EDINB. J. BOT. 47(3): 291–301 (1990)

A CRITICAL EXAMINATION OF THE STATUS OF *PERNETTYA* AS A GENUS DISTINCT FROM *GAULTHERIA*

D. J. MIDDLETON* & C. C. WILCOCK*

The taxonomic status of the genus *Pernettya* Gaud. (Ericaceae) has been assessed by comparing morphological, anatomical, chemical and cytological characters between *Pernettya*, *Gaultheria* L. and a number of other genera in the *Gaultheria* group of the tribe *Andromedeae*. It has been concluded that *Pernettya* is not sufficiently distinct from *Gaultheria* to be maintained as a separate genus. Two new names and fifteen new combinations within *Gaultheria* are here proposed.

INTRODUCTION

The genus *Pernettya* Gaud. has twice been revised by Sleumer (1935, 1985). In the earlier paper he discussed the background and taxonomic history of the genus and recognized two sections containing 13 species, with many varieties. Section *Pseudogaultheria* with a single species, *P. insana* (Molina) Gunckel (syn. *P. furiens* (Hook. & Arn.) Kl.), was distinguished by its racemose inflorescence from section *Archipernettya* (*Pernettya* in modern nomenclature), with solitary flowers, which was split into three series. In his 1985 revision Sleumer described 14 species and reduced the number of varieties recognized. The treatment included some new, although previously named species, as well as the transference of two species of *Gaultheria* L. to *Pernettya* (Burtt & Hill, 1935).

Sleumer (1985) has been taken as the model for *Pernettya* prior to this work. What has not been so clear is the generic distinction between *Pernettya* and *Gaultheria*. Hooker (1876) placed the two genera in different tribes of the Ericaceae based on fruit differences: *Pernettya* in the *Arbuteae* with *Arbutus* and *Arctostaphylos*, a tribe where the species bear fleshy fruits; *Gaultheria* in the *Andromedeae* because the fruit is a capsule.

Niedenzu (1890) included *Pernettya* and *Gaultheria* in a new tribe, *Gaultherieae*, of subfamily Arbutoideae along with *Diplycosia* Bl. and *Chiogenes* Salisb. He highlighted the similarity between *Gaultheria* and *Pernettya*, particularly in leaf anatomy, and argued that these two genera were closely related despite the obvious fruit differences. Drude (1897) in a subfamilial classification of the whole of the Ericaceae retained tribe *Gaultherieae*.

Watson et al. (1967) used a numerical taxonomic approach to construct a subfamilial classification of the Ericaceae and placed *Gaultheria* and *Pernettya* in Tribe 2 (corresponding to the *Andromedeae* of previous schemes) of subfamily III (Vaccinioids). This work has been criticized by Stevens in Burtt et al. (1970) primarily for its poor sampling, although Stevens arrived at similar conclusions for the *Andromedeae*

*Department of Plant & Soil Science, University of Aberdeen, St Machar Drive, Aberdeen, AB9 2UD.

in his work (Stevens, 1969, 1971). He placed both *Gaultheria* and *Pernettya* in tribe *Andromedeae* of subfamily Vaccinioideae and suggested that these genera, together with *Diplycosia*, *Pernettyopsis* King & Gamble, *Leucothoë* Don, *Zenobia* Don and *Tepuia* Camp, formed a distinct, but not formally recognizable, group within the *Andromedeae*. He referred to this group as the '*Gaultheria* group of genera'. He also concluded that *Pernettya* was not sufficiently distinct from *Gaultheria* to be maintained as a separate genus.

The trend in each of these schemes has been to reduce the overriding emphasis on fruit characters used to separate the two genera. The basic difference between the two genera is that the fruits of *Gaultheria* are usually a dry capsule surrounded by a fleshy calyx, whilst those of *Pernettya* are a berry with a persistent but unchanged calyx.

Hooker (1864), following a description of *Pernettya tasmanica* Hook. f. from New Zealand (the New Zealand plants of this species were later distinguished as *P. nana* Colenso) wrote: 'This is a most puzzling plant, and seems to unite the genera *Pernettya* and *Gaultheria*, as much as do the varieties of *G. antipoda*'.

Burtt & Hill (1935) suggested that this may be explained because Hooker did not fully appreciate the extent of hybridization in the group and some of the plants he described as *G. antipoda* were in fact *P. macrostigma* Colenso × *G. antipoda* hybrids. They further suggested that the calyx character is not useful for distinguishing the two genera as some of the New Zealand species of *Gaultheria* have dry calyces in fruit whereas a number of species of *Pernettya* have, to varying degrees, a fleshy calyx in fruit (Sleumer, 1935, 1985; Burtt & Hill, 1935; Stevens, 1969). Burtt & Hill (1935) argued that the 'only satisfactory distinguishing character between the two genera is in fact the fruit, *Pernettya* having a fleshy berry and *Gaultheria* a dry dehiscent capsule'.

However, it has been observed that this fruit character is also not constant. *P. lanceolata* (Hook. f.) Burtt & Hill was formerly placed in *Gaultheria* because of its large swollen calyx but Burtt & Hill (1935) removed it to *Pernettya* because the fruit is a fleshy berry. They discussed the possibility that it may be a hybrid between *Gaultheria* and *Pernettya* but stated that the uniformity of the taxon is enough to suggest it is a good species of *Pernettya*. Stevens (1969) noted that the flesh of the berry was very thin and that the type specimen of the species plus another specimen both showed 'berries' which appeared to have dehisced.

Burtt & Hill (1935) also discussed the possibility that *P. macrostigma* (formerly *G. perplexa* Kirk) could be a bigeneric hybrid but again argued that the uniformity of the taxon was too marked. Apparently this species hybridizes 'freely with many species of *Gaultheria*' (Franklin, 1962).

Sleumer (1985) has stated that where fleshy calyces occur in *Pernettya* it is due to introgression from *Gaultheria* species. He also commented that the intermediate nature of *P. lanceolata* means that it is 'presumedly [sic] of hybrid origin', speculating that the species may be either *P. tasmanica* × *G. depressa* or *P. tasmanica* × *G. hispida*. However, he added that a decision on the hybrid nature of *P. lanceolata* could only be obtained by studies in the field.

Niedenzu (1890) believed the two genera differed in the nature of the spongy

mesophyll cells in the lamina, although in his anatomical key groups of both genera key out together. Sleumer (1935), however, noted that there was virtually no difference in leaf anatomy between *P. mucronata* (L.f.) Gaud. ex Sprengel and *G. phillyreifolia* (Pers.) Sleumer, and Stevens (1969) agreed that he could find no overall leaf anatomical differences between the two genera.

Stevens (1969) concluded that 'there can be no doubt that *Pernettya* is not maintainable as a genus'. He has also suggested that *Pernettya* may be polyphyletic (Stevens, pers. comm.) which is a sentiment shared by Webb (1972).

Baas (1985) concluded that the three species of *Gaultheria* he studied covered a leaf anatomical range which overlapped that of *Pernettya*. Baas also noted that the similarities noticed by Niedenzu (1890) were even greater than Niedenzu had appreciated as some of Niedenzu's species of *Pernettya* have subsequently been transferred to *Gaultheria*. Baas states: 'In conclusion, leaf anatomy would support a broad generic concept for *Gaultheria*, including *Pernettya*. On the other hand, leaf anatomical overlap between related genera which are distinct from each other in macromorphological characters is quite common and cannot be used as a single criterium to merge genera'.

Sleumer (1985) believed that *Pernettya* should be maintained separately and listed a number of additional characters, apart from those relating to fruits, to separate the two genera. These were that: stipitate glands do not occur in *Pernettya* whilst they do in some species of *Gaultheria*; true dioecism is unknown in *Gaultheria* although it has been reported from four species of *Pernettya*; and vivipary has been recorded in *Pernettya* but not in *Gaultheria*.

This study attempts to clarify the taxonomic status of the genus *Pernettya*.

Methods and Results

Morphological, anatomical, chemical and cytological characters have been studied for all species of *Pernettya* and most of the species of *Gaultheria* (Middleton, 1989). In addition many species of *Leucothoë*, *Zenobia*, *Diplycosia*, *Pernettyopsis* and *Tepuia*, all in the *'Gaultheria* group of genera', have been studied. Morphological and anatomical characters have proved the most useful as taxonomic indicators in the group. Morphological characters studied included a wide range of vegetative, floral and fruit characters. Leaves and stem pith were used for the anatomical characters. Observations on ecology and reproductive biology were made in the field in Ecuador. The occurrence of flavonoids and simple phenols was found to be very variable within species. Quercetin was the only flavonoid which was ubiquitous in all samples; myricetin and kaempferol were variable within species. The presence of dihydroquercetin and hydroquinone was also variable within species. Base chromosome numbers were found to be invariable and are therefore of only limited taxonomic use (Middleton, 1989, 1990).

Figure 1 shows a principal components analysis (PCA) of 118 species of *Gaultheria* and *Pernettya* based on 86 binary state morphological characters. These characters are listed in Appendix 1. PCA is a form of multivariate analysis for calculating overall

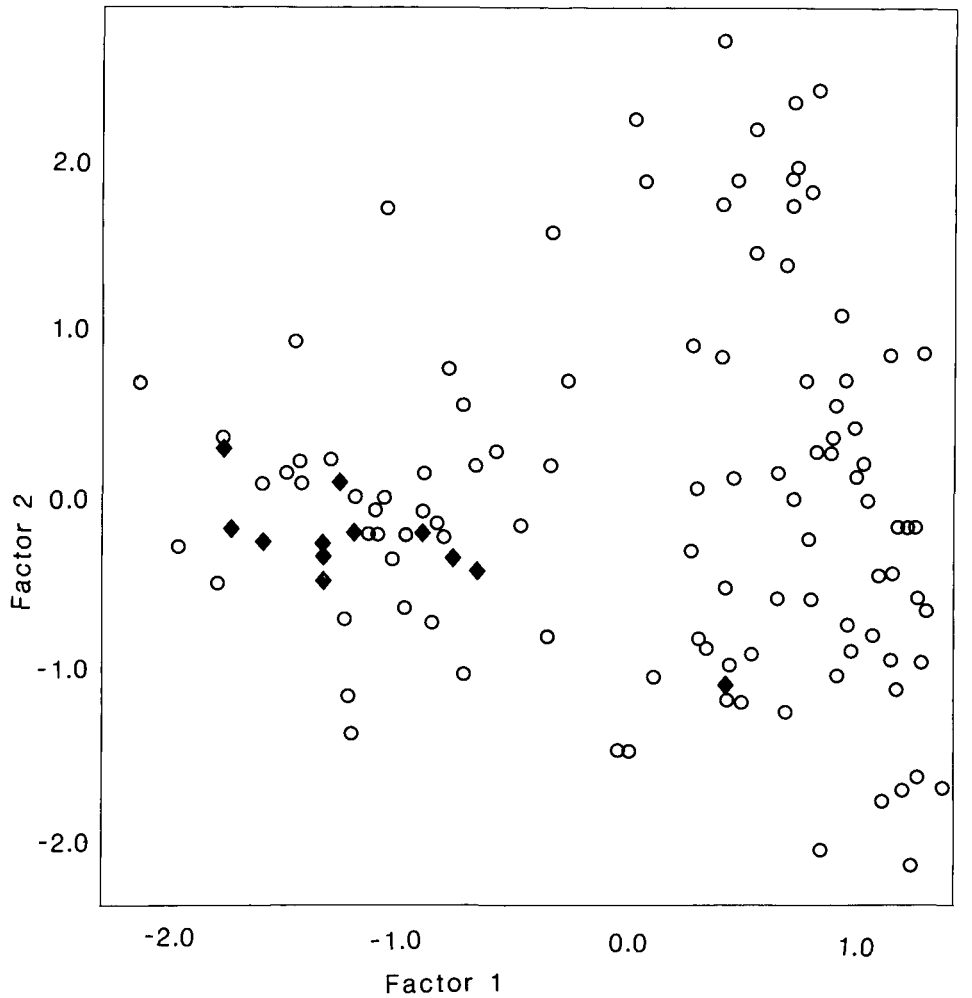

FIG. 1. Principal components analysis of 118 species of *Gaultheria* and *Pernettya* using 86 binary state characters. ○ *Gaultheria* (106 species). ◆ *Pernettya* (12 species).

similarities between species. Factor scores for each species are obtained and plotted on a graph. The first axis, factor 1, accounts for 22% of the variation, and factor 2 for a further 11%. Leaf size, inflorescence type, number of bracteoles and filament shape score most strongly on factor 1. Species with a negative score on factor 1 predominantly have solitary flowers and small leaves, whereas species with a positive score on factor 1 have racemes and larger leaves. Leaf shape and flower indumentum characters score most strongly on factor 2. The figure shows that the species of *Pernettya* do not form a cluster distinct from the species of *Gaultheria* on the first two axes. The solitary-flowered species of *Pernettya* fall within the range of variation of the solitary-flowered species of *Gaultheria* and the single racemose species of *Pernettya*,

P. insana (coordinates 0.4,1.0), falls within the range of variation of the racemose species of *Gaultheria*. There are no overall differences in the leaf and pith anatomy between *Pernettya* and *Gaultheria* (Middleton, 1989), but there are, however, many differences between *Pernettya* and the other genera of the *'Gaultheria* group' (Middleton, 1989).

Discussion

The fruit characters which have served primarily to distinguish the two genera are not reliable. A number of *Gaultheria* species have dry calyces in fruit, such as the New Zealand racemose species, *G. wardii* Marq. & Airy-Shaw, *G. nubigena* (Philippi) Burtt & Sleumer and *G. itatiaiae* Wawra, and a number of *Pernettya* species have fleshy calyces to a greater or lesser extent. *P. lanceolata* and *P. macrostigma* have well-developed fleshy calyces and *P. pumila* (L.f.) Hook., *P. insana*, *P. tasmanica*, *P. nana* and some forms of *P. prostrata* (Cav.) DC. have fleshy calyces to varying degrees. These represent half of the species of the genus from throughout their geographical range. The fruit itself is not readily divided into capsules and berries as intermediates do occur. *P. lanceolata* has a very thin flesh on the berry and sometimes dehisces. However, this may be an artefact of drying. *G. procumbens* L. has a brightly coloured 'capsule' which is more like a very thin-walled fleshy berry. The capsules of *G. rigida* HBK and *G. glomerata* (Cav.) Sleumer shrivel as a whole fruit and fall off the plant without the capsule being seen to dehisce. One specimen each of *G. tenuifolia* (Philippi) Sleumer and *G. sinensis* Anth. was seen with well-developed berries. The former case may be due to introgression from *Pernettya* as the two genera co-occur but *Pernettya* is absent from the Himalayas, the site of *G. sinensis*. There is a remarkable parallel here with the closely related genus *Diplycosia*, in which a complete range of fruit type from a fleshy berry to a dry capsule is found (Argent, pers. comm.).

In all other morphological characters *Pernettya* is not distinct, except that some species of *Pernettya* are dioecious, from *Gaultheria*. Gynodioecism, which is common in *Pernettya*, may be more common in *Gaultheria* than previously thought (Middleton, 1989). Sleumer (1985) noted that stipitate glands are absent in *Pernettya* but occur in some species of *Gaultheria*. However, their presence in a number of species of *Gaultheria* is no grounds for a separate generic status for *Pernettya* as they are also unknown in a large number of *Gaultheria* species. Sleumer (1985) also noted that vivipary has not been recorded in *Gaultheria* whereas it is known in *Pernettya*. Woods (pers. comm.) has observed vivipary in *Gaultheria leucocarpa* in cultivation. In indumentum characters, leaf shape and size, bracteole, calyx, corolla, stamen and ovary characters they overlap with *Gaultheria*. Figure 1 shows that the species of *Pernettya* are not distinguishable from *Gaultheria* in a principal components analysis using a wide range of vegetative and reproductive characters. All the solitary-flowered species of both genera are concentrated on the left hand side and all the racemose species on the right hand side on factor 1.

Pernettya also overlaps with *Gaultheria* in all anatomical characters (Middleton, 1989). Some species, notably *P. insana* and *P. pumila*, have unique combinations of

anatomical characters but the same could be claimed for a number of *Gaultheria* species, and this in no way merits separate generic status.

The combination of anatomical characters in *P. alpina* Franklin is much more like those of *G. antarctica Hook.* f. and *G. humifusa* (Graham) Rydb. than other species of *Pernettya*. Along with its morphological characters it is extremely similar to *G. antarctica*. In its original description (Franklin, 1962), and in the revision by Sleumer (1985), there is no mention of fruit characters. No fruits of *P. alpina* are known from herbarium specimens either. Franklin (1962) suggested that it was a species allied to *P. nana*, but without fruit characters it is impossible to assign a species with certainty to either *Pernettya* or *Gaultheria*. Therefore, there was no logical reason why Franklin should have placed *P. alpina* in *Pernettya* except on the grounds of its superficial resemblance to *P. nana*. The leaf anatomy, along with the morphological characters, suggests that *P. alpina* is actually more closely allied to *G. antarctica* than to the other species of *Pernettya* (Middleton, 1989).

Hydroquinone, a simple phenol, has been found in two species of *Pernettya*, *P. mucronata* and *P. myrtilloides* Zucc. ex Steudel, and has not been detected at all in *Gaultheria* (Middleton, 1989). However, its presence is not entirely consistent within species and is certainly not ubiquitous in *Pernettya*. Dihydroquercetin, detected in the same two species, also occurs in *G. nummularioides* D. Don, *G. antipoda* Forst. f. and *G. depressa* Hook. f. (Middleton, 1989). Methyl salicylate has been detected within the genus *Pernettya* only in *P. marginata* N. E. Brown, but equally this chemical is also rarely found in the solitary-flowered species of *Gaultheria*.

All species of *Pernettya* studied have a chromosome number based on $x=11$ (Middleton, 1989). Diploids, tetraploids and hexaploids are found, and *P. insana* has both tetraploids and hexaploids. The incidence of hexaploids is uncommon in the group as a whole but otherwise *Pernettya* does not differ in chromosome number or chromosome morphology from most species of *Gaultheria* (Middleton, 1989) and therefore provides no evidence for a separation.

Rollins (1953) believed that the incidence of fertile intergeneric hybrids and/or high numbers of sterile intergeneric hybrids in the angiosperms gave serious doubt as to the separation of two hybridizing genera. Mulligan (1939) and Callan (1941) have raised seedlings from the intergeneric hybrid × *Gaulnettya wisleyensis*. Camp (1939) believed *P. ciliata* (Cham. & Schldl.) Small and *P. hirsuta* (Mart. & Galeotti) Camp (both now included in *Gaultheria myrsinoides*; syn. *P. prostrata*) were the result of either a back cross from × *Gaulnettya* hybrids and *Pernettya* species, or by generic segregation from the original hybrid. This he deduced from the indumentum characters rather than from detailed population studies. Sleumer (1985) believed that *P. lanceolata* and all other *Pernettya* species with evidence of a fleshy calyx in fruit to be the result of introgression from *Gaultheria* species. All these cases would require that any original crossing of the two genera resulted in fertile progeny. Under Rollins' criteria these two genera should not be maintained separately. Whether these cases do in fact imply introgression from *Gaultheria* or not, it remains that 18 different intergeneric hybrids have now been documented (Skottsberg, 1916; Burtt & Hill, 1935; Marchant, 1937; Camp, 1939; Franklin, 1962; Corcoran, 1981; Middleton, 1989).

Stevens (1969) raised the question as to whether *Pernettya* was monophyletic. He suggested that groups of *Pernettya* species had similarities with certain groups of *Gaultheria* species. He linked *P. insana* with the American racemose species, *P. mucronata* with *G. phillyreifolia* and *P. tasmanica*, and *P. nana* with *G. caespitosa*. It is true that *P. insana* appears very different from the other species in the genus but it is difficult to pinpoint any great discontinuities within the solitary-flowered species. The examples of similarities between two of the groups given above are fairly superficial. However, there can be no doubting the great similarity between *P. mucronata* and *G. phillyreifolia*. The species are often confused and both bear the same Chilean vernacular name of 'Chaura' (Sleumer, 1985). *G. tenuifolia*, which is closely related to *G. phillyreifolia*, has a berry on one herbarium specimen seen, although this may be due to introgression from *Pernettya*.

Thus *Pernettya* should not be maintained as a separate genus from *Gaultheria*, the only character which separates them being the fruit which even then is not completely discontinuous. The 14 species of *Pernettya* recognized by Sleumer (1985) are transferred to *Gaultheria* (fuller synonymy can be found in Sleumer, 1985). A summary of the new names can be seen in Appendix 2.

Gaultheria howellii (Sleumer) Middleton, **comb. nov.**
Basionym: *P. howellii* Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 649 (1935).

Gaultheria insana (Molina) Middleton, **comb. nov.**
Basionym: *Hippomanica insana* Molina, Sag. Stor. Nat. Chili. 351 (1782).
Syn.: *Pernettya insana* (Molina) Gunckel, Not. Mens. Mus. Nac. Hist. Nat. Santiago 17(197): 6 (1972).

Gaultheria lanceolata Hook. f. in London J. Bot. 6: 267 (1847).
Syn.: *Pernettya lanceolata* (Hook. f.) Burtt & Hill, J. Linn. Soc. Bot. 49: 638 (1935).

Gaultheria macrostigma (Colenso) Middleton, **comb. nov.**
Basionym: *Pernettya macrostigma* Colenso, Trans. & Proc. New Zealand Inst. 21: 92 (1888).

Gaultheria marginata (N. E. Brown) Middleton, **comb. nov.**
Basionym: *Pernettya marginata* N. E. Brown, Trans. Linn. Soc. Lond., Bot. 6: 43 (1901).

Gaultheria mucronata (L.f.) Hook. & Arn., J. Bot. (Hooker) 1: 281 (1834).
Basionym: *Arbutus mucronata* L.f., Suppl. Pl. 239 (1781).
Syn.: *Pernettya mucronata* (L.f.) Gaud. ex Sprengel, Syst. Veg. 4(2), Cur. post. 158 (1827).

var. **angustifolia** (Lindley) Middleton, **comb. nov.**
Basionym: *Pernettya angustifolia* Lindley, Bot. Reg. 26: t.63 (1840).
Syn.: *Pernettya mucronata* var. *angustifolia* (Lindley) Reiche, Fl. Chile 5: 75 (1910).

var. **microphylla** (Hombron) Middleton, **comb. nov.**
Basionym: *Pernettya mucronata* var. *microphylla* Hombron in Dum d'Urv., Voy. Pole Sud, Bot. Phan. Dicot., Atlas t.22, X, 1–8 (1852).

Gaultheria myrsinoides Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 283 (1819).
Syn.: *Pernettya prostrata* (Cav.) DC., Prodr. 7: 609 (1839).

Gaultheria nubicola Middleton, **nom. nov.**
Syn.: *Pernettya alpina* Franklin, Trans. Roy. Soc. New Zealand, Bot. 1(13): 164, f.1, j. (1962).

Gaultheria parvula Middleton, **nom. nov.**
Syn.: *Pernettya nana* Colenso, Trans. & Proc. New Zealand Inst. 23: 389 (1891).

Gaultheria poeppigii DC., Prodr. 7: 593 (1839).
Syn.: *Pernettya myrtilloides* Zucc. ex Steudel, Nomencl. Bot. ed. 2, 2: 306 (1841).

var. **linifolia** (Philippi) Middleton, **comb. nov.**
Basionym: *Pernettya linifolia* Philippi, Linnaea 33: 172 (1864).
Syn.: *Pernettya myrtilloides* var. *linifolia* (Philippi) Kausel, Revista Univ., Santiago 34: 164 (1949).

var. **nana** (Sleumer) Middleton, **comb. nov.**
Basionym: *Pernettya poeppigii* (DC.) Klotzsch var. *nana* Sleumer, Lilloa 25: 549 (1952).
Syn.: *Pernettya myrtilloides* var. *nana* (Sleumer) Sleumer, Bot. Jahrb. Syst. 104: 473 (1985).

Gaultheria pumila (L.f.) Middleton, **comb. nov.**
Basionym: *Arbutus pumila* L.f., Suppl. Pl. 239 (1781).
Syn.: *Pernettya pumila* (L.f.) Hook., Icon. Pl. 1: t.9 (1837).

var. **leucocarpa** (DC.) Middleton, **comb. nov.**
Basionym: *Pernettya leucocarpa* DC., Prodr. 7: 586 (1839).
Syn.: *Pernettya pumila* var. *leucocarpa* (DC.) Kausel, Revista Univ., Santiago 34: 161 (1949).

var. **crassifolia** (Philippi) Middleton, **comb. nov.**
Basionym: *Pernettya crassifolia* Philippi, Linnaea 29: 10 (1858).
Syn.: *Pernettya pumila* var. *crassifolia* (Philippi) Sleumer, Lilloa 25: 539 (1952).

Gaultheria purpurascens Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 882 (1819).
Syn.: *Pernettya hirta* (Willd.) Sleumer, Bot. Jahrb. Syst. 78: 478 (1959).

Gaultheria racemulosa (DC.) Middleton, **comb. nov.**
Basionym: *Pernettya racemulosa* DC., Prodr. 7: 588 (1839).
Syn.: *Pernettya rigida* (Bertero in Colla) DC., Prodr. 7: 587 (1839).

Gaultheria tasmanica (Hook. f.) Middleton, **comb. nov.**
Basionym: *Pernettya tasmanica* Hook. f., London J. Bot. 6: 268 (1847).

Acknowledgements

Thanks are due to Dr H. Sleumer and Prof. P. Baas, of the Rijksherbarium in Leiden, for their help and to the Keepers of the following herbaria for the loan of herbarium material: AAU, B, BA, BM, C, CAL, CR, E, K, KLU, KUN, L, SP, WELT, Wisconsin. This work was carried out with the financial support of the Fullerton, Moir and Gray PhD scholarship at the University of Aberdeen.

References

Baas, P. (1985). Comparative leaf anatomy of *Pernettya* Gaud. (Ericaceae). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 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.

Burtt, B. L., Hedge, I. C. & Stevens, P. F. (1970). A taxonomic critique of recent numerical studies in Ericales and Salvia. *Notes from the Royal Botanic Garden Edinburgh* 30: 141–158.

Callan, H. G. (1941). The cytology of *Gaulthettya 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.

Corcoran, C. M. (1981). *A revision of the Mexican and Guatemalan taxa of Gaultheria (Ericaceae)*. PhD thesis, University of Wisconsin, Madison.

Drude, O. (1897). Ericaceae in Engler, A. & Prantl, K. (Eds) *Die Natürlichen Pflanzenfamilien* 4,1. Engelmann, Leipzig.

FRANKLIN, D. A. (1962). The Ericaceae in New Zealand (*Gaultheria and Pernettya*). *Transactions of the Royal Society of New Zealand (Botany)* 1: 155–173.

HOOKER, J. D. (1864). *Pernettya* in *Handbook of the New Zealand Flora*, pp. 174–176. Reeve & Co., London.

—— (1876). [Vacciniaceae and Ericaceae] in G. BENTHAM & J. D. HOOKER, *Genera Plantarum* vol. II, Part 2. pp. 564–604. Reeve & Co., London.

MARCHANT, W. J. (1937). *Choice trees, shrubs, wall plants and climbers*. Keepers Hill Nursery, Staplehill. Wimborne, Dorset.

MIDDLETON, D. J. (1989). *Taxonomic studies in the genus* Gaultheria *L. and related genera (Ericaceae)*. Unpublished PhD thesis, University of Aberdeen, Scotland.

—— & WILCOCK, C. C. (1990). Chromosome counts in *Gaultheria* and related genera. *Edinburgh Journal of Botany* 47: 303–313.

MULLIGAN, B. O. (1939). A probable bigeneric hybrid between *Gaultheria* and *Pernettya*. *Journal of the Royal Horticultural Society* 64: 125–127.

NIEDENZU, F. (1890). Über den anatomischen Bau der Laubblätter der Arbutoideae und Vaccinioideae in Beziehung zu ihrer systematischen Gruppierung und geographischen Verbreitung. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 11: 134–263.

ROLLINS, R. C. (1953). Cytogenetical approaches to the study of genera. *Chronica Botanica* 14: 133–139.

SKOTTSBERG, C. (1916). Die Vegetationsverhltnisse langs der Cordillera de los Andes S. von 41°S. *Konglingen Svenska Vetenskapsakadamiens Handligar* 56(5): 282.

SLEUMER, H. (1935). Revision der Gattung *Pernettya* Gaud. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 12: 626–655.

—— (1985). Taxonomy of the genus *Pernettya* Gaud. (Ericaceae). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 105: 449–480.

STEVENS, P. F. (1969). *Taxonomic studies in the Ericaceae*. PhD thesis, University of Edinburgh.

—— (1971). A classification of the Ericaceae: subfamilies and tribes. *Botanical Journal of the Linnean Society* 64: 1–53.

WATSON, L., WILLIAMS, W. T. & LANCE, G. N. (1967). A mixed data numerical approach to angiosperm taxonomy: the classification of Ericales. *Proceedings of the Linnean Society of London* 178: 25–35.

WEBB, D. A. (1972). Ericaceae in *Flora Europaea* 3: 5–18.

APPENDIX 1

Characters used in the principal components analysis

Plant prostrate; Plant erect < 1m; Plant erect > 1m

Leaf length 0–10mm; Leaf length 10–20mm; Leaf length 20–40mm; Leaf length 40–60mm; Leaf length > 60mm

Leaf width 0–5mm; Leaf width 5–10mm; Leaf width 10–20mm; Leaf width 20–40mm; Leaf width > 40mm

Petiole length < 1mm; Petiole length 1–3m; Petiole length > 3mm

Nervation melastomataceous; Reticulum prominent on both surfaces

Leaves deciduous

Margin entire
Leaf tip mucronate; Leaf tip acuminate; Leaf tip acute; Leaf tip obtuse
Leaf base cuneate; Leaf base obtuse; Leaf base truncate; Leaf base cordate
Multicellular hairs on leaf; Unicellular hairs on leaf
Multicellular hairs on stem; Unicellular hairs on stem
Uniseriate hairs present on the plant
Flowers solitary; Flowers fasciculate; Flowers racemose
Bracteoles 2; Bracteoles basal; Bracteoles on pedicel; Bracteoles apical
Pedicel length 0–2mm; Pedicel length 2–4mm; Pedicel length 4–6mm; Pedicel length >6mm
Multicellular hairs on pedicel; Unicellular hairs on pedicel
Flowers tetramerous
Calyx length 0–2mm; Calyx length 2–4mm; Calyx length >4mm
Calyx unicellular ciliate; Calyx glandular denticulate
Calyx with multicellular hairs; Calyx with unicellular hairs
Corolla urceolate; Corolla tubular; Corolla campanulate; Corolla infundibular
Corolla length 0–3mm; Corolla length 3–5mm; Corolla length 5–7mm; Corolla length >7mm
Corolla with multicellular hairs outside; Corolla with unicellular hairs outside; Corolla with unicellular hairs inside
Filament length 0–2mm; Filament length 2–4mm; Filament length >4mm
Filament dilated
Filament papillose; Filament pubescent
Anther length 0–1mm; Anther length 1–2mm; Anther length 2–3mm; Anther length >3mm
Tubule present on the anther
Only 1 awn
Awn length 0–0.2mm; Awn length 0.2–0.8mm; Awn length 0.8–1.5mm; Awn length >1.5mm
Ovary pilose
Style pilose
Ovary semi-inferior
Fruit a capsule
Calyx inflated in fruit

APPENDIX 2

The 14 species of *Pernettya* and their names in *Gaultheria*

P. alpina D. Franklin = *G. nubicola* Middleton
P. hirta (Willd.) Sleumer = *G. purpurascens* HBK.
P. howellii Sleumer = *G. howellii* (Sleumer) Middleton
P. insana (Molina) Gunckel = *G. insana* (Molina) Middleton
P. lanceolata (Hook. f.) Burtt & Hill = *G. lanceolata* Hook. f.
P. macrostigma Colenso = *G. macrostigma* (Colenso) Middleton
P. marginata N. E. Brown = *G. marginata* (N. E. Brown) Middleton
P. mucronata (L.f.) Gaud. ex Sprengel = *G. mucronata* (L.f.) Hook. & Arn.
P. myrtilloides Zucc. ex Steudel = *G. poeppigii* DC.
P. nana Colenso = *G. parvula* Middleton
P. prostrata (Cav.) DC. = *G. myrsinoides* HBK.
P. pumila (L.f.) Hook. = *G. pumila* (L.f.) Middleton
P. rigida (Bertero in Colla) DC. = *G. racemulosa* (DC.) Middleton
P. tasmanica Hook. f. = *G. tasmanica* (Hook. f.) Middleton