EDINB. J. BOT. 47(3): 303–313 (1990)

CHROMOSOME COUNTS IN *GAULTHERIA* AND RELATED GENERA

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

The chromosome numbers of 32 taxa in the '*Gaultheria* group' of genera of the tribe Andromedeae in the Ericaceae have been counted; 15 of these have been counted for the first time. All taxa counted in *Gaultheria* and *Leucothoë* have a chromosome number based on x = 11. The chromosome numbers counted in *Diplycosia* are 2n = 36 and in *Zenobia* 2n = c.66. *G. insana* and *G. procumbens* show different polyploid races: *G. insana* tetraploids and hexaploids and *G. procumbens* diploids, tetraploids and octoploids.

INTRODUCTION

The Ericaceae has been relatively little studied cytologically. Despite this Raven (1975) was able to make suggestions as to the ancestral basic numbers of the Ericales and Ericaceae. He proposed that the original basic chromosome number of the Ericales was x = 6 (as is found in the Epacridaceae) and that the Ericaceae was derived from this with a basic number of x = 12. From this there have been frequent dysploid derivatives especially to form x = 11 and x = 13. Chromosome numbers in the Ericaceae are summarized in Table 1.

The only large genera in the Ericaceae studied in detail are *Rhododendron* (Janaki Ammal et al., 1950; Jones & Brighton, 1972) and *Arctostaphylos* (Wells, 1968), although many smaller studies have been made on *Vaccinium* (e.g. Hall & Galleta, 1971). Chromosome numbers are known for only a very small percentage of the c.665 species of *Erica*, the second largest genus in the family.

Twenty species of the '*Gaultheria* group' have been studied cytologically. This group of genera, within the tribe Andromedeae, consists of *Gaultheria* L. (including *Chiogenes* Salisb.), *Pernettya* Gaud., *Leucothoë* Don, *Zenobia* Don, *Diplycosia* Bl., *Pernettyopsis* King & Gamble and *Tepuia* Camp (Stevens, 1969, 1971). *Diplycosia* and *Pernettyopsis* are confined to South Eastern Asia; *Tepuia* to Venezuela; *Zenobia* to North America; *Leucothoë* is found in North America and Eastern Temperate Asia; *Pernettya* in Australasia and South and Central America; and *Gaultheria* is found in North, Central and South America, Australasia and Eastern Asia. The generic limits within the group have been studied by Middleton (1989) with the conclusion that *Pernettya* cannot be maintained as a genus distinct from *Gaultheria* (Middleton & Wilcock, 1990). Half of the previous chromosome number reports for this group are from Callan (1941) and almost all are summarized in Darlington & Wylie (1955), Bohkhovskikh et al. (1969), Moore (1973, 1974, 1977) and Goldblatt (1981, 1984, 1985). These results are presented in Table 2.

The earliest report of a chromosome number in this group was by Hagerup (1928)

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

Table 1. A summary of the chromosome numbers in the Ericaceae compiled from Bohkhovskikh et al. (1969), Moore (1973, 1974, 1977), Goldblatt (1981, 1984, 1985) and Argent & Brunton (1984).

	Genus	Somatic chromosome number	Probable basic chromosome number
Rhododendroideae			
Daboecieae	Daboecia	24	12
Cladothamneae	Elliotia	22	11
Epigeae	Epigaea	24	12
Rhodoreae	Rhododendron	26, 30, 52, 78, 156	13
	Ledum	26, 52	13
	Menziesia	26	13
Phylodoceae	Leiophyllum	24	12
	Loeseleuria	24	12
	Kalmia	24, 44, 48	12, (11?)
	Phyllodoce	24	12
	Rhodothamnus	24	12
Ericoideae			
Ericeae	Erica	24	12
	Bruckenthalia	36	9 or 18
Calluneae	Calluna	16	8
Vaccinioideae			
Arbuteae	Arbutus	26	13
	Arctostaphylos	26, 39, 52, 65, 72	13, (12?)
	Arctous	26	13
Enkiantheae	Enkianthus	22, 60, 88	11, (10?)
Cassiopeae	Cassiope	26	13
	Harrimanela	32, 48	8 or 16
Andromedeae	Agarista	24	12
	Agauria	24	12
	Chamaedaphne	22	11
	Diplycosia	36	9 or 18
	Gaultheria	22, 24, 26, 44, 48, 66, 88, 96	11,12,13
	Leucothoë	22	11
	Lyonia	24	12
	Oxydendrum	24, 48	12
	Pieris	24	12
Vaccinieae	Dimorphanthera	48	12
	Diogenesia	48	12
	Gaylussacia	24, 48	12
	Gonocalyx	48	12
	Pentapterigium	24	12
	Symphysia	48	12
	Vaccinium	24, 36, 48, 72	12

where a count of n = 48 was obtained for *Gaultheria shallon*. This would make this species an octoploid based on x = 12. Callan (1941) was primarily concerned with the hybrid origin of × *Gaulnettya wisleyensis* but he also reported the chromosome numbers of 12 species of *Gaultheria* (four of which were reported as species of *Pernettya*). In the original paper he gave the chromosome number for seven species of *Pernettya* but three of these are synonyms of *P. prostrata* (= *Gaultheria myr-*

Table 2. Published chromosome numbers in the *Gaultheria* group of genera.

Species	n	2n	Range of species	Reference
Gaultheria antipoda		22	New Zealand	1
G. cuneata		22	Himalayas	1
G. domingensis		22	West Indies	2
G. fragrantissima	22		Himalayas/Khasia	3
G. fragrantissima	22		Himalayas/Khasia	4
G. glomerata		22	Andes	1
G. griffithiana		44	Himalayas	1
G. hispida		22	Tasmania	1
G. hispidula (a)		24	North America	5
G. hispidula (b)		24	North America	6
G. hispidula		24	North America	7
G. hispidula		24	North America	8
G. insana (c)		66	Temp. South America	1
G. itoana		26	Taiwan	1
G. leschenaultii (d)	24		Southern India/Sri Lanka	9
G. leucocarpa	22		Himalayas to Malesia	10
G. leucocarpa (e)		44	Himalayas to Malesia	1
G. mucronata (f)		66	Temp. South America	1
G. myrsinoides (g)		44	C & S America	1
G. myrsinoides (h)		44	C & S America	1
G. myrsinoides (i)		44	C & S America	1
G. myrsinoides (j)		44	C & S America	1
G. procumbens	24		North America	11
G. procumbens	22		North America	12
G. procumbens	44		North America	12
G. procumbens		22	North America	7
G. racemulosa (k)	33		Juan Fernandez	13
G. shallon	48		North America	14
G. shallon		88	North America	1
G. shallon	44		North America	15
G. tasmanica (l)		22	Tasmania	1
Leucothoë fontanesiana (m)		22	North America	16
Diplycosia heterophylla	18		Malesia	17

References: 1. Callan, 1941; 2. Hersey & Vander Kloet, 1976; 3. Mehra & Bawa, 1969; 4. Mehra, 1976; 5. Löve & Löve, 1966; 6. Löve & Löve, 1973; 7. Löve & Löve, 1982a; 8. Löve & Löve, 1982b; 9. Guljeet Singh & Gill, 1984; 10. Argent & Brunton, 1984; 11. Newcomer, 1941; 12. Nesom, 1978; 13. Sanders et al., 1983; 14. Hagerup, 1928; 15. Pojar, 1974; 16. Rudenberg, 1963; 17. Ratter & Milne, 1973.

Notes:

a) Löve & Löve always report *G. hispidula* as *Chiogenes hispidula*.

b) It is unclear from the paper whether this is a new count or whether they are referring to their earlier result.

c) Reported as *Pernettya furiens* which is a synonym of *G. insana*.

d) Described in the authors' paper as *G. fragrantissima* which seemed unlikely due to its site of collection. The voucher specimen has been seen and identified as *G. leschenaultii*.

e) Reported as *G. cumingiana*, a synonym of *G. leucocarpa*.

f) Reported as *Pernettya mucronata*, a synonym of *G. mucronata*.

g) Reported as *P. prostrata*, a synonym of *G. myrsinoides*.

h) Reported as *P. pentlandii*, a synonym of *G. myrsinoides*.

i) Reported as *P. ciliata*, a synonym of *G. myrsinoides*.

j) Reported as *P. buxifolia*, a synonym of *G. myrsinoides*.

k) Reported as *P. rigida*, a synonym of *G. racemulosa*.

l) Reported as *P. tasmanica*, a synonym of *G. tasmanica*.

m) Callan (1941) also reported a count for *Leucothoë acuminata* but this species is in that section of *Leucothoë* now treated as the genus *Agarista*.

sinoides—see Middleton & Wilcock, 1990). All except one of these species were found to have a chromosome number based on x = 11. *Gaultheria itoana* was reported as 2n = 26 and Callan suggested that this could have been ancestral as x = 13 is the basic number of other groups in the Ericaceae. Callan obtained a chromosome number for *G. shallon* of 2n = 88, not 2n = 96 as was reported by Hagerup (1928).

Since then only scattered work has added to this list including numbers of 2n = 22, 24, 44 and 88 for *G. procumbens* (Newcomer, 1941; Löve & Löve, 1982a; Nesom, 1978). Nesom pointed out that this would mean that both *G. shallon* and *G. procumbens* had two different basic numbers with x = 11 and x = 12 if all these counts were reliable. A basic number of x = 12 has also been reported in *G. leschenaultii*, n = 24 (Gulgeet Singh & Gill, 1984) and in *G. hispidula*, 2n = 24 (Löve & Löve, 1966, 1973, 1982a, 1982b). The reported numbers for *G. hispidula* have been used by Löve & Löve (1973) to reinstate the genus *Chiogenes*, which they suggest may be more closely related to *Vaccinium* than to *Gaultheria*.

Very few Latin American species of any genera of the Ericaceae have been studied cytologically, including *Gaultheria*. Numbers are known only for *G. domingensis*, 2n = 22, *G. glomerata*, 2n = 22, *G. insana*, 2n = 66, *G. mucronata*, 2n = 66, *G. myrsinoides*, 2n = 44, and *G. racemulosa*, n = 33, the last four species all previously being treated as species of *Pernettya*. In the other genera of the *Gaultheria* group, *Leucothoë* is known from one count of 2n = 22 for *L. fontanesiana* and *Diplycosia* from one count of n = 18 for *D. heterophylla*. Chromosome numbers are unreported for *Zenobia*, *Pernettyopsis* and *Tepuia*.

No karyotype work has been done on members of this group although Callan's diagrams show that the chromosomes are all metacentric and extremely small (1–2μm). Hall & Galleta (1971), in a more detailed study of the karyotype of some species of *Vaccinium*, found a similar morphology. All the chromosomes were metacentric with the chromosome lengths ranging from 1.2–3μm.

The work done so far suggests that the *Gaultheria* group has a chromosome complement based on x = 11 with a few exceptions: *G. itoana* x = 13, *G. hispidula* and *G. leschenaultii* x = 12, and *G. procumbens* and *G. shallon* apparently with two different basic chromosome numbers and polyploid with x = 11 and x = 12. It is not clear what the basic number of *Diplycosia* would be.

Materials and Methods

Cuttings of species of the *Gaultheria* group were collected from the Cruickshank Botanic Garden, Aberdeen, the Royal Botanic Garden Edinburgh, and the Royal Botanic Gardens, Kew, and thereafter were propagated in Aberdeen. A number of specimens were also grown from seed collected in Ecuador.

Young flower buds collected between April and May were fixed in glacial acetic acid:ethanol (1:3) overnight and then washed in two changes of 75% ethanol for an hour each time. The buds were transferred to vials with alcoholic hydrochloric acid-carmine, prepared according to Snow (1963), for bulk staining and left for at least 24 hours at room temperature. The stamens were teased open in 45% acetic acid and the pollen mother cells spread out and examined for divisions. It proved difficult to find cells undergoing meiosis and those cells which were dividing were often difficult to count as the chromosomes were prone to clumping (cf. Hagerup, 1928).

More satisfactory results were obtained for root tips. Root tips from actively growing roots were collected at noon between April and July and placed in a saturated solution of 1-bromo-naphalene for four hours. These roots were immediately fixed in 10ml of glacial acetic acid:ethanol (1:3) with a single drop of a saturated solution of $FeCl_3$ and left overnight. The roots were softened in 45% acetic acid at 60°C for ten minutes and washed in two applications of 75% ethanol for an hour each time. They were stained in the same way as the buds, squashed under a coverslip in 45% acetic acid and examined for divisions.

Voucher specimens are deposited in the Herbarium of Aberdeen University, ABD.

RESULTS

The results are presented in Table 3. Camera lucida drawings of some species are presented in Figure 1.

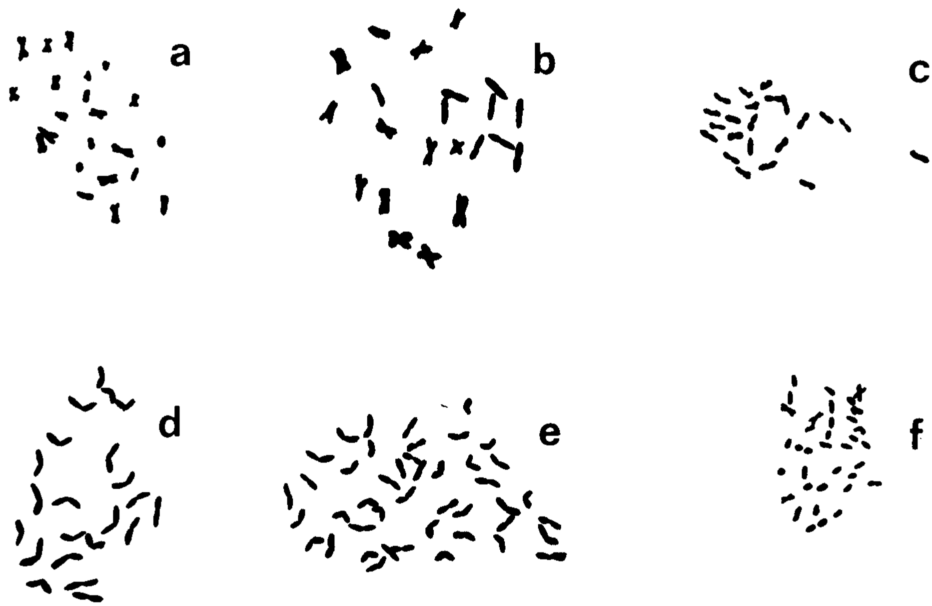

FIG. 1. Camera lucida drawings of species of *Gaultheria* and *Diplycosia*. a, *Gaultheria glomerata* 2n = 22 (*Middleton* 115); b, *G. hispidula* 2n = 22 (RBG Edinb. 715886); c, *G. itoana* 2n = 22 (RBG Edinb. 694479); d, *G. rigida* 2n = 22 (Middleton 104); e, *G. myrsinoides* (syn.: *Pernettya prostrata*) 2n = 44 (RBG Edinb. 791322); f, *Diplycosia elliptica* 2n = 36 (RBG Edinb. 680607). All × 2100.

Table 3. Chromosome numbers obtained in this study. *denotes a new count for the taxon. Edin = RBG, Edinburgh with accession number, Middleton = Collection deposited in the herbarium of Aberdeen University, Cruickshank = specimens from Cruickshank Botanic Garden, Aberdeen, K = RBG, Kew with accession number.

Species	Reference	Range of species	n	2n
Gaultheria adenothrix (Miq) Maxim	Edin 550081	Japan		22*
G. antipoda Forst. f.	Cruickshank	New Zealand		22
G. cuneata Bean	Edin 091023	Himalayas		c.22
G. cuneata Bean	Cruickshank	Himalayas	11	
G. glomerata (Cav.) Sleumer	Middleton 115	Andes		22
G. griffithiana Wight	Edin 080011	Himalayas		c.44
G. hispidula (L.) Muhlenb.	Edin 715886	North America		22
G. hookeri Clarke	Edin 760859	Himalayas		c.44*
G. insana (Molina) Middleton	Edin 754015	Temp. S America		44
G. insana (Molina) Middleton	Edin 340432	Temp. S America		44
G. itoana Hayata	Edin 694479	Taiwan		22
G. leschenaultii DC.	Edin 690828	S India/Sri Lanka		c.44
G. leucocarpa Bl.	Edin 762226	Himalayas to Malesia		44
G. mucronata (L.f.) Hook. & Arn.	Edin 590203	Temp. S America		c.66
G. mucronata var. angustifolia (Lindl.) Middleton	Edin 695629	Temp. S America	c.33*	
G. myrsinoides HBK	Edin 791322	Andes		44
G. nummularioides D. Don	Edin 762226	Himalayas to Malesia		44*
G. nummularioides D. Don	Edin 361074	Himalayas to Malesia		44
G. poeppigii DC.	Edin 761121	Temp. S America		c.66*
G. procumbens L.	Edin 752079	North America		c.44
G. pumila (L.f.) Middleton	Edin 256027	Temp. S America		44*
G. pumila var. leucocarpa (DC.) Middleton	Edin 653658	Temp. S America		44*
G. reticulata HBK	Middleton 63	Andes		44*
G. rigida HBK	Middleton 104	Andes		22*
G. shallon Pursh.	Cruickshank	North America	c.44	
G. tasmanica (Hook. f.) Middleton	Edin 695635	Tasmania		22
G. thymifolia Stapf ex Airy-Shaw	Cruickshank	Himalayas		c.44
Leucothoë axillaris (Lam.) D. Don	Edin 731434	North America		22*
L. axillaris (Lam.) D. Don	Edin 805055	North America		c.22
L. fontanesiana (Steud.) Sleumer	Edin 754011	North America	11	
L. fontanesiana (Steud.) Sleumer	Edin 754099	North America		22
L. fontanesiana (Steud.) Sleumer	Edin 754007	North America		22
L. racemosa Gray	K 010-79-00041	North America		22*
Diplycosia carrii Sleum.	Edin 820918	Malesia		c.36*
D. elliptica Ridl.	Edin 680607	Malesia		36*
D. heterophylla Bl.	Edin 842319	Malesia		36
D. myrtillus Stapf	Edin 820877	Malesia		34–36*
Zenobia pulverulenta (Bartr.) Pollard	Edin 721932	North America		c.66*

Discussion

Without exception chromosome numbers found in this study were based on x = 11 for *Gaultheria* and *Leucothoë*. *Zenobia pulverulenta* was found to be 2n = c.66, possibly x = 11. The species of *Diplycosia* studied were all 2n = 36 or 2n = 34–36. Outside this group basic numbers of x = 11 are known with certainty only in *Elliotia* of Rhododendroideae-Cladothamneae, *Chamaedaphne* of Vaccinioideae-Andromedeae and *Enkianthus* of Vaccinioideae-Enkiantheae. Where chromosome numbers are known for other members of the Andromedeae they are based on x = 12 (Table 1).

Some of the counts obtained are particularly interesting. *Gaultheria itoana* has a chromosome number of 2n = 22 (Fig. 1). Callan (1941) obtained 2n = 26 for this species. *G. itoana* is closely related to *G. cuneata* which in both Callan's and this study was found to have 2n = 22. The number 2n = 22 is in accord with most counts in the group and the same as *G. cuneata*.

A single count for *G. hispidula* of 2n = 22 was obtained (Fig. 1). This species has been treated in the past as the monotypic genus *Chiogenes* although recent authors have mostly agreed that there is no morphological basis for recognizing it as separate from *Gaultheria* (see Airy-Shaw, 1940). Three (or possibly four) previous counts by Löve & Löve were reported as 2n = 24. It is clear that more detailed study is needed on this species to interpret this variation. However, we cannot agree with the conclusions Löve & Löve (1973) reached on the status of this species based on chromosome number alone. They concluded that because x = 12 was found in *G. hispidula* and *Gaultheria* sensu stricto is based on x = 11, the genus *Chiogenes*, with the single species *C. hispidula* (including var. *japonica*), should be reinstated. To quote from their paper the two different basic chromosome numbers provide '...as clear a demonstration as possible that these taxa are distinct genera and have not evolved linearly from the same ancestor'. The morphological differences used to illustrate the differences between these two genera demonstrated that they were unaware of the range of variation in the genus *Gaultheria*. Their study also overlooked the fact that basic numbers of x = 12 had been recorded for *G. shallon* and *G. procumbens* and since then also for *G. leschenaultii*. These species are not closely related to each other. The chromosome number obtained of 2n = 22 for *G. hispidula*, which gives a basic number of x = 11, agrees with the majority of species in the genus and supports the commonly accepted view on the generic status of this taxon as *Gaultheria hispidula*.

The basic number of x = 12 previously suggested for a few species of *Gaultheria* sensu stricto and of x = 11 for *G. hispidula* in this study demonstrate that without more cytological work it is impossible to make firm conclusions on generic status based solely on chromosome number. Löve & Löve's suggestion that *Chiogenes* has its affinities with *Vaccinium*, based on the same basic number of x = 12, overlooks the fact that even if *Chiogenes* were reinstated its morphological similarities are with the tribe Andromedeae in which a number of genera with x = 12 have already been reported (see Table 1).

Numbers of 2n = 44 for two individuals of *Gaultheria insana* were obtained. Callan (1941) found this species to have 2n = 66 (referring to it as *Pernettya furiens*). This suggests that this species has both tetraploid as well as hexaploid races. Similarly *G. procumbens* has been reported as diploid, tetraploid and octoploid (Nesom, 1978; Löve & Löve, 1982a). All other species where more than one specimen has been studied showed no variation in chromosome number. It would be interesting to have a clearer idea of the geography of these different chromosome races and to determine whether there are any other characters associated with them.

From this work and from previous counts it can be seen that the larger Asian species of Airy-Shaw's section *Leucothoides* (all species in Asia which have been counted except for *G. nummularioides*, *G. leucocarpa* and *G. thymifolia*) are tetraploid. Those Airy-Shaw recognized as a group of species with a sympodial relation of the inflorescence to the main vegetative axis, *G. cuneata* and *G. itoana*, are diploids. This may suggest at least two lines of evolution within this section, one proceeding after an initial tetraploid increase and one remaining at the diploid level.

One each of Airy-Shaw's section *Gymnobotrys* and series *Trichophyllae* are known chromosomally, *G. leucocarpa* and *G. thymifolia* respectively. Both are tetraploids.

There is a great lack of cytological information in the large group of tropical Latin American species of *Gaultheria*. Counts are known for only five species: *G. glomerata* (Fig. 1), *G. domingensis*, *G. rigida* (Fig. 1), *G. reticulata* and *G. myrsinoides* (Fig. 1). Both diploids and tetraploids occur in this group of species.

The species counted which were previously included in the genus *Pernettya* (*G. insana*, *G. mucronata*, *G. myrsinoides*, *G. poeppigii*, *G. pumila*, *G. racemulosa* and *G. tasmanica*) have rather high chromosome numbers, generally speaking, with hexaploids recorded in four species and tetraploids in three. Only one species is so far known to be diploid, *G. tasmanica*.

Knaben & Engelskjøn (1968) suggested that polyploidy was an important mode of species formation in many genera of the Ericaceae. Wells (1968) stated that in *Arctostaphylos* there was morphological evidence to suggest that some of the tetraploids had been derived through allopolyploidy, i.e. from hybridization of two diploid species followed by chromosome doubling. Distributional and ecological facts also provided strong support for their origin through amphidiploidy. In the light of the common occurrence of hybrids, this may also have been an important mode of species formation in the *Gaultheria* group.

Janaki Ammal (1950) suggested that 'polyploidy has been one of the ways in which [*Rhododendron*] species have been able to combat the difficulties of altitude'. In Gaultheria there does not appear to be a noticeable increase in polyploidy with altitude. Instead the hexaploids and octoploids have so far been found only in temperate regions of North and South America although diploids are also found at these latitudes. Also, in *Rhododendron* there are strong concentrations of polyploids geographically and taxonomically: almost all the polyploids in this genus are confined to the Himalayas and none have been found in the tropics (Janaki Ammal, 1950; Jones & Brighton, 1972). Diploids have been found only in the elepidote *Rhododendron* species, considered to be the most primitive group.

These conclusions cannot be reached in *Gaultheria*. Referring to *Gaultheria* and *Pernettya* Camp (1947) stated that 'there seems to be a concentration of diploid species in the far South'. More recent information has shown this to be incorrect. It is true that all three Australian and New Zealand species so far studied are diploids, but diploids are also present in the Himalayas (*G. cuneata*), Taiwan (*G. itoana*) and North America (*G. procumbens*, *G. adenothrix*). He claimed that the basic number of x = 11 was 'known only from the lower three fourths' of the range of *Gaultheria* and that x = 12 and x = 13 were found only in the 'upper (northern) part'. This was incorrect even with the information he had access to as it was known at that time that *G. shallon* from North America had a basic chromosome number of x = 11 (Callan, 1941). In the *Gaultheria* group both diploids and tetraploids occur throughout the geographical distribution and across the range of morphological variation. Diploids and tetraploids occur in North and South America and in Asia. They also occur in species with flowers in racemes and species with solitary flowers. It is interesting that only diploids have so far been found in *Leucothoë* which Airy-Shaw (1940) thought may be a more primitive type closely linked to *Gaultheria*. *Zenobia*, however, has a chromosome number of 2n = c.66 indicating that it is a possible hexaploid.

Argent & Brunton (1984) pointed out that *Gaultheria* differed from *Diplycosia* in chromosome number based on a count for *D. heterophylla* of n = 18 (Ratter & Milne, 1973). The new counts for four species of *Diplycosia*, all of which are 2n = 36 or about 2n = 36 (e.g. *D. elliptica*—Fig. 1), add further support to the cytological difference between the two genera.

Figure 1 shows that the chromosomes vary in size between species but not enough sampling within species or detailed studies on the chromosome size has been done to know whether this is significant or not. The chromosomes are all metacentric and 0.5–2.1 μm long.

No chromosome counts exist for *Pernettyopsis* and *Tepuia*. It would be interesting to know the chromosome number for *Pernettyopsis* to see if it is similar to *Diplycosia* with which it is closely related and possibly congeneric. Despite the uniformity of basic numbers in *Gaultheria*, *Leucothoë* and *Zenobia* considerable interest still remains for further study, particularly into the apparent occurrence of two basic chromosome numbers in *G. hispidula*, *G. procumbens*, *G. shallon* and *G. leschenaultii*.

Acknowledgements

The authors would like to thank Dr Kwiton Jong for his help and suggestions with the chromosome counts. Thanks are also due to the Royal Botanic Gardens at Edinburgh and Kew and the Cruickshank Botanic Garden, Aberdeen for the use of material.

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