

Flower size variation in *Danhatchia* (Orchidaceae)

Matt A.M. Renner

*National Herbarium of New South Wales, Royal Botanic Garden and Domain Trust,
Mrs Macquaries Road, Sydney NSW 2000, Australia*

Abstract

Danhatchia novaehollandiae D.L.Jones & M.A.Clem. and *D. australis* (Hatch) Garay & Christenson were separated at species rank due to differences in petal length and flower opening, with the Australian species having smaller, tardily opening flowers. From this, flower lengths for Australia and New Zealand are expected to be bi-modally distributed with peaks at *c.* 3 mm and *c.* 5 mm respectively. Flowers on all available herbarium specimens in AK, CANB, and NSW were measured, and flower length was found to be unimodal, with nearly identical ranges in Australian and New Zealand plants. Flower size variation in Australian and New Zealand *Danhatchia* specimens has two significant contributing components, inter-individual variation, and ontogenetic variation where flowers increase in size as they age. Dimensions previously recorded for the two species reflect upper and lower limits on the range of variation in flower size present in *both* New Zealand and Australia, respectively. Within herbarium material, 20% of flowers on New Zealand specimens, and 40% of flowers on Australian specimens exhibited signs of opening. There was no correlation between flower size and opening, as might be expected if the two species were both present in Australia and/or New Zealand. Neither the biogeographic context, pollination system, nor morphological evidence support *Danhatchia australis* and *D. novaehollandiae* as distinct species.

Introduction

Danhatchia Garay & Christenson is a genus of obligate mycoheterotrophic orchids found in Australia and Aotearoa/New Zealand. In New Zealand *D. australis* occurs from Waipoua Forest to Mt Pirongia in the North Island, and also Aotea, Hauturu, and the Mokohinau Islands off the north east coast of the Auckland region, and has an outlying occurrence in the north-west of the South Island. *Danhatchia australis* is often found in taraire (*Beilschmiedia taraire*) forest, on alluvial terraces and hill slopes. But it also occurs within other communities, including houpara (*Pseudopanax lessonii*) scrub, and kanuka (*Kunzea linearis*) forest, so is not an obligate associate of *Beilschmiedia*. It has a reputation for being a challenging orchid to find, with a distinct summer flowering season.

Danhatchia australis was initially proposed as a species of *Yoania* by Hatch (1963). Earliest specimens were collected in 1955 at Waipoua River, and subsequent collections in 1962 from Glorit, Kaipara Harbour by Ross and Jessica Beever. Hatch (1963 p.186) noted that New Zealand plants differed from the Japanese type species (*Yoania japonica*) in their short pedicels, lack of labellum spur, fleshy obtuse column wings and two pollinia, differences which 'so strain the original generic description that I propose creating a new subgenus'. *Yoania australis* transferred to the new genus *Danhatchia* by Garay and Christenson (1995).

Danhatchia was thought to be endemic to New Zealand until it was discovered at two widely separated localities on the east coast of New South Wales in 2010, during a wet spring, after a particularly wet winter, first near Bundanoon on the south Coast, then independently and around three weeks later at Borganna, on the Comboyne Plateau. At both sites *Danhatchia* grew in mixed warm temperate rainforest. Australian plants were described as a new species, *D. novaehollandiae* D.L.Jones & M.A.Clem. because they differed from New Zealand plants by their smaller, tardily opening flowers (Jones and Clements 2018). A third species, *D. copelandii* D.L.Jones & M.A.Clem., has since been described from near Coffs Harbour, New South Wales (Jones and Clements 2019).

The differences cited as distinguishing *D. australis* from *D. novaehollandiae* are not fully compatible with statements made by Moore and Edgar (1970) regarding the variability of *D. australis* in New Zealand. In the *Flora of New Zealand* Volume 2, Moore and Edgar (1970) noted that ‘some capsules are full of seeds although perianths appear never to have opened and pollinia are intact in situ’. They also lamented the paucity of ‘good fresh flowers’, which made the precise limits of stigmatic surfaces and column-wings difficult to establish. Moore and Edgar (1970) described New Zealand plants as having a perianth around 6 mm long, however a preliminary assessment of living plants and herbarium specimens suggested flower sizes in Australian and New Zealand plants are more variable than indicated by either Moore and Edgar (1970) or Jones and Clements (2018). In this paper patterns of flower size variation in Australian and New Zealand *Danhatchia*, including one specimen of *D. copelandii*, are quantified, to better understand factors contributing to flower size variation.

Methods

Flower length was measured to quantify patterns of flower size variation. Flower length was the length of the lateral sepals measured from their insertion on the ovary to their apex, in the flattened conformation preserved in dry herbarium material. The difference between dehydrated and hydrated lengths was estimated by measuring lateral sepals from three different flowers when dry, and after soaking for 2 hours in water. Wet lengths were c. 0.5 mm longer than dry lengths. Measurements were made with Carrera Precision digital calipers accurate to 0.01 mm. Measurement error was estimated at 0.06 mm by repeated measures of five flowers, selected haphazardly.

A total of 232 mature *Danhatchia* flowers from 31 specimens – 26 from New Zealand (all *D. australis*) and 5 from Australia (4 *D. novaehollandiae* and 1 *D. copelandii*) were measured, the specimens included are listed under specimens examined in the Taxonomic Treatment. Mature flowers were those whose anther had dehisced, which was confirmed by either swelling of the ovary or visual inspection of the anther. The node number from the first mature flower closest to the inflorescence apex was recorded, node number is a proximate measure of relative flower age within each inflorescence. Whether the flowers were fertilized and whether or not the flowers exhibited evidence of opening (segments separated) was also recorded. The date of collection was included as a predictor variable by scoring the earliest collection date as 1 and adding the number of subsequent days for all other specimens. All analyses were performed on dry-length measurements.

Homoscedasticity of variance was confirmed with the Breusch-Pagan test for linear regressions of flower length on day with the `bptest` function of the `lmtest` package (Zeileis and Hothorn 2002), and with the Levene’s test for the factors in the anova model, with the `leveneTest` function of the `car` package (Fox and Weisberg 2019). Relationships between flower length and flowering time were estimated with a generalized linear model, using the `lm` function. An association between flower size and country (a proxy for the species *D. australis* and *D. novaehollandiae*), specimen, and node number was assessed in a four-way analysis of variance (anova) with interaction terms for node and specimen, and node and inflorescence, with the function `aov`. The single specimen of *D. copelandii* was excluded from the anova. The correlation between flower length and flower opening was estimated with a binary logistic regression, performed by the `glm` function. Regression, correlation and analysis of variance were all completed using the `stats` package (R Core Team 2018), and all analyses were performed in R 3.5.2 (R Core Team 2018).

Results

Variances were homoscedastic for all predictor variables and factors. Flower length was not significantly different between Australian and New Zealand plants (Table 1, Fig. 1A), nor different between inflorescences on the same herbarium sheet (Table 1). However, flower length was significantly different among specimens (Table 1, Fig. 1B), and among flowers at different node numbers on the inflorescence, across all specimens (Table 1, Fig. 1C, 1D). Flower length was not significantly correlated with date of collection ($R^2=0.015$, $F_{(1, 255)}=3.42$, $p=0.066$, Fig. 2A). There was a significant positive correlation between flower size and position on inflorescence, with flowers further from the apex, and having higher nodal number from the apex, being longer on average ($R^2=0.166$, $F_{(1, 255)}=45.64$, $p=1.9 \times 10^{-10}$, Fig. 2B). There was no correlation between flower length and whether flowers opened or remained closed (Table 2).

Table 1. Summary statistics from anova of flower length, showing significant contribution to variation from specimens and inflorescence node number, but no significant differences among Australia or New Zealand, or among flowers from different inflorescences on the same herbarium sheet.

| | Df | Sum Sq | Mean Sq | F-value | P |
|-----------------|-----|--------|---------|---------|-------------------------------|
| Country | 1 | 0.004 | 0.0044 | 0.033 | 0.857 |
| Specimen | 28 | 26.653 | 0.9519 | 7.145 | 7.4 × 10⁻¹⁴ |
| Stem | 1 | 0.036 | 0.0361 | 0.271 | 0.604 |
| Node | 6 | 14.903 | 2.4838 | 18.643 | 1.7 × 10⁻¹⁴ |
| Specimen : node | 78 | 7.551 | 0.0968 | 0.727 | 0.929 |
| Stem : node | 4 | 0.585 | 0.1462 | 1.097 | 0.362 |
| Residuals | 101 | 13.456 | 0.1332 | | |

Table 2. Summary statistics from binary logistic regression describing the relationship between flower length and flower opening. There was no significant relationship, meaning flowers of any length could open or remain closed.

| | Estimate | Std. Error | z value | P |
|---------------|----------|------------|---------|-------|
| (Intercept) | 0.07144 | 1.28966 | 0.055 | 0.956 |
| Flower length | -0.30495 | 0.29950 | -1.018 | 0.309 |

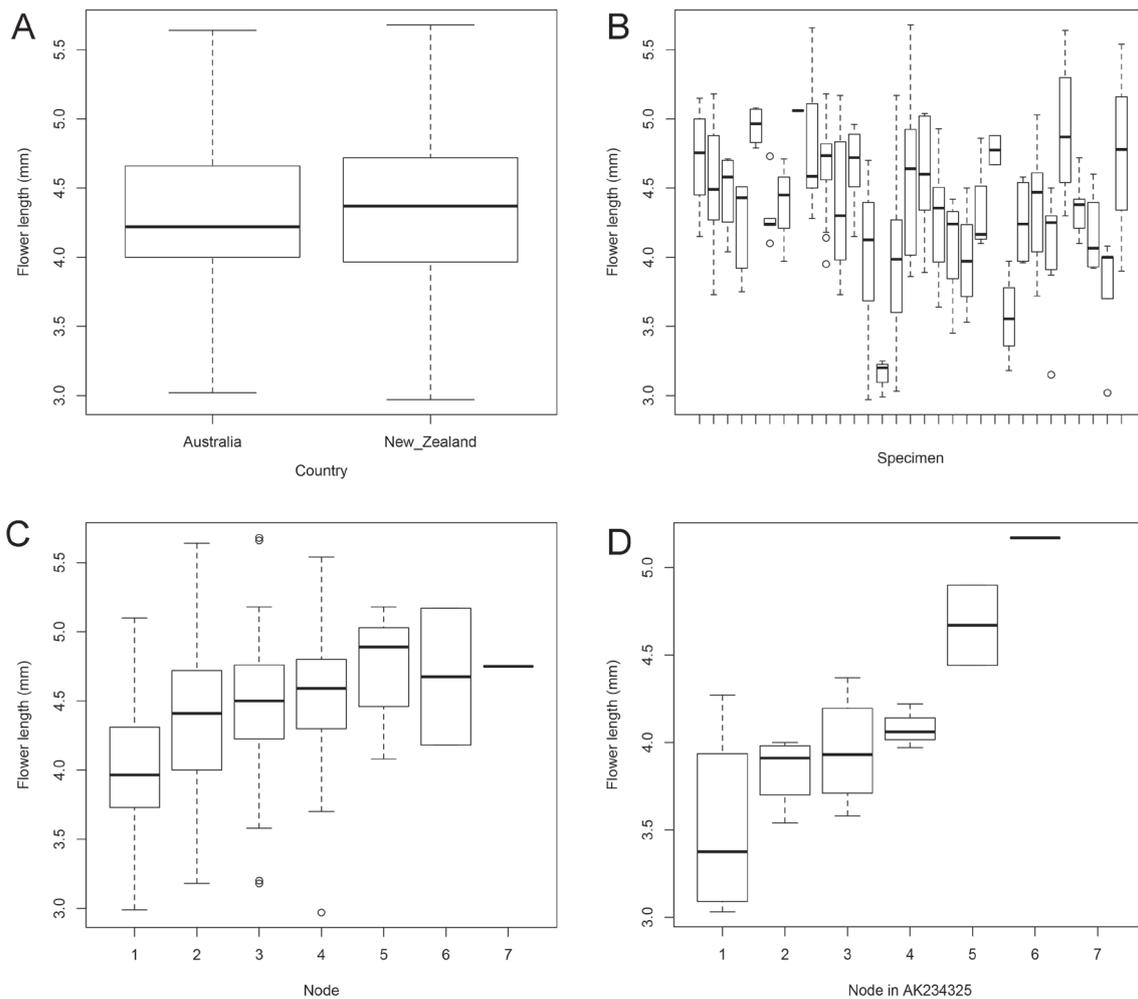


Fig 1. Boxplots showing flower length variation for (A) country including the one specimen of *D. copelandii* – boxplots without *D. copelandii* had the same range and equivalent interquartile range and median; (B) specimen; (C) node number for all data and (D) node number for inflorescences on one herbarium sheet.

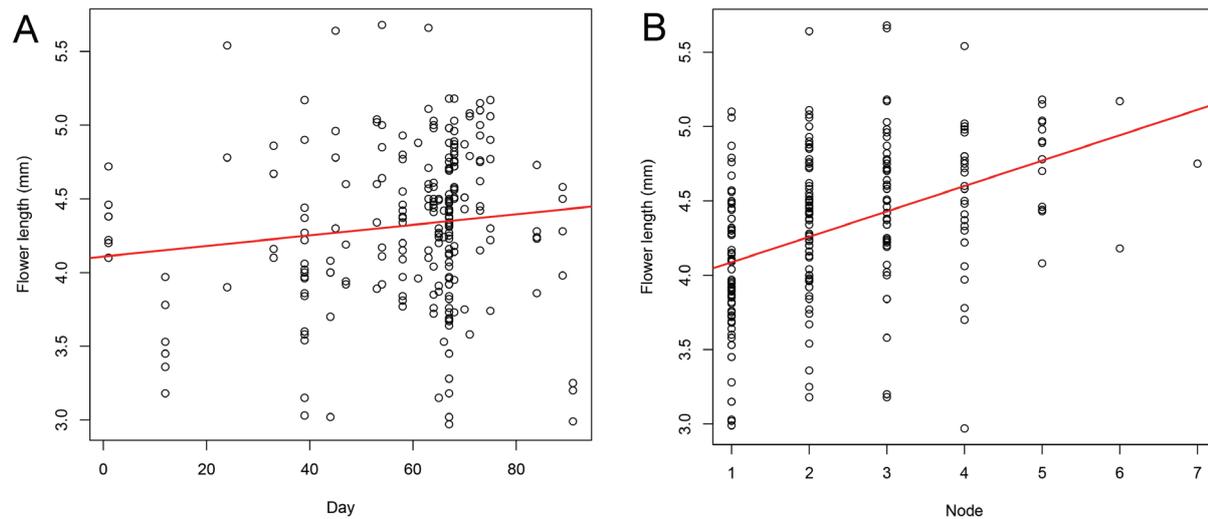


Fig. 2. Linear models describing the relationship between of flower length and (A) day of collection; and (B) node number on inflorescence where node number increases with distance from the inflorescence apex.

Discussion

The species circumscriptions proposed for *Danhatchia australis* and *D. novaehollandiae* predict a bi-modal distribution of flower lengths with peaks at *c.* 3 mm and *c.* 5 mm in samples containing representatives from Australia and New Zealand. Contrary to this expectation flower size was unimodal, samples from Australia and New Zealand exhibited the same range and inter-quartile ranges of flower size variation. Embedded within both Australia and New Zealand was considerable variation among individuals within both regions, such that individuals have significantly different and sometimes non-overlapping flower sizes (Fig. 1B). Examples are presented by the type specimen of *D. novaehollandiae*, whose flowers vary from 3.02 to 4.08 mm long, and another Australian specimen, from Borganna, whose flowers vary from 3.92 to 4.6 mm long. Similar inter-individual variation is present within New Zealand, for example AK 185189 whose flowers vary from 2.99 to 3.25 mm long, and AK 246921 whose flowers range from 3.89 to 5.04 mm long. Dimensions quoted by Edgar and Moore (1970) and Jones and Clements (2018) reflect the upper and lower limits on the range of variation in flower size shared by populations in *both* New Zealand and Australia, respectively.

Flower lengths within single inflorescences also vary in a consistent pattern. The flowers of *Danhatchia* increase in length with distance from the inflorescence apex, suggesting they get longer as they age, and continue to increase in length after fertilization. The linear model describing the relationship between length and node number returned a positive slope of 0.17, on average flower length increased by 0.17 mm from one node to the next. For inflorescences with five mature flowers this implies that the lowermost and oldest flower is on average 0.85 mm longer than the uppermost. This general trend emerges from the considerable variation in flower lengths at each node along the inflorescence, particularly flowers at younger nodes whose lengths are more variable than those at older nodes. The variation in flower lengths within inflorescences is such that for some specimens it is possible to assign the uppermost mature flower to *D. novaehollandiae* and the lowermost to *D. australis* on the basis of floral dimensions, for example AK 234325 (Fig. 1D). Flower length increase with age may be due to ongoing cell expansion within otherwise mature floral segments, and measurements of cell lengths and their correlation with inflorescence node number would establish whether this is indeed the case. The expansion could also be linked to fruit development.

Petal lengths, for which lengths were cited as the defining difference separating *D. australis* and *D. novaehollandiae*, were not measured in this study – they are challenging to access and measure in herbarium material without dissecting flowers. However, a qualitative assessment suggests that open flowers on single *Danhatchia* inflorescences have the same shape regardless of position on the inflorescence, in other words the same proportional relationships between petal and sepal length are maintained independent of overall flower size, and the results presented here for flower length generalize to petal length.

The species circumscription proposed by Jones and Clements (2018) therefore appears to overlook ontogenetic and inter-individual variance components that both contribute to variation in flower size, within individuals and within populations. These are 1) post-anthesis flowers continue to increase in size as they age; and 2) individuals within populations differ in their flower sizes.

In both Australia and New Zealand some individuals may open their flowers while others do not, a feature previously noted by Moore and Edgar (1970) for New Zealand plants. Within herbarium material, 20% of flowers on New Zealand specimens, and 40% of flowers on Australian specimens exhibited separation of sepals. Regardless of whether flowers open or not, seed set occurs at high frequency, more than 90% of flowers in Australian herbarium specimens exhibited evidence of fertilization in the form of a swollen ovary, for New Zealand specimens the fertilization rate was nearly 80%. Many of the fertilized flowers in New Zealand specimens had not opened, and there was no correlation between flower size and flower opening, as might be expected if there were two species that occurred in *both* Australia and New Zealand.

Danhatchia flowers are evidently capable of self-fertilisation, and the pollinium is friable and readily disaggregates. The column structure in *Danhatchia* is a little unusual, being cylindrical at the base, having two column wings, and a long narrow-triangular rostellum according to Hatch (1963) and Edgar and Moore (1970). However, in two specimens of New Zealand plants examined, AK 169131 and AK 253760, both had what appeared to be a three-lobed stigma whose margin and inner surface were translucent, hyaline, somewhat fleshy, and continuous around the margin of all three lobes; and whose medial outer surface was brown pigmented. The anther rested flush with the fleshy inner surface of all three stigma lobes, and pollen contacted that same surface, after anther dehiscence (Fig. 3). Pollen tubes were observed growing into contact with the hyaline inner surface of all three stigma lobes. It is possible that all three stigmatic lobes are fertile in *Danhatchia*, including the medial lobe, which is not then modified into a rostellum. The absence of a physical barrier separating pollen and stigma, in combination with the fragile pollen masses may guarantee self-fertilisation in the absence of any floral visitation, and indeed flower opening.

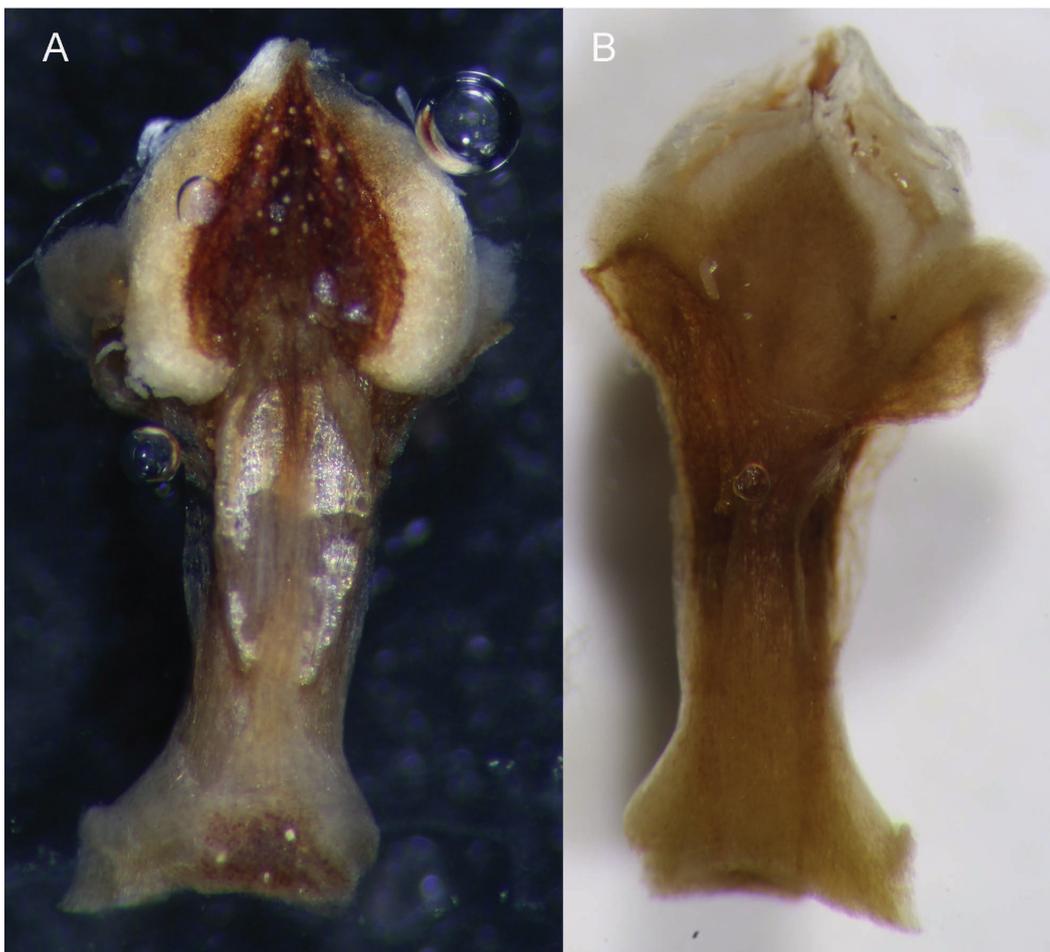


Fig. 3. The column of *Danhatchia australis*. (A) abaxial surface showing the anther connective and anther sacs, with the lateral stigma lobes protruding beyond and behind the pollen sac. (B) adaxial surface showing brown column wings partially fused to lateral stigma lobes, between which is situated a large triangular medial stigma lobe whose margin of fleshy hyaline receptive surface is continuous with the lateral lobes and sits flush with the two pollen sacs.

Australia was hypothesized as the source of the New Zealand plants (Jones and Clements 2018), due to the predominating west wind drift across the Tasman Sea. While dispersal from Australia to New Zealand has been inferred to occur three times more frequently than dispersal from New Zealand to Australia (Sanmartín *et al.* 2007), east to west dispersal between New Zealand and Australia, in seed plants and ferns, does occur (Wanntorp and Wanntorp 2003; Cook and Crisp 2005; Bush *et al.* 2009; Lockhart *et al.* 2010; Perrie *et al.* 2010; Pirie *et al.* 2010). It is therefore not possible to resolve biogeographic areas of origin from distributions alone. There are many species shared across the Tasman, including the orchids *Cryptostylis subulata*, *Pterostylis alveata*, and *P. tasmanica*, seed plants such as *Gaultheria depressa* and *Myosotis australis*, many ferns, and just under half of the liverwort flora of New Zealand (Engel and Glenny 2008). Some of these species have dispersed from Australia, others from New Zealand (Perrie *et al.* 2010). Some species may remain in limited genetic contact despite the distance of open ocean separating populations, as suggested by the occurrence of multiple trans-Tasman dispersals in some orchids such as *Pterostylis nutans* a species which, due the absence of a pollinator, is vagrant in New Zealand but has colonized at least three times in the last Century. As such, trans-Tasman disjunctions in the distributions of single species, including orchids, are not unknown.

In summary, neither the biogeographic context, pollination system, nor morphological evidence support the distinction between *Danhatchia australis* and *D. novaehollandiae*. Rather, the evidence is consistent with the existence of a single species distributed on both sides of the Tasman Sea, and the synonymisation of *D. novaehollandiae* with *D. australis* is formalized below. The relationship between *D. australis* and *D. copelandii*, however, requires further scrutiny, the latter was predicated in part on separate species status for *D. novaehollandiae*, from which *D. copelandii* differed by its larger flowers that open, in combination with differences in flower colour. Flower sizes for *D. copelandii* fall within the range exhibited by *D. australis*, and some individuals in New Zealand also bear yellow pigmentation on the labellum of open flowers, meaning both the status and circumscription of *D. copelandii* require further investigation on combined molecular and morphological data appropriate to tests of species circumscription.

Taxonomic Treatment

Danhatchia australis (Hatch) Garay & Christenson, *The Orchadian* 11(10): 470 (1995)

Basionym: *Yoania australis* Hatch, *Transactions of the Royal Society of New Zealand. Botany* 2(14): 185 (1963).

Type: New Zealand, North Island, Rodney County, (Kaipara), Glorit, 150 m, 24 Dec 1962, R.E. Beever & J.E. Beever (holotype: AK 108769!)

=*Danhatchia novaehollandiae* D.L.Jones & M.A.Clem., *Australian Orchid Review* 83(4): 56 (2018) *syn. nov.*

Type: Australia, New South Wales, Southern Tablelands, Morton National Park, Bundanoon Creek Walking Track, 11 Dec 2016, S. Okada ORG 7641 (holotype: CANB 907493.1! and CANB 907493.2 material in spirit is a second part of the holotype).

Specimens examined: NEW ZEALAND: North Island: Coromandel Ecological Region, Colville Ecological District, forest above Taiharuru Bay, 10 Jan 1982, K. Rabarts, J.C. Smith-Dodsworth (AK 156545); Coromandel Ecological Region, Great Barrier Island Ecological District, northern Great Barrier Island, Rangiwahakaea Bay, stream flowing into Burrill's Bay, 4 Jan 1983, A.E. Wright 5426 (AK 160936); Coromandel Ecological Region, Great Barrier Island Ecological District, northern Great Barrier Island, Rangiwahakaea Bay, near mouth of Kokako Bay Stream, 4 Jan 1983, A.E. Wright 5433 (AK 160943); Coromandel Ecological Region, Great Barrier Ecological District, northern Great Barrier Island: on true left bank of stream running into bay south of Miner's Head, 7 Jan 1983, A.E. Wright 5488, (AK 160998); Coromandel Ecological Region, Great Barrier Ecological District, northern Great Barrier Island : in head of "hanging valley" above coast between Paradise and Deep Bays, 8 Jan 1983, A.E. Wright 5507 (AK 161016); Auckland Ecological Region, Manukau Ecological District, Papakura, Kirks Bush, 21 Jan 1967, J. Horsman (AK 163375); Auckland, Waitakere Ranges, Karekare: Lone Kauri Road, 31 Dec 1973, V.P. Hatch (AK 163376); Kaipara, Glorit, Atuanui State Forest (Mount Auckland), 31 Dec 1980, J. Beever s.n. (AK169129); Kaipara, Glorit, Atuanui State Forest (Mount Auckland), 31 Dec 1980, J. Beever s.n. (AK169130); Auckland Ecological Region, Rodney Ecological District, Glorit, 5 Jan 1964, E.D. Hatch s.n. (AK 169131); Auckland Ecological Region, Rodney Ecological District, Wayby : junction of Waitaraire Stream and Hoteo River, 12 Jan 1985, M.E. Young s.n. (AK 172969); Auckland Ecological Region, Rodney Ecological District, Kaipara Flats, 5 Jan 1986, M.E. Young s.n. (AK 172970); Great Barrier Island, northern block, major catchment draining into Miner's Cove, 4 Jan 1989, A.E. Wright 8547 (AK 184236); banks of Waipoua River, 28 Jan 1955, E. Kulka s.n. (AK 185189); Eastern Northland Ecological Region, Taranga Ecological District, Mokohinau Islands, Motukino (Fanal) Islands, Pahuhunui, 7 Dec 1997, P.J. de Lange 3386 & D.A. Norton (AK 234325); Auckland Ecological Region, Awhitu Ecological District, Awhitu Peninsula, Matakawau, Hamiltons

Bush QEII Covenant, 22 Dec 1999, *P.J. de Lange 4052* (AK 246920); Auckland Ecological Region, Rodney Ecological District, Warkworth (Pohuehue), Cowan Bay Road, McElroy's Reserve, 21 Dec 1999, *P.J. de Lange 4048* & *M.E. Young* (AK 246921); Auckland Ecological Region, Awhitu Ecological District, Matakawau, off main Awhitu Road, Hamilton's property, QEII Trust, 20m off road, on spur and to north, 26 Dec 2000, *P.A. Aspin s.n.* (AK 253760); outer Hauraki Gulf, N E Great Barrier Island, Rangiwhakaea Bay, Burrells Bay, 3 Jan 1983, *E.K. Cameron 2071a* & *A.B. Grace* (AK 271448); outer Hauraki Gulf, N E Great Barrier Island, Rangiwhakaea Bay, near Burrells Stream, 4 Jan 1983, *E.K. Cameron 2071b* (AK271449); Auckland Ecological Region, Inner Gulf Islands Ecological District, Waiheke Island, behind Opopo Bay, Dec 2002, *H.A. Cox* & *C.D. Kilgour s.n.* (AK 280127); Auckland Ecological Region, Rodney Ecological District, Leigh, Mt. Tamahunga, 29 Dec 2001, *M.E. Young s.n.* (AK 281848); Little Barrier Island, Waipawa Stream, 10 Nov 2001, *P.J. de Lange 5433* (AK 286236); Auckland Ecological Region, Rodney Ecological District, south of Warkworth near SH1, Woodlands Estate, 26 Jan 2009, *M.E. Young* (AK304823); Glorit, Mt Auckland Reserve, Jan 1963, *R.E. Beever s.n.* (AK 369646); Great Barrier Island, Miners Cove, 2 Jan 1988, *R.E. Beever 890 02* (AK 369689). AUSTRALIA: New South Wales: Lamington National Park; O'Reilly's [Resort], Morans Valley, 12 Dec 2018, *D. Fowler s.n.* (CANB 909801); Borganna Nature Reserve, Walking track to Rawson Falls, 15 Dec 2010, *P.H. Weston 3405* (NSW 870437); without locality or date *Riley s.n.* (CANB).

Also examined: *Danhatchia copelandii* D.L.Jones & M.A.Clem.: AUSTRALIA: New South Wales: Coffs Harbour, 'Delachco Farm', private property 300 m N of Cassidy's Road, c. 2.5 km due NW of Bonville Post Office, 29 Oct 2018, *L.M. Copeland 4550* (CANB 906265).

Acknowledgements

I thank Ewen Cameron for allowing me to examine and measure *Danhatchia* specimens held by the Auckland War Memorial Museum Herbarium (AK); Dr Mark Clements for allowing me to measure herbarium material of *Danhatchia* held by CSIRO (CANB) and for discussions of the status of *D. novaehollandiae*; and two reviewers for suggesting improvements to the submitted manuscript.

References

- Bush CM, Wagstaff SJ, Fritsch PW, Kron KA (2009) The phylogeny, biogeography and morphological evolution of *Gaultheria* (Ericaceae) from Australia and New Zealand. *Australian Systematic Botany* 22, 229–242. <https://doi.org/10.1071/SB08049>
- Cook LG, Crisp MD (2005) Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. *Journal of Biogeography* 32, 741–754. <https://doi.org/10.1111/j.1365-2699.2005.01261.x>
- Engel JJ, Glenny D (2008) *A Flora of the liverworts and hornworts of New Zealand. Vol. 1.* (Missouri Botanical Garden Press: St Louis, Missouri)
- Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Garay LA, Christenson EA (1995) *Danhatchia*, a new genus for *Yoania australis*. *The Orchadian* 11, 469–470.
- Hatch ED (1963) Notes on New Zealand orchids – II. *Transactions of the Royal Society of New Zealand. Botany* 2, 185–188.
- Jones DL, Clements MA (2018) *Danhatchia novaehollandiae* (Orchidaceae: Goodyerinae), a new species from south-eastern Australia. *Australian Orchid Review* 83, 56–57.
- Jones DL, Clements MA (2019) *Danhatchia copelandii* (Orchidaceae: Goodyerinae), a newly discovered species of leafless orchid from northern New South Wales. *Australian Orchid Review* 84, 41–43.
- Lockhart PJ, McLenachan PA, Havell D, Glenny D, Huson D, Jensen U (2001) Phylogeny, radiation, and transoceanic dispersal of New Zealand alpine buttercups: molecular evidence under split decomposition. *Annals of the Missouri Botanical Garden* 88, 458–477. <https://doi.org/10.2307/3298586>
- Moore LB, Edgar E (1970) *Flora of New Zealand. Volume II.* Government Printer: Wellington.
- Perrie LR, Ohlsen DJ, Shepherd LD, Garrett M, Brownsey PJ, Bayly MJ (2010) Tasmanian and Victorian populations of the fern *Asplenium hookerianum* result from independent dispersals from New Zealand. *Australian Systematic Botany* 23, 387–392. <https://doi.org/10.1071/SB10028>
- Pirie MD, Lloyd KM, Lee WG, Linder HP (2010) Diversification of *Chionochloa* (Poaceae) and biogeography of the New Zealand Southern Alps. *Journal of Biogeography* 37, 379–392. <https://doi.org/10.1111/j.1365-2699.2009.02205.x>
- R Core Team (2018) *R: A language and environment for statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>

- Sanmartín I, Wanntorp L, Winkworth RC (2007) West wind drift revisited: testing for directional dispersal in the southern hemisphere using event-based tree fitting. *Journal of Biogeography* 34, 398–416. <https://doi.org/10.1111/j.1365-2699.2006.01655.x>
- Thorsen MJ, Dickinson KJM, Seddon PJ (2009) Seed dispersal systems in the New Zealand flora. *Perspectives in Plant Ecology, Evolution and Systematics* 11, 285–309. <https://doi.org/10.1016/j.ppees.2009.06.001>
- Wanntorp L, Wanntorp H-E (2003) The biogeography of *Gunnera* L.: vicariance and dispersal. *Journal of Biogeography* 30, 979–987. <https://doi.org/10.1046/j.1365-2699.2003.00895.x>
- Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. *R News* 2, 7–10. <https://CRAN.R-project.org/doc/Rnews/>

Submitted 27 May 2020, accepted 21 August 2020