN, H. H., 1961. *Gaultheria* L. In *Flora of New Zealand*, 1: 506–513. Wellington: R. E. Owen.
- BAAS, P., 1985. Comparative leaf anatomy of *Pernettya* Gaud. (Ericaceae). *Botanische Jahrbücher*, 105: 481–495.
- BURTT, B. L. & HILL, A. W., 1935. The genera *Gaultheria* and *Pernettya* in New Zealand, Tasmania and Australia. *Journal of the Linnean Society (Botany)*, 49: 611–644.
- CALLAN, H. G., 1941. The cytology of *Gaultheria wisleyensis* (Marchant) Rehder. A new mode of species formation. *Annals of Botany*, 5: 579–585.
- CAMP, W. H., 1939. Studies in the Ericales IV. Notes on *Chimaphila*, *Gaultheria* and *Pernettya* in Mexico and adjacent regions. *Bulletin of the Torrey Botanical Club*, 66: 7–28.
- CANDOLLE, A. L. P. DE, 1839. Ericaceae. *Prodromus Systematis Naturalis Regni Vegetabilis*, 7: 580–773.
- COPELAND, H. F., 1931. Philippine Ericaceae III. A taxonomic revision. Genus *Gaultheria* L. *Philippine Journal of Science*, 47: 57–63.
- CORCORAN, C. M., 1981. *A revision of the Mexican and Guatemalan taxa of Gaultheria (Ericaceae)*. Unpublished Ph.D. thesis of the University of Wisconsin, Madison.
- HERSEY, R. E. & VANDER KLOET, S. P., 1976. Taxonomy and distribution of *Gaultheria* in the Caribbean. *Canadian Journal of Botany*, 54: 2465–2472.
- HOOKER, J. D., 1876. Vacciniaceae and Ericaceae. In G. Bentham & J. D. Hooker, *Genera Plantarum*, 2(2): 564–604. London: Reeve & Co.
- HOWARD, R. A., 1975. *Gaultheria swartzii* nom. nov. and the combinations in Raeschels Nomenclator. *Journal of the Arnold Arboretum*, 56: 240–242.
- HSU, T., 1981. Preliminary study of the classification of Chinese *Gaultheria*. *Acta Botanica Yunnanica*, 3: 417–434.
- LINNAEUS, C., 1751. *Nova Plantarum Genera*. Uppsala.
- LINNAEUS, C., 1753. *Species Plantarum I*. Uppsala.
- LÖVE, Å. & LÖVE, D., 1973. *Chiogenes* or *Gaultheria*, a question of generic definition. *American Rock Garden Society Bulletin*, 31: 127–129.
- MIDDLETON, D. J., 1989. *Taxonomic studies in the genus Gaultheria L. and related genera (Ericaceae)*. Unpublished Ph.D. thesis of the University of Aberdeen.
- MIDDLETON, D. J. & WILCOCK, C. C., 1990a. A critical examination of the status of *Pernettya* Gaud. as a genus distinct from *Gaultheria* L. *Edinburgh Journal of Botany*, 47: 291–301.
- MIDDLETON, D. J. & WILCOCK, C. C., 1990b. Chromosome counts in the genus *Gaultheria* and related genera. *Edinburgh Journal of Botany*, 47: 303–313.
- MIDDLETON, D. J., 1991. Ecology, reproductive biology and hybridization in *Gaultheria* L. *Edinburgh Journal of Botany*, 48: 81–89.
- SCHULTES, R. E., 1941. Plantae Mexicanae X: New or critical species from Oaxaca. *Botanical Museum Leaflets*, 9: 165–217.
- SLEUMER, H., 1935. Revision der Gattung *Pernettya* Gaud. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem*, 12: 626–655.
- SLEUMER, H., 1952. Die Arten der Gattung *Gaultheria* L. in Brasilien. *Botanische Jahrbücher*, 75: 443–450.
- SLEUMER, H., 1957. Florae Malesiana praecursores XV. A revision of the genus *Gaultheria* (Ericaceae). *Reinwardtia*, 4: 163–188.
- SLEUMER, H., 1966. Ericaceae. *Flora Malesiana ser. I*, 6: 469–668.
- SLEUMER, H., 1967. Ericaceae. *Flora Malesiana ser. I*, 6: 669–914.
- SLEUMER, H., 1985. Taxonomy of the genus *Pernettya* Gaud. (Ericaceae). *Botanische Jahrbücher*, 105: 449–480.
- STEVENS, P. F., 1969. *Taxonomic studies in the Ericaceae*. Unpublished Ph.D. thesis of the University of Edinburgh.
- STEVENS, P. F., 1971. A classification of the Ericaceae: subfamilies and tribes. *Botanical Journal of the Linnean Society*, 64: 1–53.
- TOWERS, G. H. N., AIDE TSE & MAAS, W. S. G., 1966. Phenolic acids and phenolic glycosides of *Gaultheria* species. *Phytochemistry*, 5: 677–681.