

## New combinations and new and resurrected names in *Gaultheria* (Ericaceae)

K.A. Kron<sup>1</sup>, P.W. Fritsch<sup>2</sup>, L. Lu<sup>3</sup> & W.S. Judd<sup>4</sup>

<sup>1</sup>Department of Biology, 226 Winston Hall, Box 7325 Reynolda Station, Wake Forest University, Winston-Salem, North Carolina 27109, USA

<sup>2</sup>Botanical Research Institute of Texas, 1700 University Drive, Fort Worth, TX 76107, USA  
pfritsch@brit.org

<sup>3</sup>School of Pharmaceutical Sciences and Yunnan Key Laboratory of Pharmacology for Natural Products, Kunming Medical University, CN-650500 Kunming, Yunnan, China

<sup>4</sup>Department of Biology, University of Florida, 220 Bartram Hall, P.O. Box 118525, Gainesville, Florida 32611, USA

**ABSTRACT.** The Wintergreen Group clade of the tribe Gaultherieae (Ericaceae: subfam. Vaccinioideae) comprises the genera *Diplycosia* Blume, *Gaultheria* L., and *Tepuia* Camp. Phylogenetic analysis has demonstrated that *Gaultheria* is not monophyletic, with *Diplycosia* and *Tepuia* nested within it. On morphological grounds, the recognition of a single genus in the Wintergreen Group to establish monophyly as the basis for the classification is favoured over subdivision into smaller genera. Here, we make the taxonomic changes necessary for recognising *Gaultheria* as the sole genus constituting the Wintergreen Group. We make 126 new combinations, erect 17 new names, and resurrect four species names in *Gaultheria* for all species, varieties, and forms heretofore recognised in the literature under *Diplycosia* or *Tepuia*. Additionally we make two new combinations in *Gaultheria* at the sectional level to accommodate the species from *Diplycosia* and *Tepuia*, and provide lectotypes for *Pernettyopsis* King & Gamble and *Gaultheria* [unranked] *Amphicalyx* Endl.

**Keywords.** *Diplycosia*, Gaultherieae, *Tepuia*, wintergreen

### Introduction

The tribe Gaultherieae (Ericaceae: subfam. Vaccinioideae) comprises seven genera and c. 292 species distributed in East Asia, the Indian Subcontinent, Southeast Asia, Australasia, and the Americas (Middleton, 1991; Argent, 2002; Stevens et al., 2004; Bush et al., 2010; Lu et al., 2019a). Phylogenetic studies based on DNA sequence data have shown that three of these genera, i.e., *Gaultheria* L., *Diplycosia* Blume, and *Tepuia* Camp, form a strongly supported clade known informally as the Wintergreen Group (Kron et al., 1999; Powell & Kron, 2001; Bush et al., 2009; Fritsch et al., 2011). These studies also show that *Gaultheria* is not monophyletic and that *Diplycosia* and *Tepuia* are nested within it.

For the classification of the Gaultherieae to be based on monophyly, the number of genera in the Wintergreen Group requires either expansion or reduction. Expansion would impel the recognition of three more genera in the clade, two of which, i.e., the clades corresponding to *Gaultheria* ser. *Hispidulae* Airy Shaw and *Gaultheria* ser. *Gymybotrys* (Airy Shaw) D.J.Middleton (see Middleton, 1991 and Fritsch et al., 2011), would be straightforward in their morphological definitions. However, the third clade, i.e., that comprising *Gaultheria* sect. *Amblyandra* Airy Shaw through the Australia/New Zealand clade in Fritsch et al. (2011: Fig. 3), has never been named or otherwise recognised in any classification of the Gaultherieae. Moreover, we can detect no solid morphological basis that could warrant its recognition other than a possible reduction in seed size (Lu et al., 2010), despite its strong statistical support in DNA sequence-based phylogenetic studies (Bush et al., 2009; Fritsch et al., 2011; Lu et al., 2019b). We therefore consider it more appropriate to instead recognise the sole genus *Gaultheria* as comprising the entirety of the Wintergreen Group clade. The recognition of this one large genus is also in line with the general trend of recognising larger plant genera under the criterion of monophyly based at least in part on molecular phylogenetic data (Humphreys & Linder, 2009). With this circumscription, *Gaultheria* has the putative morphological synapomorphy of methyl salicylate produced in damaged tissues, and possibly an accrescent mature fleshy calyx and obliquely pyramidal seeds, although all of these features apparently have been lost or modified in some derived lineages within the clade multiple times (Powell & Kron, 2001; Bush et al., 2009; Lu et al., 2010; Fritsch et al., 2011).

We are preparing a formal revised sectional classification of *Gaultheria* based on a synthesis of morphological and molecular data. During the process of completing the revision, the need for the timely publication of the revised species taxonomy based on the phylogenetic data has become apparent. For example, ongoing floristic projects such as the *Flora of Peninsular Malaysia* series (Kiew et al., 2007) often wish to base their taxonomy on monophyletic groups whenever possible. Accordingly, here we provide the new combinations and new and resurrected names in *Gaultheria* (Ericaceae) resulting from the placement of *Diplycosia* and *Tepuia* into the synonymy of *Gaultheria*.

## Methods

The infrageneric names transferred (species, varieties, and forms) are those of taxa currently recognised in major publications that cover the entirety of the infrageneric taxonomy of *Diplycosia* and *Tepuia*. The names transferred from *Diplycosia* are those accepted in Sleumer's (1957) revision of *Diplycosia*, Sleumer's *Flora Malesiana* treatment (1966–1967), and new taxa from the region published since (Argent, 1982, 1989, 2002, 2013, 2014, 2018; Ferreras & Argent, 2011; Argent & Widjaja, 2015; Fritsch & Bush, 2016; Fritsch & Amoroso, 2016, 2017; Wilkie & Argent, 2016; Mustaqim & Ardi, 2019; Mustaqim et al., 2019, 2020). Watthana (2010) and (2015) were also consulted for a more recent treatment of *Diplycosia* for Thailand. Panda

et al. (2012) consider *D. indica* Debta & H.J.Chowdhery, J. Bot. Res. Inst. Texas 3: 147 (2009) to be a heterotypic synonym of *Gaultheria akaensis* S.Panda & Sanjappa, Edinburgh J. Bot. 63: 15 (2006), and so a new combination is not made in *Gaultheria* for this species. The names transferred from *Tepuia* are those recognised by Luteyn (1995) in the treatment of the genus for *Flora Neotropica*. Most of the transferred names retain the original epithet as described in *Diplycosia* or *Tepuia*. In cases where a new (replacement) name was required, the epithets often refer to either the locality of the type of the taxon as indicated in the original description, or a botanist in honour of significant contributions to science.

### Taxonomy

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

*Brossaea* L., Sp. Pl. 2: 1190 (1753). – TYPE: *Brossaea coccinea* L. (= *Gaultheria domingensis* Urb.).

*Hippomanica* Molina, Sag. Stor. Nat. Chili 126 (1782). – TYPE: *Hippomanica insana* Molina (= *Gaultheria insana* (Molina) D.J.Middleton).

*Chiogenes* Salisb., Trans. Hort. Soc. London 2: 94 (1817). – TYPE: *Vaccinium hispidulum* L. (= *Gaultheria hispidula* (L.) Muhl. ex Bigelow).

*Shallonium* Raf., Amer. Monthly Mag. & Crit. Rev. 2(4): 266 (1818). – TYPE: *Shallonium serrulatum* Raf. (= *Gaultheria shallon* Pursh).

*Pernettya* Gaudich., Ann. Sci. Nat. (Paris) 5: 102 (1825) [as ‘*Pernettia*’]. – TYPE: *Pernettya pumila* (L.f.) Hook. (= *Gaultheria pumila* (L.f.) D.J.Middleton).

*Diplycosia* Blume, Bijdr. Fl. Ned. Ind. 15: 857 (1826). – TYPE: *Diplycosia heterophylla* Blume, lectotype designated by Sleumer (1957) (= *Gaultheria heterophylla* (Blume) Endl. ex Hassk.).

*Pernettyopsis* King & Gamble, J. Asiat. Soc. Bengal, Pt. 2, 74: 79 (1906 [‘1905’]). – TYPE: *Pernettyopsis malayana* King & Gamble, lectotype designated here (= *Gaultheria macrocalyx* Kron & P.W.Fritsch).

*Tepuia* Camp in Gleason & Killip, Brittonia 3: 178 (1939). – TYPE: *Tepuia tatei* Camp (= *Gaultheria campii* Kron & P.W.Fritsch).

*Distribution.* Approximately 292 species in East Asia (including Japan), Indian Subcontinent, Southeast Asia, Australasia, Americas.

***Gaultheria* sect. *Diplycosia*** (Blume) Kron & P.W.Fritsch, **comb. & stat. nov.** – *Diplycosia* Blume, Bijdr. Fl. Ned. Ind. 15: 857 (1826). – TYPE: *Diplycosia heterophylla* Blume, lectotype designated by Sleumer (1957) (= *Gaultheria heterophylla* (Blume) Endl. ex Hassk.).

*Gaultheria* [unranked] *Amphicalyx* Endl., Gen. Pl. 756 (1839). – TYPE: *Diplycosia heterophylla* Blume, lectotype designated here (= *Gaultheria heterophylla* (Blume) Endl. ex Hassk.).

*Pernettyopsis* King & Gamble, J. Asiat. Soc. Bengal, Pt. 2, 74: 79 (1906 [‘1905’]). – TYPE: *Pernettyopsis malayana* King & Gamble, lectotype designated above (= *Gaultheria macrocalyx* Kron & P.W.Fritsch).

*Distribution.* A section of 125 species in Thailand, Vietnam, Malaysia, Brunei, Indonesia and Papua New Guinea.

*Notes.* Almost all species previously described in *Diplycosia* and *Pernettyopsis* are now accommodated in *Gaultheria* sect. *Diplycosia*. As there is no competing name at the rank of section, we make the new combination *Gaultheria* sect. *Diplycosia* to preserve the connection to the genus name. “*Gaultheria* sect. *Amphicalyx* Endl.” was placed in synonymy of *Diplycosia* by Sleumer (1966–1967) but the name has never been validly published. This name was based on *Gaultheria* [unranked] *Amphicalyx* Endl. but as Sleumer included it only in synonymy it was not validated (see Turland et al., 2018: Art. 33.1).

1. *Gaultheria abanii* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia abanii* Argent, Gard. Bull. Singapore 54: 218 (2002).
2. *Gaultheria abscondita* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia abscondita* Sleumer, Blumea 11: 4 (1961).
3. *Gaultheria amboinensis* (Becc.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia amboinensis* Becc., Malesia 1: 210 (1878).
4. *Gaultheria annamensis* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Vaccinium pilosum* A.Chev. ex Dop in Lecomte, Fl. Indo-Chine 3: 705 (1930), non *Gaultheria pilosa* (Blume) Zoll. & Moritzi, Natuur- Geneesk. Arch. Ned.-Indië 2: 9 (1845). – *Diplycosia annamensis* Sleumer, Reinwardtia 4: 139 (1957).

*Notes.* Sleumer (1957) conferred the name *Diplycosia annamensis* to this taxon because of the name *Diplycosia pilosa* Blume, Bijdr. Fl. Ned. Ind. 15: 858 (1826). The epithet ‘*pilosa*’ cannot be used in *Gaultheria* for this species because of *Gaultheria pilosa* (Blume) Zoll. & Moritzi (1845).

5. *Gaultheria aperta* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia aperta* J.J.Sm., Bot. Jahrb. Syst. 68: 208 (1937).
6. *Gaultheria apiculifera* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia apiculifera* J.J.Sm., Repert. Spec. Nov. Regni Veg. 35: 296 (1934).
7. *Gaultheria apoensis* (Elmer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia apoensis* Elmer, Leaflet. Philipp. Bot. 3: 1101 (1911).
8. *Gaultheria argentii* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia hirtiflora* Argent, Notes Roy. Bot. Gard. Edinburgh 46: 17 (1989), non *Gaultheria hirtiflora* Benth., Pl. Hartw. 66 (1840).

*Notes.* The new epithet honours the British botanist Dr Graham Charles George Argent (1941–2019), leading authority on the taxonomy of the Ericaceae and who originally named this species.

9. *Gaultheria aurea* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia aurea* Sleumer, Bot. Jahrb. Syst. 71: 148 (1940).
10. *Gaultheria balgooyi* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia balgooyi* Argent, Edinburgh J. Bot. 71: 88 (2014).
11. *Gaultheria barbiger*a (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia barbiger*a Sleumer, Bot. Jahrb. Syst. 71: 149 (1940).
12. *Gaultheria bartolomei* (Ferreras & Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia bartolomei* Ferreras & Argent, Edinburgh J. Bot. 68: 39 (2011).
13. *Gaultheria beamanii* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia crenulata* Sleumer, Bot. Jahrb. Syst. 71: 153 (1940), non *Gaultheria crenulata* Kurz, J. Bot. 11: 195 (1873).

*Notes.* The new epithet honours Dr John H. Beaman (1929–2015) for significant contributions to our knowledge of the flora of Mt Kinabalu, to which this species is endemic, and who encouraged many undergraduate and graduate students to pursue plant systematics as a profession.

14. *Gaultheria beccarii* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia acuminata* Becc., Malesia 1: 212 (1878), non *Gaultheria acuminata* Cham. & Schltdl., Linnaea 5: 126 (1830).

*Notes.* The new epithet honours the Italian botanist Odoardo Beccari (1843–1920), a contemporary of Charles Darwin and Joseph Hooker, who made significant

contributions to the botany of Malesia, and who originally named this species and collected its type.

15. *Gaultheria benitotanii* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia benitotanii* Argent, Philipp. J. Syst. Biol. 12: 73 (2018).
16. *Gaultheria benomensis* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia lancifolia* Ridl., J. Straits Branch Roy. Asiat. Soc. 39: 15 (1903), non *Gaultheria lancifolia* Small, N. Amer. Fl. 29: 78 (1914).  
  
*Notes.* The new epithet refers to Gunung [Mount] Benom [= Benum], the locality from which the type specimen was collected.
17. *Gaultheria benomensis* Kron & P.W.Fritsch var. *calvescens* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia lancifolia* Ridl. var. *calvescens* Sleumer, Reinwardtia 4: 149 (1957).
18. *Gaultheria brachyantha* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia brachyantha* Sleumer, Reinwardtia 4: 138 (1957).
19. *Gaultheria brachyantha* (Sleumer) Kron & P.W.Fritsch var. *parvula* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia brachyantha* Sleumer var. *parvula* Sleumer, Reinwardtia 4: 139 (1957).
20. *Gaultheria capitata* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia capitata* Sleumer, Bot. Jahrb. Syst. 71: 149 (1940).
21. *Gaultheria capitata* (Sleumer) Kron & P.W.Fritsch var. *crassiramea* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia crassiramea* Sleumer, Reinwardtia 4: 141 (1957). – *Diplycosia capitata* Sleumer var. *crassiramea* (Sleumer) Argent, Edinburgh J. Bot. 71: 91 (2014).
22. *Gaultheria carrii* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia carrii* Sleumer, Reinwardtia 4: 129 (1957).
23. *Gaultheria caryophylloides* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia caryophylloides* J.J.Sm., Bot. Jahrb. Syst. 68: 209 (1937).
24. *Gaultheria caryophylloides* (J.J.Sm.) Kron & P.W.Fritsch var. *longipes* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia caryophylloides* J.J.Sm. var. *longipes* Sleumer, Reinwardtia 4: 144 (1957).
25. *Gaultheria caudatifolia* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia caudatifolia* Sleumer, Bot. Jahrb. Syst. 71: 150 (1940).



26. *Gaultheria celebensis* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia celebensis* J.J.Sm., Bull. Jard. Bot. Buitenzorg ser. 3, 1: 406 (1920).
27. *Gaultheria chrysothrix* (Stapf) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia chrysothrix* Stapf, Trans. Linn. Soc. London, Bot. 4: 191 (1894).
28. *Gaultheria ciliolata* (Hook.f.) F.Muell., Trans. Roy. Soc. Victoria 1(2): 21. (1889). – *Diplycosia ciliolata* Hook.f., Icon. Pl. 9: t. 894 (1852).
- Notes.* Although a combination in *Gaultheria* already exists for this species, it was recognised in *Diplycosia* by Sleumer (1957, 1966–1967); it is here returned to *Gaultheria*.
29. *Gaultheria cinnabarina* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia cinnabarina* Sleumer, Reinwardtia 4: 146 (1957).
30. *Gaultheria cinnamomifolia* (Stapf) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia cinnamomifolia* Stapf, Trans. Linn. Soc. London, Bot. 4: 195 (1894).
31. *Gaultheria clementium* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia clementium* Sleumer, Bot. Jahrb. Syst. 71: 151 (1940).
32. *Gaultheria coi* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia coi* Argent, Philipp. J. Sci. 142 (special issue): 52 (2013) [as *D. 'coii'*].
33. *Gaultheria commutata* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia commutata* Sleumer, Reinwardtia 4: 153 (1957).
34. *Gaultheria consobrina* (Becc.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia consobrina* Becc., Malesia 1: 211 (1878).
35. *Gaultheria edulis* (Schltr.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia edulis* Schltr., Bot. Jahrb. Syst. 55: 163 (1918).
36. *Gaultheria ensifolia* (Merr.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia ensifolia* Merr., J. Straits Branch Roy. Asiat. Soc. 76: 107 (1917).
37. *Gaultheria epiphytica* (H.R.Fletcher) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia epiphytica* H.R.Fletcher, Bull. Misc. Inform. Kew 1936: 40 (1936).
38. *Gaultheria eymae* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia stenophylla* Sleumer, Reinwardtia 4: 147 (1957), non *Gaultheria stenophylla* P.W.Fritsch & Lu Lu, Phytotaxa 201(1): 22 (2015).

*Notes.* The new epithet honours the Dutch botanist Dr Pierre Joseph Eyma (1903–1945), who collected the type of this species.

39. *Gaultheria filipes* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia filipes* Sleumer, Reinwardtia 4: 133 (1957).
40. *Gaultheria fimbriata* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia fimbriata* Sleumer, Blumea 12: 120 (1963).
41. *Gaultheria gajoensis* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia atjehensis* Sleumer, Reinwardtia 4: 132 (1957), non *Gaultheria atjehensis* J.J.Sm., Repert. Spec. Nov. Regni Veg. 35: 293 (1934).

*Notes.* The new epithet refers to the Gajo [Gayo] land, the locality of the type collection in Aceh Province on the island of Sumatra, Indonesia.

42. *Gaultheria gallowayana* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia gallowayana* Argent, Edinburgh J. Bot. 71: 96 (2014).
43. *Gaultheria glaucicaulis* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia glaucicaulis* Argent, Edinburgh J. Bot. 71: 99 (2014).
44. *Gaultheria glauciflora* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia glauciflora* Sleumer, Reinwardtia 4: 137 (1957).
45. *Gaultheria gracilipes* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia gracilipes* J.J.Sm., Bull. Jard. Bot. Buitenzorg ser. 3, 1: 407 (1920).
46. *Gaultheria haemantha* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia haemantha* Sleumer, Reinwardtia 4: 150 (1957).
47. *Gaultheria hendrianiana* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia hendrianiana* Argent, Edinburgh J. Bot. 71: 103 (2014) [as *D. 'hendriana'*].
48. *Gaultheria heterophylla* (Blume) Endl. ex Hassk., Cat. Hort. Bog., 160 (1844). – *Diplycosia heterophylla* Blume, Bijdr. Fl. Ned. Ind. 15: 858 (1826).

*Notes.* Although a combination in *Gaultheria* already exists for this species, it was recognised in *Diplycosia* by Sleumer (1957, 1966–1967); it is here returned to *Gaultheria*.

49. *Gaultheria heterophylla* (Blume) Endl. ex Hassk. var. *latifolia* (Blume) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia latifolia* Blume, Bijdr. Fl. Ned. Ind. 15: 858 (1826). – *Gaultheria latifolia* (Blume) Endl. ex Hassk., Cat. Hort. Bog.:



- 160 (1844). – *Diplycosia heterophylla* Blume var. *latifolia* (Blume) Sleumer, *Reinwardtia* 4: 156 (1957).
50. *Gaultheria jiewhoei* (Mustaqim) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia jiewhoei* Mustaqim, *Telopea* 22: 194 (2019).
51. *Gaultheria kalimantanensis* (P.Wilkie & Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia kalimantanensis* P.Wilkie & Argent, *Edinburgh J. Bot.* 73: 140 (2016).
52. *Gaultheria kalmiifolia* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia kalmiifolia* Sleumer, *Bot. Jahrb. Syst.* 71: 154 (1940).
53. *Gaultheria kemulensis* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia kemulensis* J.J.Sm., *Bull. Jard. Bot. Buitenzorg ser. 3*, 13: 459 (1935).
54. *Gaultheria kinabaluensis* (Stapf) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia kinabaluensis* Stapf, *Trans. Linn. Soc. London, Bot.* 4: 193 (1894).
55. *Gaultheria kitangladensis* (P.W.Fritsch) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia kitangladensis* P.W.Fritsch, *Nat. Hist. Bull. Siam Soc.* 62: 22 (2017).
56. *Gaultheria kjellbergii* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia kjellbergii* J.J.Sm., *Bot. Jahrb. Syst.* 68: 206 (1937).
57. *Gaultheria kosteri* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia kosteri* Sleumer, *Blumea* 12: 117 (1963).
58. *Gaultheria kostermansii* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia kostermansii* Sleumer, *Blumea* 11: 5 (1961).
59. *Gaultheria lamii* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia lamii* J.J.Sm., *Nova Guinea* 18: 99 (1936).
60. *Gaultheria lavandulifolia* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia lavandulifolia* Sleumer, *Blumea* 12: 121 (1963).
61. *Gaultheria ledermannii* (Schltr.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia ledermannii* Schltr., *Bot. Jahrb. Syst.* 55: 165 (1918).
62. *Gaultheria lilianae* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia lilianae* J.J.Sm. in Gibbs, *Fl. Arfak Mts.*: 170 (1917).

63. *Gaultheria loheri* (Merr.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia loheri* Merr., Philipp. J. Sci. 27: 44 (1925).
64. *Gaultheria lorentzii* (Koord.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia lorentzii* Koord., Nova Guinea 8: 881 (1912).
65. *Gaultheria lotungensis* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia lotungensis* Argent, Notes Roy. Bot. Gard. Edinburgh 46: 19 (1989).
66. *Gaultheria luzonica* A.Gray, Proc. Amer. Acad. Arts 5: 324. (1861). – *Diplycosia luzonica* (A.Gray) Merr., Philipp. J. Sci., C 2: 293 (1907).

*Notes.* Although originally described in *Gaultheria*, this species was recognised in *Diplycosia* by Sleumer (1957, 1966–1967); it is here returned to *Gaultheria*.

67. *Gaultheria luzonica* A.Gray var. *calelanensis* (Elmer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia calelanensis* Elmer, Leaf. Philipp. Bot. 3: 1103 (1911) [as *D. 'calelanense'*]. – *Diplycosia luzonica* (A.Gray) Merr. var. *calelanensis* (Elmer) Sleumer, Reinwardtia 4: 144 (1957).
68. *Gaultheria luzonica* A.Gray var. *merrittii* (Merr.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia merrittii* Merr., Philipp. J. Sci., C 2: 293 (1907). – *Diplycosia luzonica* (A.Gray) Merr. var. *merrittii* (Merr.) Sleumer, Reinwardtia 4: 144 (1957).
69. *Gaultheria luzonica* A.Gray var. *pubens* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia luzonica* (A.Gray) Merr. var. *pubens* Sleumer, Reinwardtia 4: 143 (1957).
70. *Gaultheria lysolepis* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia lysolepis* Sleumer, Bot. Jahrb. Syst. 72: 209 (1942).
71. *Gaultheria macrocalyx* Kron & P.W.Fritsch, **nom. nov.** – *Pernettyopsis malayana* King & Gamble, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74: 79 (1906 ['1905']), non *Gaultheria malayana* Airy Shaw, Bull. Misc. Inform. Kew 1940: 304 (1941). – *Diplycosia malayana* (King & Gamble) Argent, Gard. Bull. Singapore 54: 236 (2002).

*Notes.* The new epithet refers to the notably large calyx in the flowers of this species.

72. *Gaultheria mantorii* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia mantorii* Argent, Gard. Bull. Singapore 54: 224 (2002).

73. *Gaultheria kingii* (Merr.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia kingii* Merr., Pap. Michigan Acad. Sci. 1933, 19: 182 (1934).

*Diplycosia microphylla* Becc., Malesia 1: 212 (1878).

*Diplycosia elliptica* Ridl., J. Fed. Malay States Mus. 10: 145 (1920).

*Diplycosia cordifolia* Ridl., J. Fed. Malay States Mus. 10: 145 (1920).

*Notes.* Sleumer (1966–1967) treated *Diplycosia elliptica* Ridl. as a distinct species but Watthana (2015) treated it as a synonym of *D. microphylla* Becc., considering the differences to be taxonomically trivial. Of the names here considered to be heterotypic synonyms, the specific epithets ‘*microphylla*’, ‘*elliptica*’ and ‘*cordifolia*’ are not available for use in *Gaultheria* because of the names *Gaultheria microphylla* Hook.f., Bot. Antarct. Voy. 1: 327 (1846), *Gaultheria elliptica* Cham., Linnaea 8: 502 (1833), and *Gaultheria cordifolia* Kunth in Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. 3: 285 (1819), respectively.

Watthana (2015) excluded *Diplycosia cordifolia* Ridl. from *D. microphylla* but did not further comment on its taxonomic status other than to mention that the type may comprise more than one element. We, however, follow Sleumer’s (1966–1967) synonymy in treating it as a synonym of *Gaultheria kingii* pending further clarification of its status.

74. *Gaultheria megabracteata* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Pernettyopsis megabracteata* Argent, Bot. J. Linn. Soc. 85: 10 (1982). – *Diplycosia megabracteata* (Argent) Argent, Gard. Bull. Singapore 54: 237 (2002).

75. *Gaultheria mekonggaensis* (Argent & Widjaja) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia mekonggaensis* Argent & Widjaja, Edinburgh J. Bot. 72: 239 (2015).

76. *Gaultheria memecyloides* (Stapf) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia memecyloides* Stapf, Trans. Linn. Soc. London, Bot. 4: 194 (1894).

77. *Gaultheria merrillii* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia parvifolia* Merr., Philipp. J. Sci., C 5: 211 (1910), non *Gaultheria parvifolia* Small, N. Amer. Fl. 29: 78 (1914).

*Notes.* The new epithet honours the American Elmer Drew Merrill (1876–1956), renowned botanist and taxonomic expert on the plants of East and Southeast Asia, and who originally named this species and collected its type.

78. *Gaultheria microsalicifolia* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia microsalicifolia* Argent, Bot. J. Linn. Soc. 85: 8 (1982).

79. *Gaultheria minutiflora* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia minutiflora* Sleumer, Reinwardtia 4: 151 (1957).

80. *Gaultheria minutiflora* (Sleumer) Kron & P.W.Fritsch var. *glandulifera* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia minutiflora* Sleumer var. *glandulifera* Argent, Edinburgh J. Bot. 71: 106 (2014).
81. *Gaultheria mogeana* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia mogeana* Argent, Gard. Bull. Singapore 54: 221 (2002).
82. *Gaultheria morobeensis* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia morobeensis* Sleumer, Bot. Jahrb. Syst. 72: 210 (1942).
83. *Gaultheria morobeensis* (Sleumer) Kron & P.W.Fritsch var. *ovatifolia* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia morobeensis* Sleumer var. *ovatifolia* Sleumer, Reinwardtia 4: 140 (1957).
84. *Gaultheria muluensis* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia salicifolia* Sleumer, Blumea 12: 122 (1963), non *Gaultheria salicifolia* Phil., Anales Univ. Chile 90: 192 (1895).
- Notes.* The new epithet refers to Mt Mulu, the locality where the type specimen was collected in Sarawak State, Malaysia, on the island of Borneo.
85. *Gaultheria muluensis* Kron & P.W.Fritsch f. *gigantea* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia salicifolia* Sleumer f. *gigantea* Argent, Gard. Bull. Singapore 54: 227 (2002).
86. *Gaultheria muscicola* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia muscicola* Sleumer, Blumea 12: 118 (1963).
87. *Gaultheria myrtillus* (Stapf) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia myrtillus* Stapf, Trans. Linn. Soc. London, Bot. 4: 192 (1894).
88. *Gaultheria ngii* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia ngii* Argent, Gard. Bull. Singapore 54: 233 (2002).
89. *Gaultheria orophila* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia orophila* Sleumer, Bot. Jahrb. Syst. 71: 155 (1940).
90. *Gaultheria othmanii* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia othmanii* Argent, Gard. Bull. Singapore 54: 227 (2002).
91. *Gaultheria papuana* (Mustaqim, Utteridge & Heatubun) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia papuana* Mustaqim, Utteridge & Heatubun, Kew Bull. 74-68: 1 (2019).

92. *Gaultheria paulsmithii* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia paulsmithii* Argent, Gard. Bull. Singapore 54: 230 (2002).
93. *Gaultheria pendens* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia pendens* Sleumer, Blumea 12: 119 (1963).
94. *Gaultheria penduliflora* (Stapf) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia penduliflora* Stapf, Trans. Linn. Soc. London, Bot. 4: 193 (1894).
95. *Gaultheria piceifolia* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia piceifolia* Sleumer, Reinwardtia 4: 147 (1957).
96. *Gaultheria pilosa* (Blume) Zoll. & Moritzi, Natuur-Geneesk. Arch. Ned.-Indië 2: 9 (1845). – *Diplycosia pilosa* Blume, Bijdr. Fl. Ned. Ind. 15: 858 (1826).
- Notes.* Although a combination in *Gaultheria* already exists for this species, it was recognised in *Diplycosia* by Sleumer (1957, 1966–1967); it is here returned to *Gaultheria*.
97. *Gaultheria pinifolia* (Stapf) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia pinifolia* Stapf, Trans. Linn. Soc. London, Bot. 4: 192 (1894).
98. *Gaultheria pittosporifolia* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia pittosporifolia* J.J.Sm., Bull. Jard. Bot. Buitenzorg ser. 3, 13: 460 (1935).
99. *Gaultheria pittosporifolia* (J.J.Sm.) Kron & P.W.Fritsch var. *punctiloba* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia pittosporifolia* J.J.Sm. var. *punctiloba* Sleumer, Reinwardtia 4: 152 (1957).
100. *Gaultheria platyphylla* (P.W.Fritsch) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia platyphylla* P.W.Fritsch, PhytoKeys 69: 33 (2016).
101. *Gaultheria puradyatmikai* (Mustaqim, Utteridge & Heatubun) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia puradyatmikai* Mustaqim, Utteridge & Heatubun, Phytotaxa 442(2): 53 (2020).
102. *Gaultheria pseudorufescens* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia pseudorufescens* Sleumer, Bot. Jahrb. Syst. 71: 157 (1940).
103. *Gaultheria pseudorufescens* (Sleumer) Kron & P.W.Fritsch var. *elliptifolia* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia pseudorufescens* Sleumer var. *elliptifolia* Sleumer, Reinwardtia 4: 136 (1957).

104. *Gaultheria pubivertex* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia pubivertex* Sleumer, Reinwardtia 4: 131 (1957).
105. *Gaultheria punctulata* (Stapf) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia punctulata* Stapf, Trans. Linn. Soc. London, Bot. 4: 193 (1894).
106. *Gaultheria retusa* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia retusa* Sleumer, Bot. Jahrb. Syst. 71: 156 (1940).
107. *Gaultheria rhombica* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia rhombica* Argent, Gard. Bull. Singapore 54: 223 (2002).
108. *Gaultheria rigidifolia* (P.W.Fritsch & C.M.Bush) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia rigidifolia* P.W.Fritsch & C.M.Bush, Nordic J. Bot. 34: 699 (2016).
109. *Gaultheria rosea* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia rosea* Sleumer, Reinwardtia 4: 135 (1957).
110. *Gaultheria rosmarinifolia* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia rosmarinifolia* Sleumer, Bot. Jahrb. Syst. 71: 156 (1940).
111. *Gaultheria rubella* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia rubella* Sleumer, Reinwardtia 4: 148 (1957).
112. *Gaultheria rubidiflora* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia rubidiflora* J.J.Sm., Repert. Spec. Nov. Regni Veg. 30: 172 (1932).
113. *Gaultheria rufa* (Stapf) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia rufa* Stapf, Trans. Linn. Soc. London, Bot. 4: 191 (1894).
114. *Gaultheria rupicola* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia rupicola* Sleumer, Reinwardtia 4: 140 (1957).
115. *Gaultheria sagittanthera* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia sagittanthera* J.J.Sm., Bot. Jahrb. Syst. 68: 205 (1937).
116. *Gaultheria sanguinolenta* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia sanguinolenta* Sleumer, Bot. Jahrb. Syst. 71: 157 (1940).
117. *Gaultheria saurauoides* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia saurauoides* J.J.Sm., Bull. Jard. Bot. Buitenzorg ser. 3, 13: 456 (1935).
118. *Gaultheria scabrida* (Becc.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia scabrida* Becc., Malesia 1: 211 (1878).



119. *Gaultheria schramii* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia schramii* Sleumer, *Blumea* 12: 116 (1963).

120. *Gaultheria schultzei* (Schltr.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia schultzei* Schltr., *Bot. Jahrb. Syst.* 55: 163 (1918).

121. *Gaultheria sepikensis* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia rufescens* Schltr., *Bot. Jahrb. Syst.* 55: 165 (1918), non *Gaultheria rufescens* DC., *Prodr.* 7: 595 (1839).

*Notes.* The new epithet refers to the area of Papua New Guinea known as the Sepik region, to which the species is endemic.

122. *Gaultheria setiloba* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia setiloba* Sleumer, *Blumea* 12: 121 (1963).

123. *Gaultheria smithii* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia setosa* J.J.Sm., *Bull. Jard. Bot. Buitenzorg ser. 2*, 8: 51 (1912), non *Gaultheria setosa* Small, *N. Amer. Fl.* 29: 77 (1914).

*Notes.* The new epithet honours the Dutch botanist Johannes Jacobus Smith (1867–1947), who named many species of Malesian Ericaceae, including this species.

124. *Gaultheria soror* (Becc.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia soror* Becc., *Malesia* 1: 210 (1878).

125. *Gaultheria soror* (Becc.) Kron & P.W.Fritsch var. *nuda* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia soror* Becc. var. *nuda* Sleumer, *Blumea* 12: 118 (1963).

126. *Gaultheria sphenophylla* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia sphenophylla* Sleumer, *Bot. Jahrb. Syst.* 71: 158 (1940).

127. *Gaultheria steenisii* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia tetramera* Sleumer, *Reinwardtia* 4: 136 (1957), non *Gaultheria tetramera* W.W.Sm., *Notes Roy. Bot. Gard. Edinburgh* 11: 211 (1920).

*Notes.* The new epithet honours the Dutch botanist Dr Cornelis Gijsbert Gerrit Jan van Steenis (1901–1986), renowned expert on the flora of Malesia and general editor of the *Flora Malesiana* series, who collected the type of this species.

128. *Gaultheria stellaris* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia stellaris* Sleumer, *Blumea* 11: 6 (1961).

129. *Gaultheria subglobularis* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia subglobularis* Sleumer, Blumea 11: 5 (1961).
130. *Gaultheria sulawesiensis* Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia hirsuta* Sleumer, Bot. Jahrb. Syst. 71: 154 (1940), non *Gaultheria hirsuta* M.Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9: 540 (1842).
- Notes.* The new epithet refers to the Indonesian island of Sulawesi, to which the species is endemic.
131. *Gaultheria sulcinervia* (Sleumer) Kron & P.W.Fritsch, **nom. nov.** – *Diplycosia viridiflora* Sleumer, Bot. Jahrb. Syst. 71: 159 (1940), non *Gaultheria viridiflora* Sleumer, Reinwardtia 4: 176 (1957).
- Notes.* The new epithet refers to the deeply sulcate midvein of the leaf blade adaxially in this species.
132. *Gaultheria sulcinervia* (Sleumer) Kron & P.W.Fritsch var. *megalantha* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia viridiflora* Sleumer var. *megalantha* Sleumer, Reinwardtia 4: 155 (1957).
133. *Gaultheria sumatrensis* (Merr.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia sumatrensis* Merr., Pap. Michigan Acad. Sci. 1933, 19: 181 (1934).
134. *Gaultheria supyanii* (Argent) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia supyanii* Argent, Edinburgh J. Bot. 71: 111 (2014).
135. *Gaultheria triangularanthera* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia triangularanthera* J.J.Sm., Bot. Jahrb. Syst. 68: 207 (1937).
136. *Gaultheria trinervia* (Elmer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia trinervia* Elmer, Leafl. Philipp. Bot. 3: 1102 (1911).
137. *Gaultheria undata* (J.J.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia undata* J.J.Sm., Repert. Spec. Nov. Regni Veg. 30: 171 (1932).
138. *Gaultheria urceolata* (Stapf) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia urceolata* Stapf, Trans. Linn. Soc. London, Bot. 4: 191 (1894).
139. *Gaultheria urdanetensis* (Elmer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia urdanetensis* Elmer, Leafl. Philipp. Bot. 7: 2628 (1915). – *Diplycosia trinervia* Elmer var. *urdanetensis* (Elmer) Sleumer, Reinwardtia 4: 143 (1957).

140. *Gaultheria varians* (Sleumer) Kron & P.W.Fritsch, **comb. nov.** – *Diplycosia varians* Sleumer, Blumea 12: 342 (1964).

**Gaultheria** sect. **Tepuia** (Camp) Kron & P.W.Fritsch, **comb. & stat. nov.** – *Tepuia* Camp in Gleason & Killip, Brittonia 3: 178 (1939). – TYPE: *Tepuia tatei* Camp (= *Gaultheria campii* Kron & P.W.Fritsch).

*Distribution.* A section of seven species from the Guayana Highlands of southeastern Venezuela (Bolívar State).

1. *Gaultheria auyantepuiensis* Kron & P.W.Fritsch, **nom. nov.** – *Tepuia intermedia* Steyerl., Acta Bot. Venez. 2: 303 (1967), non *Gaultheria intermedia* J.J.Sm., Meded. Rijks-Herb. 30: 1 (1916).

*Notes.* The new epithet refers to Auyán-tepui, the table-top mountain to which this species is endemic.

2. *Gaultheria campii* Kron & P.W.Fritsch, **nom. nov.** – *Tepuia tatei* Camp in Gleason & Killip, Brittonia 3: 179 (1939), non *Gaultheria tatei* A.C.Sm., Bull. Torrey Bot. Club 60: 99 (1933).

*Notes.* The new epithet honours Dr W.H. Camp (1904–1963) for his important contributions to the Modern Synthesis unified theory of evolution and our understanding of Ericaceae systematics, and who originally named this species.

3. *Gaultheria cardonae* (A.C.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Tepuia cardonae* A.C.Sm., Contr. U.S. Natl. Herb. 29: 338 (1950).

4. *Gaultheria empetrifolia* Kron & P.W.Fritsch, **nom. nov.** – *Tepuia venusta* Camp in Gleason & Killip, Brittonia 3: 181 (1939), non *Gaultheria venusta* DC., Prodr. 7: 597 (1839).

*Notes.* The new epithet refers to the leaves of this species, which superficially resemble those of *Empetrum nigrum* L.

5. *Gaultheria multiglandulosa* (Steyerl. & Maguire) Kron & P.W.Fritsch, **comb. nov.** – *Tepuia multiglandulosa* Steyerl. & Maguire, Acta Bot. Venez. 2: 301 (1967).

6. *Gaultheria speciosa* (A.C.Sm.) Kron & P.W.Fritsch, **comb. nov.** – *Tepuia speciosa* A.C.Sm., Contr. U.S. Natl. Herb. 29: 336 (1950).

7. *Gaultheria vareschii* (Steyerl.) Kron & P.W.Fritsch, **comb. nov.** – *Tepuia vareschii* Steyerl., Acta Bot. Venez. 2: 306 (1967).

ACKNOWLEDGEMENTS. We thank Dr David Middleton for helpful comments on the manuscript. This work was supported by U.S. National Science Foundation grants DEB-0103795 and DEB-0717711; National Geographic Society grant 148057; National Natural Science Foundation of China grants 41671052 and 31960080; and Program Innovative Research Team in Science and Technology in Yunnan Province 202005AE160004.

## References

- Argent, G.C.G. (1982). New taxa and combinations and comments on Ericaceae. *Bot. J. Linn. Soc.* 85: 2–17.
- Argent, G.C.G. (1989). *Diplycosia* in Borneo. Two new species and a provisional key to *Diplycosia* and close allies. *Notes Roy. Bot. Gard. Edinburgh* 46: 17–26.
- Argent, G.C.G. (2002). New taxa and combinations in the genus *Diplycosia* (Ericaceae) of Borneo and Peninsular Malaysia. *Gard. Bull. Singapore* 54: 217–238.
- Argent, G.C.G. (2013). A new species of *Diplycosia*: *D. coii* Argent (Ericaceae) is described in honour of Leonardo Co. *Philipp. J. Sci.* 142(Special Issue): 51–55.
- Argent, G. (2014). A contribution to the study of the genus *Diplycosia* (Ericaceae) in Sulawesi, Indonesia. *Edinburgh J. Bot.* 71: 83–115.
- Argent, G. (2018). A new species of *Diplycosia*: *D. benitotanii* Argent (Ericaceae) from Mt. Halcon in the Philippines is described in honour of the late Dr. Benito Tan. *Philipp. J. Syst. Biol.* 12: 73–76.
- Argent, G. & Widjaja, E.A. (2015). *Diplycosia mekonggaensis* (Ericaceae, Gaultherieae), a new species from Sulawesi, Indonesia. *Edinburgh J. Bot.* 72: 239–242.
- Bush, C.M., Lu, L., Fritsch, P.W., Li, D.-Z. & Kron, K.A. (2009). Phylogeny of Gaultherieae (Ericaceae: Vaccinioideae) based on DNA sequence data from *matK*, *ndhF*, and nrITS. *Int. J. Pl. Sci.* 170: 355–364.
- Bush, C.M., Judd, W.S., Frazier, L. & Kron, K.A. (2010). The phylogeny of *Leucothoe* s.l. (Ericaceae: Vaccinioideae) based on morphological and molecular (*ndhF*, *matK*, and nrITS) data. *Syst. Bot.* 35: 201–206.
- Ferreras, U.F. & Argent, G.C.G. (2011). *Diplycosia bartolomei* (Ericaceae), a new species from the Philippines. *Edinburgh J. Bot.* 68: 39–42.
- Fritsch, P.W. & Amoroso, V.B. (2016). *Diplycosia platyphylla* (Ericaceae), a new species from Mindanao, Philippines. *PhytoKeys* 69: 31–38.
- Fritsch, P.W. & Amoroso, V.B. (2017). *Diplycosia kitangladensis* sp. nov. from Mindanao, the Philippines, and a taxonomic reassessment of *D. trinervia*. *Nat. Hist. Bull. Siam Soc.* 62: 21–27.
- Fritsch, P.W. & Bush, C.M. (2016). *Diplycosia rigidifolia* sp. nov. (Ericaceae) from Borneo, Sabah, Malaysia. *Nordic J. Bot.* 34: 699–702.
- Fritsch, P.W., Lu, L., Bush, C.M., Cruz, B.C., Kron, K.A. & Li, D.Z. (2011). Phylogenetic analysis of the Wintergreen Group (Ericaceae) based on six genic regions. *Syst. Bot.* 36: 990–1003.
- Humphreys, A.M. & Linder, H.P. (2009). Concept versus data in delimitation of plant genera. *Taxon* 58: 1054–1074.
- Kiew, R., Chung, R.C.K., Saw, L.G. & Rafidah, R. (2007). The Flora of Peninsular Malaysia project. In: *Conference on Forestry & Forest Products Research 2007*, pp. 16–25. Kepong, Kuala Lumpur: Forest Research Institute Malaysia.
- Kron, K.A., Judd, W.S. & Crayn, D.M. (1999). Phylogenetic analyses of Andromedeae (Ericaceae subfam. Vaccinioideae). *Amer. J. Bot.* 86: 1290–1300.

- Lu, L., Fritsch, P.W., Bush, C.M., Dong, L.-N., Wang, H. & Li, D.-Z. (2010). Systematic implications of seed coat diversity in Gaultherieae (Ericaceae). *Bot. J. Linn. Soc.* 162: 477–495.
- Lu, L., Fritsch, P.W., Matzke, N.J., Wang, H., Kron, K.A., Li, D.-Z. & Wiens, J.J. (2019a). Why is fruit colour so variable? Phylogenetic analyses reveal relationships between fruit-colour evolution, biogeography and diversification. *Global Ecol. Biogeogr.* 28: 891–903.
- Lu, L., Fritsch, P.W., Bush, C.M., Wang, H., Kron, K.A. & Li, D.-Z. (2019b). Allopolyploidy in the Wintergreen Group of tribe Gaultherieae (Ericaceae) inferred from low-copy nuclear genes. *Nordic J. Bot.* 2019: e02077.
- Luteyn, J.L. (1995). *Tepuia*. In: J.L. Luteyn (ed.) *Flora Neotropica Monograph, Monograph 66. Ericaceae Part II. The Superior-Ovaried Genera*, pp. 351–364. New York: New York Botanical Garden.
- Middleton, D.J. (1991). Infrageneric classification of the genus *Gaultheria* L. (Ericaceae). *Bot. J. Linn. Soc.* 106: 229–258.
- Mustaqim, W.A. & Ardi, W.H. (2019). Ericaceae of Sulawesi: A new species of *Diplycosia*, a new variety of *Vaccinium paludicolum* and one rediscovery. *Telopea* 22: 193–204.
- Mustaqim, W.A., Utteridge, T.M.A. & Heatubun, C.D. (2019). *Diplycosia papuana* (Ericaceae: Vaccinioideae: Gaultherieae): A new endemic species from central New Guinea. *Kew Bull.* 74: 68.
- Mustaqim, W.A., Chikmawati, T., Utteridge, T.M. & Heatubun, C.D. (2020). A new species of *Diplycosia* (Ericaceae) from Mount Jaya, western New Guinea. *Phytotaxa* 442(2): 52–60.
- Panda, S., Reveal, J.L. & Sanjappa, M. (2012). Reduction of *Diplycosia indica* (2009) to *Gaultheria akaensis* (2006) (Ericaceae). *Phytoneuron* 2012-35: 1–7.
- Powell, E.A. & Kron, K.A. (2001). An analysis of the phylogenetic relationships in the wintergreen group (*Diplycosia*, *Gaultheria*, *Pernettya*, *Tepuia*; Ericaceae). *Syst. Bot.* 26: 808–817.
- Sleumer, H. (1957). Florae Malesianae praecorsores XIV. A revision of the genus *Diplycosia* (Ericaceae). *Reinwardtia* 4: 119–161.
- Sleumer, H. (1966–1967). Ericaceae. In: van Steenis, C.G.G.J. (ed.) *Flora Malesiana*, ser. 1, Seed Plants, vol. 6, pp. 469–914. Groningen, Netherlands: Wolters-Noordhoff.
- Stevens, P.F., Luteyn, J., Oliver, E.G.H., Bell, T.L., Brown, E.A., Crowden, R.K., George, A.S., Jordan, G.J., Ladd, P., Lemson, K., McLean, C.B., Menadue, Y., Pate, J.S., Stace, H.M. & Weiller, C.M. (2004). Ericaceae. In: Kubitzki, K. (ed.) *The Families and Genera of Vascular Plants*, vol. 6, pp. 145–194. Berlin: Springer-Verlag.
- Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K. et al. (eds) (2018). *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books.
- Wattana, S. (2010). The genus *Diplycosia* Blume (Ericaceae) in Thailand. *Thai J. Bot.* 2: 127–132.
- Wattana, S. (2015). Ericaceae. In: Newman, M. & Barfod, A. (eds) *Flora of Thailand*, vol. 13, part 1, pp. 101–141. Bangkok: The Forest Herbarium, Department of National Parks, Wildlife and Plant Conservation.
- Wilkie, P. & Argent, G.C.G. (2016). A new species of *Diplycosia* (Ericaceae) from South Kalimantan, Indonesia. *Edinburgh J. Bot.* 73: 139–142.

